

Ecological connectivity, adult animal movement, and climate change: Implications for
marine protected area design when data are limited

by

Sarah K. Friesen
Bachelor of Science, University of Victoria, 2011

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Supervisory Committee

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Abstract

Marine protected areas (MPAs) are important conservation tools that can support the resilience of marine ecosystems. Many countries, including Canada, have committed to protecting at least 10% of their marine areas under the Convention on Biological Diversity's Aichi Target 11, which includes connectivity as a key aspect. Connectivity, the movement of individuals among habitats, can enhance population stability and resilience within and among MPAs. This thesis aimed to understand regional spatial patterns of marine ecological connectivity, specifically through the mechanism of adult movement, and how these patterns may be affected by climate change. I used the Northern Shelf Bioregion in British Columbia, Canada, as a case study for four objectives: (1) evaluate potential connectivity via adult movement for the entire bioregion, using habitat proxies for distinct ecological communities; (2) assess potential connectivity via adult movement among existing and potential MPAs, using the same habitat proxies; (3) model potential connectivity via adult movement among marine protected areas for two focal species (*Metacarcinus magister* and *Sebastolobus alascanus*) and predict how this interconnectedness may shift based on projected ocean temperature changes; and (4) contribute the results of these analyses to the MPA technical team's ongoing planning process so that connectivity may be considered in the implementation of a new MPA network in the bioregion. This thesis developed an approach to assess and design MPA networks that maximize inferred connectivity within habitat types for adult movement when ecological data are limited. It applied least-cost theory and circuit theory to model MPA suitability and interconnectedness, finding that these are projected to decrease for *Sebastolobus alascanus* but increase for *Metacarcinus*

magister. I showcased some methods that may be used in MPA design and evaluation, with lessons for other contexts. Importantly, this thesis informed an ongoing MPA planning process, enabling ecological connectivity to be considered in the establishment of a new MPA network in the bioregion. Overall, this work provided examples for incorporating connectivity and climate change into MPA design, highlighting what is possible even when data are limited.

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Chapter 1 – Introduction

Marine biodiversity is under increasing threat from human activities, such as fishing, pollution, and climate change (Harley et al. 2006, Day et al. 2012). Marine protected areas (MPAs) are important biodiversity conservation tools because they can eliminate or restrict human activities, thereby enabling marine ecosystems to recover from direct impacts (Lubchenco et al. 2003). Under the Convention on Biological Diversity's Strategic Plan for 2011-2020, countries are working towards establishing protected areas in 10% of their coastal and marine waters by 2020 (Convention on Biological Diversity 2010). Canada has further emphasized the importance of this with a set of national biodiversity goals and targets; Canada Target 1 is 10% marine protection by 2020 (Environment and Climate Change Canada 2016). MPAs are intended to increase depleted populations of key species and/or to protect important ecological features (Magris et al. 2014). Their effectiveness in achieving these objectives is well-documented (Lester et al. 2009, Afonso et al. 2011, Sciberras et al. 2015), particularly when key MPA design attributes are considered in the planning process, such as representation and persistence (Margules and Pressey 2000). MPAs are likely to provide greater conservation benefit if they are well-enforced no-take areas, and these benefits tend to increase with duration of protection (Edgar et al. 2014). While they can be effective in eliminating some anthropogenic impacts such as from fishing or oil and gas exploration (Lester et al. 2009), MPAs cannot prevent other human-caused impacts such as from point-source pollution or climate change from spreading to protected waters (Partelow et al. 2015, Abessa et al. 2018, Bruno et al. 2018).

In order to meet their ecological objectives, MPAs must either have sufficient self-recruitment and immigration from non-protected areas to offset mortality and emigration, or be connected with other MPAs to facilitate sufficient immigration (Botsford et al. 2001). Connectivity contributes to the stability and resilience of populations, both of which are key factors in determining long term population persistence (Botsford et al. 2001, Green et al. 2014). Thus ecological connectivity is a key attribute of MPA design, especially in the case of MPA networks (Carr et al. 2017, Magris et al. 2018b). Because of this, it is critical to incorporate the best available information about connectivity into MPA planning processes, alongside other MPA design objectives such as representation and replication. However, our understanding of ecological connectivity is limited, particularly at the regional scale. This thesis is focused on addressing this gap in knowledge and enabling connectivity to be considered in MPA design.

Connectivity is a broad term that encompasses many processes in marine ecosystems including dispersal (by larvae, juveniles, and adults), migration, ontogenetic shifts, oceanographic conditions, nutrient flow physically and through food webs, and risk due to anthropogenic impacts or disease (Gillanders et al. 2003, Robinson et al. 2005, Blowes and Connolly 2012). Carr *et al.* (2017) define four types of ecological connectivity that are important for MPAs: population, genetic, community, and ecosystem connectivity. Population and genetic connectivity are focused on a particular study species, where connections result from the movement of individuals between distinct areas and the movement of genes between populations respectively (Carr et al.

2017). Community and ecosystem connectivity pertain to broader scales, relating to the movement of multiple species within an ecological community among spatially distinct patches (such as eelgrass meadows) and the movement of species, chemicals, energy, and materials between distinct ecosystems respectively (Carr et al. 2017). For this thesis, I focus on population connectivity, which is the type of connectivity that is typically considered for MPA design (e.g., Treml et al. 2008, Magris et al. 2016, Weeks 2017).

The individual dispersal of larvae, juveniles, and adults determines source-sink dynamics between areas (Botsford et al. 2001, Botsford et al. 2009, Cowen and Sponaugle 2009). Dispersal may have many drivers, such as seeking out potential reproductive partners, avoiding intra- or inter-species competition, or searching for suitable habitat and available resources. For some marine species, there may be ontogenetic shifts that also influence population connectivity, which is where life stages exhibit different habitat preferences (Gillanders et al. 2003). Dispersal commonly occurs during a planktonic larval stage (Roberts 1997). Individual larvae may be passively transported by prevailing currents, or exhibit behaviours that influence where they settle (Roberts 1997). If the juvenile and adult stage of a species is mobile, connectivity typically results from the active movement of individuals. However, as these individuals move between protected areas, they may be exposed to fishing mortality or other anthropogenic impacts. Dispersal abilities vary between species and life history stages of the same species, based on different home range sizes for adults and amount of time spent in the water column as larvae (known as the planktonic larval duration) (Magris et al. 2016). Two MPAs may be functionally connected for one species but not another

(Botsford et al. 2001). In addition, dispersal may be affected by physical barriers, such as land or strong opposing currents, and anthropogenic disturbance, such as water pollution. Studies on larval dispersal typically incorporate oceanic current models and passive particle tracking (e.g., Treml et al. 2008, Magris et al. 2016), while studies focused on benthic adult phases typically incorporate active movement of individuals and seascape connectivity (e.g., Pittman et al. 2014). The type of measurement or modeling possible is often limited by data availability, which may restrict the life stages or species considered in analyses. In my thesis, I thus investigate methods that are possible with limited data.

The role of adult movement in ecological connectivity patterns has been understudied relative to other life stages, even though it is important for population persistence (Frisk et al. 2014, Bryan-Brown et al. 2017, but see Pittman et al. 2014) – hence it is the focus of my thesis. Previous studies on adult movement have focused on MPA sizing to balance beneficial economic spillover effects with long term population persistence (Palumbi 2004, Green et al. 2015), as well as implications of adult fishing mortality on larval connectivity patterns and MPA efficacy (Moffitt et al. 2009, Grüss et al. 2011b). Species with medium adult movement distances have been identified as the best focus for MPA connectivity applications (Gerber et al. 2005); short dispersal ranges (e.g., less than 1 km) should be considered in determining individual MPA sizes, while highly mobile species may spend large proportions of their time outside MPAs, limiting the protection afforded by MPAs (Kaplan et al. 2009, Moffitt et al. 2009, Green et al. 2014, Carr et al. 2017). That being said, MPAs can be valuable conservation tools for

highly mobile species if they are large and positioned to protect critical areas, such as aggregation hotspots or breeding areas (Roberts et al. 2003, Daly et al. 2018).

Benthic adult stages tend to exhibit habitat associations; if these preferences are known, it may be possible to use benthic habitat as a proxy for a species' adult distribution (Ban 2009, Grober-Dunsmore et al. 2009, Weeks 2017). Because of this, simplistic connectivity modeling for adult movement may still be possible in data-limited regions, where benthic habitat data may be the only information available (Brooks et al. 2004). Where possible, connectivity modeling should also incorporate other species-specific parameters such as movement behaviour, resistance to movement within and between habitat types, influence of oceanic currents, mortality risk, larval dispersal, density-dependence, and species interactions (e.g., Rocha et al. 2002, Gillanders et al. 2003, Treml et al. 2008, Baggio et al. 2011, Caldwell and Gergel 2013, Pittman et al. 2014, Magris et al. 2016, Treml and Kool 2018).

1.1 Climate change impacts on MPAs and population connectivity

Climate change is causing many physical changes in marine systems, including warming temperatures, deoxygenation, acidification, and changes in ocean circulation (Harley et al. 2006, Okey et al. 2014). The impacts of these on species may be direct and indirect, plus may interact with each other additively, synergistically, or antagonistically (Harley et al. 2006). Climate change has already resulted in changes to species distributions, with more drastic shifts in species' ranges anticipated in the future (Cheung et al. 2008, Weatherdon et al. 2016). This has significant implications for population

connectivity (Munday et al. 2009, Magris et al. 2014). In this thesis, I focus on temperature, which has been shown to be an important determinant of species' spatial distributions (Sunday et al. 2012, Poloczanska et al. 2013). Normal species distribution limits typically correspond to pejus temperature limits, defined as the threshold at which metabolic function declines (Pörtner 2012). If warming temperatures in a given location exceed a species' upper pejus limit, a population is unlikely to persist there (Morley et al. 2018). Conversely, where temperatures warm above the lower pejus limit, there will be more suitable thermal habitat available and the distribution range may expand into the area (Morley et al. 2018).

Physiological effects from temperature changes may also alter reproductive output, individual fitness and survival, phenology, trophic interactions, and population connectivity (Harley et al. 2006, Mumby et al. 2011, Andrello et al. 2015, Álvarez-Romero et al. 2018). Endothermic larvae develop faster in warmer water temperatures, resulting in decreased time spent in the water column before settling in a new location. Climate change may thus decrease dispersal distances because of the direct relationship between time spent in the water column and distance dispersed (O'Connor et al. 2007, Munday et al. 2009, Andrello et al. 2015). However, climate change may alter oceanic current direction or magnitude, so larval dispersal distance may instead increase in certain areas. Changes in oceanic conditions and circulations may also facilitate or inhibit juvenile and adult movements (Caldwell and Gergel 2013). Species within an ecosystem will be affected differently depending on their thermal tolerances and individual dispersal abilities (Magris et al. 2016). These predicted changes in population viability, species

distributions, and connectivity will have ecosystem-wide implications. Climate change effects may be partially ameliorated through species acclimatization or adaptation, although high connectivity between regions may limit capacity for local adaptation (Jump and Penuelas 2005, Somero 2010).

Ideally, MPAs are situated such that they will continue to protect species of conservation interest, even as their distributions shift (Carr et al. 2017). However, habitat suitability for particular species may change within an MPA, with resulting shifts in community composition (Bruno et al. 2018). If the MPA has species-specific conservation objectives, this may enhance or inhibit the MPA's ability to meet those objectives. While MPAs will not prevent physical changes, such as temperature and pH, they may provide refugia from local stressors like fishing (Carr et al. 2017). Evidence is also emerging that well-designed MPAs may increase resilience to climate change because there are fewer local stressors, such as overfishing (Halpern and Warner 2002, Lester et al. 2009, McLeod et al. 2009). This reduction in stressors helps maintain ecosystem functions, which contributes to resistance and recovery from climate impacts (Bellwood et al. 2004, Sala and Knowlton 2006, Micheli et al. 2012). However, other research suggests that protection may instead decrease ecosystem resistance to stressors, although still enhance ecosystem recovery (Côté and Darling 2010, Mumby et al. 2011). Because larval dispersal can facilitate ecosystem recovery in unprotected areas, MPAs may play a role in maintaining genetic diversity as climate change progresses (Munguía-Vega et al. 2015).

Climate change impacts will not be uniform across regions so MPAs will be variably affected with respect to suitability for species and contributions to ecological connectivity (Carr et al. 2017, Bruno et al. 2018). MPA planners may want to prioritize areas with the potential to act as climate refugia, if those can be identified (Groves et al. 2012). In order to maintain larval connectivity, MPAs may need to be situated closer to each other to account for decreased dispersal distance (Álvarez-Romero et al. 2018). It is possible that decreased dispersal may lead to higher levels of self-recruitment within MPAs, with implications for local adaptation and population extinction vulnerability (Coleman et al. 2017). Given the inherent uncertainty in predicting future environmental conditions, planners may want to spread risk when implementing MPAs by including greater representation and replication of conservation priorities, plus ensuring spatial separation of some replicates (McLeod et al. 2009). It is important that these conservation tools remain flexible to adapt as scientific understanding increases (Groves et al. 2012).

1.2 Theories that have been used for modeling population connectivity

Many theories have been applied to develop population connectivity modeling approaches (Rudnick et al. 2012, Correa Ayram et al. 2016, Treml and Kool 2018). In this thesis, I use graph theory, least-cost theory, and circuit theory to inform my analyses.

1.2.1 Graph theory

Marine ecological connectivity studies commonly use graph theory (Treml and Kool 2018), a mathematical field of research that is focused on discrete entities and the

connections between them (Harrary 1969). Graphs are constructed out of the entities (termed 'nodes') and connections ('edges'; West 2001). In marine connectivity applications, nodes are typically habitat patches or MPAs, while edges generally refer to dispersal or genetic connections (e.g., Treml et al. 2008). Graphs may be undirected (each edge implies a symmetrical relationship between node pairs) or directed, where a connection occur from one patch to another, but not in the reverse direction (Minor and Urban 2007, Galpern et al. 2011). In addition, graphs may be unweighted, such that each connection is considered equal, or weighted if connection strength varies between node pairs (e.g., due to number of larvae transported between areas or resistance to movement through the interpatch area; Urban and Keitt, 2001, Treml et al. 2008). Nodes may also vary in their attributes, such as area or patch quality (Urban and Keitt 2001). If there are multiple types of edges, these may be represented in a multiplex network, where each node and type of link ensemble is a unique layer within the network (Battiston et al. 2014, De Domenico et al. 2014). In an ecological application, layers may represent connectivity for different life stages, multiple species, or within various habitat types. The simplest method for calculating connections between nodes is Euclidean distance between habitat patches, where connection strength is assumed to weaken as distance increases (Urban and Keitt 2001, Galpern et al. 2011). Other potential approaches to assess these connections in marine systems include species-specific dispersal distance thresholds, passive particle tracking models, least-cost methods, circuit theory methods, genetic sequencing, and tagging or tracking studies (Urban and Keitt 2001, Galpern et al. 2011, Correa Ayram et al. 2016, Treml and Kool 2018). While more complex methods

have greater data and computational requirements, they may enable a more realistic representation of actual connectivity patterns (Galpern et al. 2011, Treml and Kool 2018).

Once the graph has been constructed, it can be evaluated using a wide range of network analysis methods (West 2001). For example, centrality metrics (e.g., degree, eigenvector, betweenness) calculate the relative importance of nodes and/or edges for network connectivity, while graph-level analyses (like network density) evaluate the network as a whole (Treml and Kool 2018). Selection of specific network analysis tools should be based on which network attributes are most highly valued in a given study or planning process (Minor and Urban 2007, Treml and Kool 2018). For MPA design, graph theory can be a powerful and highly flexible tool to assess ecological connectivity, provided areas or entities of interest are discrete. Depending on the methods used to determine network connections, a key limitation in the graph theory approach is that it may not have the capacity to consider the role of interpatch areas in facilitating or impeding connections (Galpern et al. 2011, Correa Ayram et al. 2016).

1.2.2 Least-cost theory

Least-cost theory is fundamentally about minimizing accumulated cost along a path, based on cost-weighted distance instead of Euclidean distance. The type of cost (e.g., effective distance, time, energy expenditure, predation risk) may vary between studies (Adriaensen et al. 2003, Caldwell and Gergel 2013, García-Rangel and Pettorelli 2013, Correa Ayram et al. 2016). This type of analysis requires a landscape (or seascape) matrix for movement to occur through, so enough data must be available for an

individual cost value to be assigned to each landscape pixel (generating a cost surface). Costs may be derived in many ways, such as from literature reviews, expert opinion, or habitat suitability models (Stevenson-Holt et al. 2014). When applied to animal movement across a landscape, least-cost path analysis determines the single lowest-accumulated-cost or optimal route between two habitat patches in the matrix. An inherent assumption is that animals have complete knowledge of the landscape and all associated costs when making movement decisions (Adriaensen et al. 2003, McClure et al. 2016). Despite this, it tends to be more realistic of animal movements than patch-based network analysis because it considers the entire landscape and resistances or barriers to movement (Carroll et al. 2012).

Least-cost corridor analysis is an extension of least-cost path analysis, where the accumulated cost of movement is calculated for each landscape pixel (Rudnick et al. 2012). While least-cost paths determine a route that is only one pixel wide, least-cost corridors show the accumulated cost gradient across the landscape, identifying areas of similarly low resistance to movement that may also be important for dispersal (Beier et al. 2009, Rudnick et al. 2012). Narrow sections of the corridor indicate where there are pinch points to movement because the path is mostly surrounded by costly landscape pixels (Beier et al. 2009). Least-cost corridors are likely to be more representative of dispersal pathways than least-cost paths, thus are more informative for conservation planning (Beier et al. 2009, Rudnick et al. 2012, Correa Ayram et al. 2016).

Because movement costs are species- and life-stage specific (Correa Ayram et al. 2016), data availability may limit the application of this theory to connectivity analyses or restrict the costs that may be incorporated. For example, Stevenson-Holt *et al.* (2014) used costs derived from land cover type and some anthropogenic features in a grey squirrel connectivity model, but not predation risk. Directional costs, such as ocean currents, may be considered in least-cost analysis such that the accumulated cost of movement with the current from Patch A to B may be lower than against the current from B to A (Caldwell and Gergel 2013). However, the energetic costs incurred from swimming against given current strengths (e.g., as measured through oxygen consumption rates) must be known in order for ocean currents to be incorporated into the landscape matrix (Caldwell and Gergel 2013). Both types of analyses have been applied in a wide range of marine and terrestrial systems, including in connectivity assessments to inform conservation planning (Correa Ayram et al. 2016). As with all modeling approaches, however, least-cost analyses alone do not indicate if or to what extent animals are actually using the optimal paths or corridors (LaPoint et al. 2013). If input data have high uncertainty, a least-cost model may have low predictive value and it may be no better than using a simple Euclidean distance-based model (Pullinger and Johnson 2010).

1.2.3 Circuit theory

Similar to least-cost theory, circuit theory involves movement through a landscape matrix, but pixels are assigned resistance values rather than costs (McRae et al. 2008). Circuit theory methods simulate electrical current flow through resistors equal to

pixel resistance values, passing from source habitat patch to ground habitat patch (McRae et al. 2008). In electrical circuits, the voltage drop across an individual resistor does not change based on the flow direction, so connectivity analyses based on circuit theory cannot accommodate directionally-variable contributors to resistance (such as ocean currents with potential upstream and downstream movements) that would present asymmetrical effective resistances (McRae et al. 2008, but see Dambach et al. 2016 for a genetic example). Parameterization of the resistance surface is species- and life-stage specific so data requirements and limitations are similar to least-cost theory applications (Correa Ayram et al. 2016). A key distinction is that circuit theory incorporates random walk theory; movement occurs via a random and unpredictable path, plus past movements cannot be used to predict future movements (McRae et al. 2008). When applied to ecological connectivity analyses, this is analogous to random exploratory movements by animals without prior knowledge of the landscape and associated resistances (McRae and Shah 2009, Correa Ayram et al. 2016). Despite this, least-cost methods and circuit theory methods often identify similar connectivity patterns (Carroll et al. 2012, St-Louis et al. 2014).

Electrical current flows along paths of least resistance, so circuit theory determines probabilistic dispersal routes, plus alternative paths (McRae and Shah 2009). For conservation planning, this presents an advantage over graph theory and least-cost theory methods which only identify the single best path between two habitat patches (Correa Ayram et al. 2016). Redundancy decreases the effective resistance of dispersal pathways. High electrical current density identifies areas with high dispersal likelihood or

where animals are likely to concentrate while moving through the landscape (McRae et al. 2008, Dutta et al. 2016). However, it does not necessarily indicate whether animals are actually using these dispersal pathways. Nevertheless, these areas may be considered conservation priorities in MPA planning processes, as impacts on these areas could potentially have disproportional impacts on overall MPA network connectivity (McRae et al. 2008, Dutta et al. 2016). To my knowledge, circuit theory analyses have thus far only been applied to conservation planning in terrestrial systems (Correa Ayram et al. 2016), but it is anticipated that use of these methods will increase.

1.3 The Northern Shelf Bioregion planning process

For this thesis, I use the Northern Shelf Bioregion as a case study. It is one of thirteen ecologically defined bioregions within Canada's Exclusive Economic Zone (Government of Canada 2011). It is approximately 102,000 square kilometres in size, encompassing many marine ecosystems ranging from coastal fjords and shallow nearshore areas to the deep continental slope (Figure 1). In this bioregion, MPAs have been established individually on an ad hoc basis, with varying levels of protection under federal and/or provincial jurisdictions. As part of its commitments under the Convention on Biological Diversity and Canada Target 1, Canada is implementing MPA networks in all of its bioregions; five bioregions (including the Northern Shelf) were selected as priorities for MPA planning processes (Government of Canada 2011). Upon completion, the Northern Shelf Bioregion will contain the first MPA network in the Pacific Region.

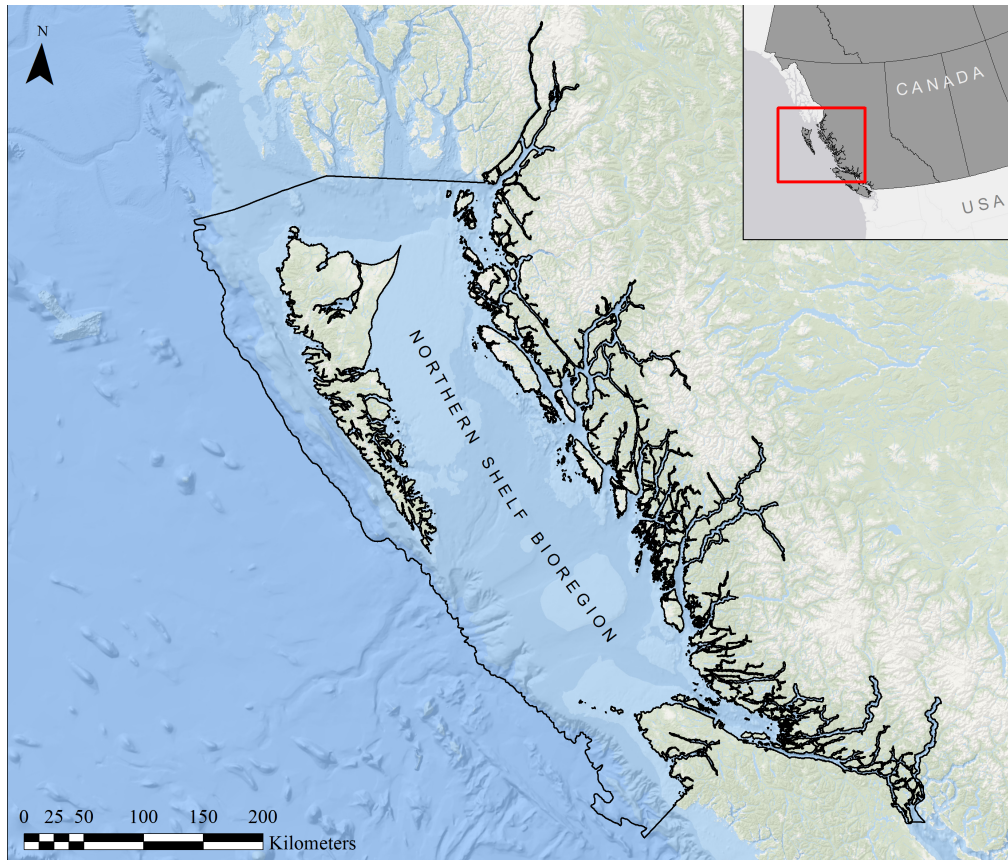


Figure 1. The Northern Shelf Bioregion in British Columbia, Canada.

The Northern Shelf Bioregion planning process is unique compared to others in Canada because the process is co-led by federal, provincial and 16 First Nations partners collaborating as the Marine Protected Area Technical Team (MPATT). The *National Framework for Canada's Network of Marine Protected Areas* includes representativity, replication, viability, and connectivity as critical MPA design attributes, recognizing their importance for MPA effectiveness (Government of Canada 2011). While MPATT is incorporating these MPA design attributes into the planning process, the team has recognized that ecological connectivity represents a key gap in knowledge within the British Columbia (B.C.) context. I have co-developed this project with MPATT representatives to address this knowledge gap and ensure that this work has direct

application to marine spatial planning in B.C. One limitation is that species distribution data for this region are limited; however, abiotic data have been used as a proxy in other studies (e.g., Brooks et al. 2004, Ban 2009). Planning processes are often constrained by data availability, but time and resources may not permit the collection of additional data (Ban 2009, Hansen et al. 2011). In the face of ongoing anthropogenic threats, delaying implementation of protected areas in order to collect more data may actually lead to less effective protection (Grantham et al. 2008, Grantham et al. 2009). While it would be possible to find out much more about connectivity through further research (such as tagging studies or genetic sequencing), this project seeks to contribute this additional MPA design element to the ongoing marine planning process in B.C. and there is no time to wait.

1.4 Research goal and objectives

The goal of this project is to examine potential connectivity in the Northern Shelf Bioregion through the mechanism of adult movement, using existing readily available information. This study had four research objectives:

- 1) Evaluate potential connectivity via adult movement for the entire bioregion, using habitat proxies for distinct ecological communities;
- 2) Assess potential connectivity via adult movement among existing and potential MPAs, using the same habitat proxies;
- 3) Model potential connectivity via adult movement among marine protected areas for two focal species (*Metacarcinus magister* and *Sebastolobus*

alascanus) and predict how this interconnectedness may shift based on projected ocean temperature changes; and

- 4) Contribute the results of these analyses to MPATT's ongoing planning process so that connectivity may be considered in the implementation of a new MPA network in the bioregion.

My thesis is comprised of two substantive chapters that seek to fulfill these objectives, plus a final chapter to synthesize key results, discuss limitations, and draw final conclusions. Chapter 2 is focused on the first two objectives, developing a novel approach to modeling connectivity using graph and multiplex network theory. I identify connectivity hotspots and evaluate the MPA network with respect to potential connectivity. In Chapter 3, I apply least cost and circuit theory to model MPA interconnectedness for the two focal species, then examine the effects of climate change upon these connectivity patterns (addressing objective 3). It is important to note that this thesis is comprised of modeling exercises rather than measurement of actual realized connectivity. However, modeling may be the only way to assess ecological connectivity in areas with limited data. This project is both timely and urgently needed as it will inform the placement of MPAs by working closely with MPA planners and contribute to ensuring resilient marine ecosystems in B.C. In the Conclusion (Chapter 4), I discuss my contribution to MPATT's planning process (objective 4).

The two substantive chapters (Chapters 2 and 3) have been designed as stand-alone manuscripts with the intention of publication in peer-reviewed journals, so there

may be some repetition within the thesis. I lead the conception, design, methods, data collation, analysis, and writing components of all chapters.

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Chapter 2 – An approach to incorporating inferred connectivity of adult movement into marine protected area design with limited data¹

2.1 Introduction

Countries are working towards protecting 10% of their coastal and marine areas as part of the Convention on Biological Diversity's Aichi Target 11, of which connectivity is a key aspect (Convention on Biological Diversity 2010). Connectivity is a fundamental attribute of MPA design and network development because of its importance for population persistence (Carr et al. 2017, Magris et al. 2018). Marine populations must have sufficient inputs of new individuals, whether through self-recruitment or immigration from other areas, to avoid or recover from local extinctions (Botsford et al. 2001, Carr et al. 2017). Greater connectivity increases the stability and resilience of populations, thereby enabling MPAs to meet their ecological objectives (Botsford et al. 2001, Green et al. 2014). However, too much connectivity can also be detrimental to system stability, favoring the diffusion of diseases and other negative perturbations, as well as reducing the ability of prey to find refugia (Dakos et al. 2015, Hermoso et al. 2015).

Despite its ecological importance, connectivity is difficult to characterize and measure in marine ecosystems because data are limited and it encompasses many

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Data from the connectivity analyses in this chapter are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ts0jb2s>

ecological processes, including dispersal (by larvae, juveniles, and adults), oceanographic conditions, ontogenetic shifts, migration, physical and ecological nutrient flow, invasive species, and risk due to anthropogenic impacts or disease (Blowes and Connolly 2012, Gillanders et al. 2003, Robinson et al. 2005). There are four commonly defined types of ecological connectivity: population, genetic, community, and ecosystem connectivity (Carr et al. 2017). Population and genetic connectivity pertain to a single species, resulting from the movement of individuals (e.g. adults, juveniles, larvae) between distinct areas and the movement of genes between populations, respectively (Carr et al. 2017). On a broader scale, community connectivity relates to the movement of multiple species within the same ecological community among spatially segregated patches (such as different patches of kelp forest beds), while ecosystem connectivity results from the movement of species, chemicals, energy, and materials between distinct ecosystems (Carr et al. 2017). Data necessary for measuring or modeling these types of connectivity are often limited, particularly at the regional scale, so methods that require large amounts of data may not be possible (e.g. Bode et al. 2016, Castorani et al. 2017). Studies incorporating connectivity into MPA planning have primarily focused on identifying locations that are important for these various types of connectivity as potential MPAs (e.g. Engelhard et al. 2017, Treml et al. 2008), but do not determine if these potential MPAs are connected to each other.

Population connectivity – the type of connectivity most commonly considered in MPA planning (e.g. Magris et al. 2016, Treml et al. 2008, Weeks 2017) – is complex, with patterns varying by species and life history stage (Magris et al. 2014). The dispersal

of individuals is an important ecological process, as it determines source-sink dynamics between areas (Botsford et al. 2001, Cowen and Sponaugle 2009). To be effective, MPAs must have sufficient self-recruitment and/or immigration from other areas, protected or not, to offset mortality and emigration (Botsford et al. 2001). For many marine species, dispersal occurs through the movement of larvae, juveniles, and adults while seeking out potential reproductive partners, avoiding intra- or inter-species competition, or searching for suitable habitat and available resources. Species may also exhibit ontogenetic shifts, where different life stages display different habitat preferences, which will influence overall population connectivity (Gillanders et al. 2003). However, when juveniles and adults are moving between MPAs, they may be at risk of fishing or other human activities. Because dispersal abilities vary between species and life history stages, two MPAs may be functionally connected for one species or life history stage, but not another (Botsford et al. 2001).

Within the marine environment, connectivity due to adult movement has not been as well studied as for other life stages despite its importance for population persistence (Frisk et al. 2014, Bryan-Brown et al. 2017). Adult movement distances are often reported as home ranges or maximum distance traveled, determined through methods such as tagging or tracking individuals (Gillanders et al. 2003, Grober-Dunsmore et al. 2009). Connectivity via adult movement is most relevant in MPA planning for species with moderate adult movement distances, as individual MPA size rather than network connectivity should enable self-recruitment for species with short distance adult dispersal (e.g. less than 1 km) (Kaplan et al. 2009, Carr et al. 2017), while the movement of wide-

ranging or pelagic species (e.g. turtles and tuna) may limit the effectiveness of MPAs as a conservation tool for these species (Moffitt et al. 2009, Green et al. 2014). Ideally, when species-specific data are available, connectivity analysis incorporates details such as adult habitat preferences, resistance to movement within and between habitat types, influence of oceanic currents on adult movement, larval dispersal, density-dependence, and species interactions (e.g. Rocha et al. 2002, Gillanders et al. 2003, Treml et al. 2008, Baggio et al. 2011, Caldwell and Gergel 2013, Pittman et al. 2014, Magris et al. 2016). However, such data rarely exist for multiple species.

In MPA planning processes where data are limited, benthic habitat data may be the only information available (Brooks et al. 2004). Indeed, conservation planners are often faced with limited data with which to make decisions, and may not have the time or resources to collect additional data (Ban 2009, Hansen et al. 2011). Benthic habitat data may be useful as a proxy for benthic-associated species or communities, where species distributions are inferred based on the presence of suitable habitats (Ban 2009, Grober-Dunsmore et al. 2009, Weeks 2017). It is uncertain how connectivity patterns identified using habitat proxies and modeling align with actual population connectivity for individual species. I coin the phrase ‘inferred connectivity’ to emphasize this uncertainty, and use it rather than ‘potential connectivity’ – which combines landscape attributes with some information about species’ dispersal ability (Calabrese and Fagan 2004) or probability of dispersal between patches (Watson et al. 2010) – because the latter implies a more detailed species-specific understanding of connectivity patterns than a habitat proxy approach can provide. Delaying conservation action to collect more data may

result in less effective protection, particularly in the presence of ongoing threats (Grantham et al. 2008, Grantham et al. 2009). Therefore, it is critical to incorporate the best available information about ecological connectivity into MPA design (Carr et al. 2017), alongside other design objectives such as feature representation and replication (Margules and Pressey 2000, Roberts et al. 2003).

Graph theory is a common method to explore ecological connectivity (Galpern et al. 2011, Grober-Dunsmore et al. 2009, Urban and Keitt 2001) and incorporate it into marine conservation (Anadón et al. 2013, Andrello et al. 2015, Treml et al. 2008). The graph's main components are 'nodes', typically the center of habitat patches or protected areas, and 'edges' that each indicate an ecological connection between two nodes (Urban and Keitt 2001, Grober-Dunsmore et al. 2009, Treml and Kool 2018). Metrics to assess network connectivity include eigenvector centrality, betweenness, and network density among others (D'Aloia et al. 2017, Sayles and Baggio 2017, Treml et al. 2008). Multiplex networks are networks in which nodes are connected via multiple types of linkages (Battiston et al. 2014, De Domenico et al. 2014). Hence, in a multiplex network, a node (such as a location) is connected to another node via different ecological processes or different ecological attributes (Pilosof et al. 2017). Each node and type of link ensemble is called a layer (Battiston et al. 2014). Multiplex networks have recently been used to analyze and understand how structure may affect function in different complex systems (e.g. Battiston et al. 2014, Kivelä et al. 2014, Baggio et al. 2016), but their application is only just emerging in ecology (Pilosof et al. 2017).

The objective of this research was to develop a method for incorporating connectivity into MPA planning through the mechanism of adult movement when data are limited, using a case study along the Pacific coast of Canada. I used the Northern Shelf Bioregion in British Columbia (BC), Canada, as my case study because MPA network planning is actively being pursued jointly by the Government of Canada, Province of British Columbia, and 16 First Nations who are working together as the Marine Protected Area Technical Team (MPATT) (Department of Fisheries and Oceans Canada 2017), and my research is informing the planning process. Although tagging studies and genetic analyses can deepen our understanding of connectivity, such data are limited to only a few species and areas in the study region (e.g. Withler et al. 2001, Fong and Dunham 2007, Rechisky et al. 2017). I thus explore using existing habitat data, which are available, to ensure that a component of ecological connectivity can be incorporated into the MPA network planning process. I developed two ways to include inferred connectivity in MPA planning: (1) identifying sites important for inferred connectivity as proposed candidate MPAs, and (2) assessing the inferred connectivity of existing and potential MPAs.

2.2. Methods

2.2.1 Case Study Description

Canada is committed to developing MPA networks in all 13 of its bioregions (Government of Canada 2011), with planning underway in 5 priority bioregions across the country. In BC, the Northern Shelf (approximately 102,000 square kilometres in size) was selected as the planning area for the first MPA network in the Pacific Region. The

planning team has identified connectivity as a key knowledge gap, and as a highly important ecological attribute. MPATT has identified multiple marine conservation priorities in this planning process, including 55 fish, 15 crustaceans, and 19 molluscs (for complete list, see Department of Fisheries and Oceans Canada 2017). Of these, 26 are benthic conservation priority species with known adult movement ranges as reported by Burt *et al.* (2014) (Appendix S1: Table S1), and 8 of these have moderate adult movement ranges. Fisheries and Oceans Canada does fishery-independent surveys for many of these species, but these surveys do not cover the full extent of the bioregion as they do not venture into fjords, inlets, or parts of Hecate Strait (Chandler *et al.* 2017). Thus they were not appropriate for use in this analysis.

Prior to the MPA Network planning process, there were 124 existing MPAs in the Northern Shelf Bioregion (Figure 2) established in an ad hoc manner and with varying levels of protection from industry, fishing, and other anthropogenic impacts. I evaluated inferred connectivity to assess connections among existing MPAs and to inform the selection of new MPAs to ensure the resulting network was well connected. I also considered 311 “potential MPAs”: areas with boundaries but not yet designated as MPAs, which are likely to be considered in the MPA network planning process (i.e. Protection Management Zones (PMZs) proposed by the Marine Plan Partnership for the North Coast (MaPP) (MaPP 2016a, 2016b); and Rockfish Conservation Areas (RCAs), partial fishing closures established to protect rockfish) (Figure 2). At the time of this study, the MPA planning process in B.C. was considering upgrading areas that had limited protection. My

analysis assumes that the MPAs, including existing ones, would need enhanced protection to provide ecological connectivity benefits.

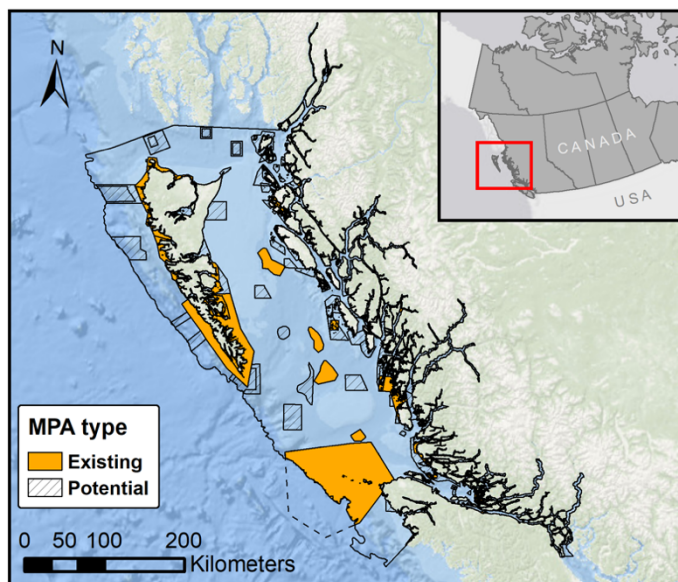


Figure 2. Existing and potential marine protected areas (MPAs) in the Northern Shelf Bioregion, British Columbia. Many small MPAs are not visible at the regional scale.

2.2.2 Data

I assessed inferred connectivity within benthic habitat types because species-specific distribution and movement data were not available. For this study, habitat types were defined by their physical characteristics (e.g. rocky areas) or presence of canopy-forming species (i.e. kelp beds and eelgrass meadows), resulting in six major benthic habitat types that comprise the Northern Shelf Bioregion. The region's entirety has been broadly classified into rocky, sandy, muddy, and 'unknown' habitat types (Province of BC 2002), and biogenic habitat types: kelp beds, eelgrass meadows, and estuaries (Appendix S1: Table S2). Each habitat type was split into five biologically-relevant depth ranges (Province of BC 2002) to generate distinct habitat patches in ArcGIS version

10.4.1 (ESRI Inc. 2016): 0 – 20 m (shallow), 20 – 50 m (photic), 50 – 200 m (mid-depth), 200 – 1000 m (deep), and 1000+ m (abyssal). Although the best available data were used, there is some uncertainty associated with each of the spatial habitat datasets (e.g., positional accuracy, and variation in data resolution (see Appendix S1: Table S2 for details)). I defined ‘habitat category’ as a specific combination of benthic habitat type and depth range. If a particular habitat category contained only one habitat patch, it was excluded as connectivity between habitat patches would not exist. Only habitat patches that were greater than one square kilometre in area were included in the analysis due to computational feasibility.

2.2.3 Analyses

Given the lack of population level or individual movement data, I assumed that Euclidean distance between habitat patches is correlated to adult movement. Not only has this assumption been used in other studies on connectivity (Minor and Urban 2008, Engelhard et al. 2017), previous studies have suggested that using distance as a proxy for connection probability involves the fewest additional assumptions, and therefore potential introduction of error, compared to more parameter-rich methods like dispersal modeling or least cost path analysis in the absence of movement information (Minor and Urban 2007, Galpern et al. 2011). I measured the distance from the centroid of each habitat patch to the centroids of all other patches within the same habitat category using visibility graphing (Tandy 1967, O’Sullivan and Turner 2001) and network analysis (Curtin 2007). Geographic Resources Analysis Support System software version 7.2.2 (GRASS Development Team 2017) was used to generate the visibility graphs, which were then

processed in ArcGIS to find the shortest path from one habitat patch to another, while accounting for deviation around BC's complex coastline. The connectivity analyses were performed in R version 3.3.3 (R Core Team 2017), with the 'igraph' package (Csardi and Nepusz 2006) using two approaches: (1) regional analyses, whereby I divided the Northern Shelf Bioregion into 1597 100 km² planning units (smaller adjacent to land due to the complexity of the region's coastline); (2) MPA analyses, where I assessed the distance between habitat patches within existing or potential MPAs. Although some biological processes occur on finer scales, planning unit resolution was restricted to 100 km² due to data availability and computational feasibility. For planning units or MPAs with more than one habitat patch of the same category, the shortest distance to a habitat patch in another planning unit or MPA was used.

To assess inferred connectivity via adult movement, I used two different threshold distances to capture moderate adult movement ranges. Burt *et al.* (2014) conducted a literature review of BC marine species movement and dispersal in order to inform MPA design processes, assigning species to broad adult movement categories (0, <0.05 km, <1 km, 1-10 km, 10-50 km, 50-1000 km, or >1000 km). These natural groupings indicated that (a) 10 km and (b) 50 km were generalized moderate distance thresholds across BC species. Because the 10 km distance threshold was the same size as the planning unit width, I adjusted that distance threshold to 15 km to capture diagonal connections, and therefore to minimize distortion. Based on these inferred connections, adjacency matrices for each habitat category were generated at 15 km and 50 km distance thresholds.

I used graph theory to evaluate inferred connectivity between planning units or MPAs, constructing networks with planning units or MPAs as nodes, and the inferred connections between them as edges (Figure 3). The edges were undirected, indicating that movement could occur in both directions between the two nodes. A separate network was generated for each habitat category at each distance threshold, resulting in 32 networks.

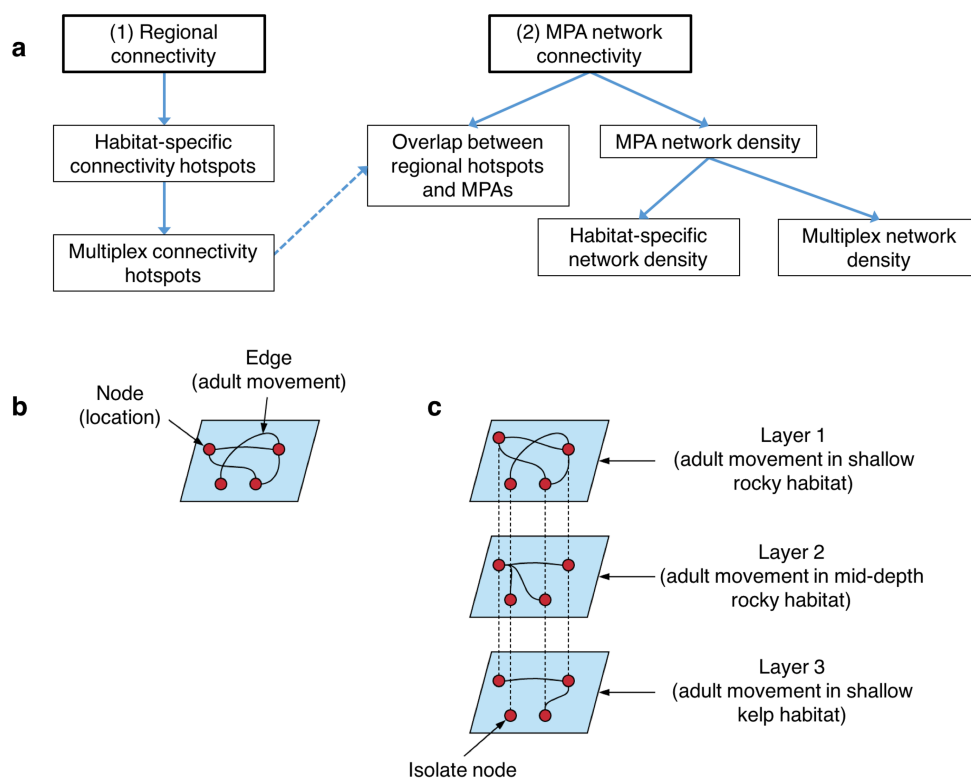


Figure 3. Conceptual diagram of the a) analysis approach overview; b) graph or network, showing key components; c) multiplex network structure. Node or location may refer to a planning unit or MPA. ‘Isolate node’ refers to a node that exists, but does not contain a particular habitat category or is not connected to any other nodes within that habitat category.

2.2.4 Approaches

Regional connectivity

I carried out regional analyses for the whole planning region to identify key areas for connectivity that could be considered in the MPA network planning process (Figure 3). Dividing the study region into planning units enabled evaluation of the relative contribution of individual planning units to regional connectivity. I used two centrality indices to address different aspects of network connectivity: betweenness and eigenvector centrality. Nodes with the highest betweenness scores link otherwise disconnected parts of the network, acting as key stepping stone patches for animal movement (Freeman 1977, Urban and Keitt 2001, Gilarranz et al. 2015, Treml and Kool 2018). Eigenvector centrality evaluates the relative contribution of nodes to overall network connectivity, such that planning units with well-connected neighbours may facilitate animal movement through a greater portion of the network (Battiston et al. 2014, De Domenico et al. 2014, White et al. 2014, Shanafelt et al. 2017).

For each habitat category, I calculated the centrality metrics (betweenness and eigenvector centrality) for all nodes that contained the habitat category, in the networks at the 15 km and 50 km distance thresholds. This ensured that scores of 0 accurately reflected nodes that were not connected but had the potential to be. For every habitat category and distance threshold, I calculated the *z*-score (number of standard deviations from the mean) associated with each planning unit's betweenness and eigenvector centrality metrics. *Z*-scores ≥ 2 indicated a network hub (as in Battiston *et al.* 2014) for that habitat category, which was identified as a connectivity hotspot. These planning units

may be important (with respect to connectivity only) to consider as possible areas to include in the MPA network to ensure the resulting network is well connected.

I then evaluated the planning units as a multiplex network, in which each layer represents a different habitat network type (Figure 3). Analyzing the planning units as a multiplex allows consideration of the different types of links between areas (Baggio *et al.* 2016), where each link type represents a connection for a specific habitat category. I thus incorporated all of the habitat category matrices at the 15 km distance threshold into a supra-adjacency matrix, representing the layers in a multiplex, repeating this to create a separate multiplex for the 50 km distance threshold. At each distance threshold, the same metrics for each planning unit in the multiplex were calculated (betweenness and eigenvector centrality, associated z -scores), as well as the multiplex participation coefficient for each planning unit following the method described by Battiston *et al.* (2014). The participation coefficient (P_i) of node i indicates how evenly spread the node's connections are across the habitat categories, where values close to 0 reflect participation in only a few habitat categories and values close to 1 reflect participation in most habitat categories. Participation is calculated for each multiplex, so there is only one set of highly participatory hot spots at each distance threshold (i.e. no difference between the centrality metrics). Planning units that were network hubs ($z \geq 2$) or had a high participation coefficient ($P_i > 0.66$) were identified as connectivity hotspots (the same thresholds as in Battiston *et al.* 2014). To assess how representative the multiplex connectivity hotspots were, I determined the proportion of hotspots identified in each

habitat category that were also identified as multiplex hotspots, for each centrality metric at both distance thresholds.

MPA network connectivity

To assess the current state of inferred connectivity within existing and potential MPAs, I evaluated MPA network configurations rather than planning units (Figure 3). I carried out two analyses: evaluating inferred connectivity for (1) existing MPAs, and (2) existing and potential MPAs. In order to evaluate the MPA network's performance with respect to regional connectivity, existing and potential MPAs were overlaid with the hotspots identified in the habitat networks and multiplexes, for all centrality metrics and distance thresholds (Figure 3). I determined the proportion of hotspots that intersected (1) existing MPAs, and (2) existing and potential MPAs.

In addition to assessing the MPAs' performance for inferred regional connectivity, I evaluated inferred connectivity between MPAs to see how they functioned as a network (Figure 3). For each habitat category and distance threshold, the network density, or the proportion of inferred connections to possible connections in the network (if every node was connected to every other node), was determined. The (1) existing MPA network densities and (2) existing and potential MPA network densities were compared at each distance threshold. MPA multiplex networks were created for each distance threshold the same way as in the regional planning unit analyses, where each habitat category formed a unique layer and MPAs corresponded to nodes that were present across layers. I summed the total number of inferred connections across the

habitat categories for each distance threshold, and determined the total number of possible connections, then calculated the network densities of both network configurations (Battiston et al. 2014). The multiplex participation coefficients (P_i) for all nodes were calculated, then averaged to determine the participation coefficient for the entire multiplex (P) at each distance threshold, as in Battiston *et al.* (2014). The multiplex network densities were used to compare the MPA network configurations for each distance threshold.

2.3 Results

2.3.1 Regional analysis

Out of 1597 planning units, 1261 were included in the analysis, comprised of 3727 habitat patches (Appendix S1: Figure S1). Some planning units were excluded because they contained only habitat patches that were of 'unknown' type or less than one square kilometre in area; many naturally small discrete patches (like kelp, eelgrass, and some estuaries) were excluded because of the area minimum. The sixteen habitat categories had variable patch numbers, from 6 patches in eelgrass meadows to 527 patches in mid-depth rocky habitat (Appendix S1: Table S3). Eelgrass, kelp, estuaries, and abyssal rocky areas were more spatially restricted and had fewer habitat patches than the other categories. More links were present in habitat categories with more habitat patches because of the higher potential. The nearshore planning units tended to have the highest habitat diversity.

There was low similarity in the multiplex network hubs identified for each distance threshold and centrality metric (Figure 4). This indicates that the planning units identified as important for connectivity, and perhaps as candidate MPAs, are highly dependent on the centrality metric and distance threshold (or model species) used in the planning process. No network hubs were identified with the eigenvector centrality metric at the 15 km distance threshold, indicating that planning unit contributions to inferred regional connectivity were fairly similar across the bioregion. All 87 network hubs based on eigenvector centrality at the 50 km distance threshold intersected the largest habitat patch in the bioregion; eigenvector centrality helps to confirm the importance of contiguous habitat for animal movement. In contrast, the network hubs identified using betweenness were often at the edge of habitat patches, where they would act as critical links to other patches in the same habitat category.

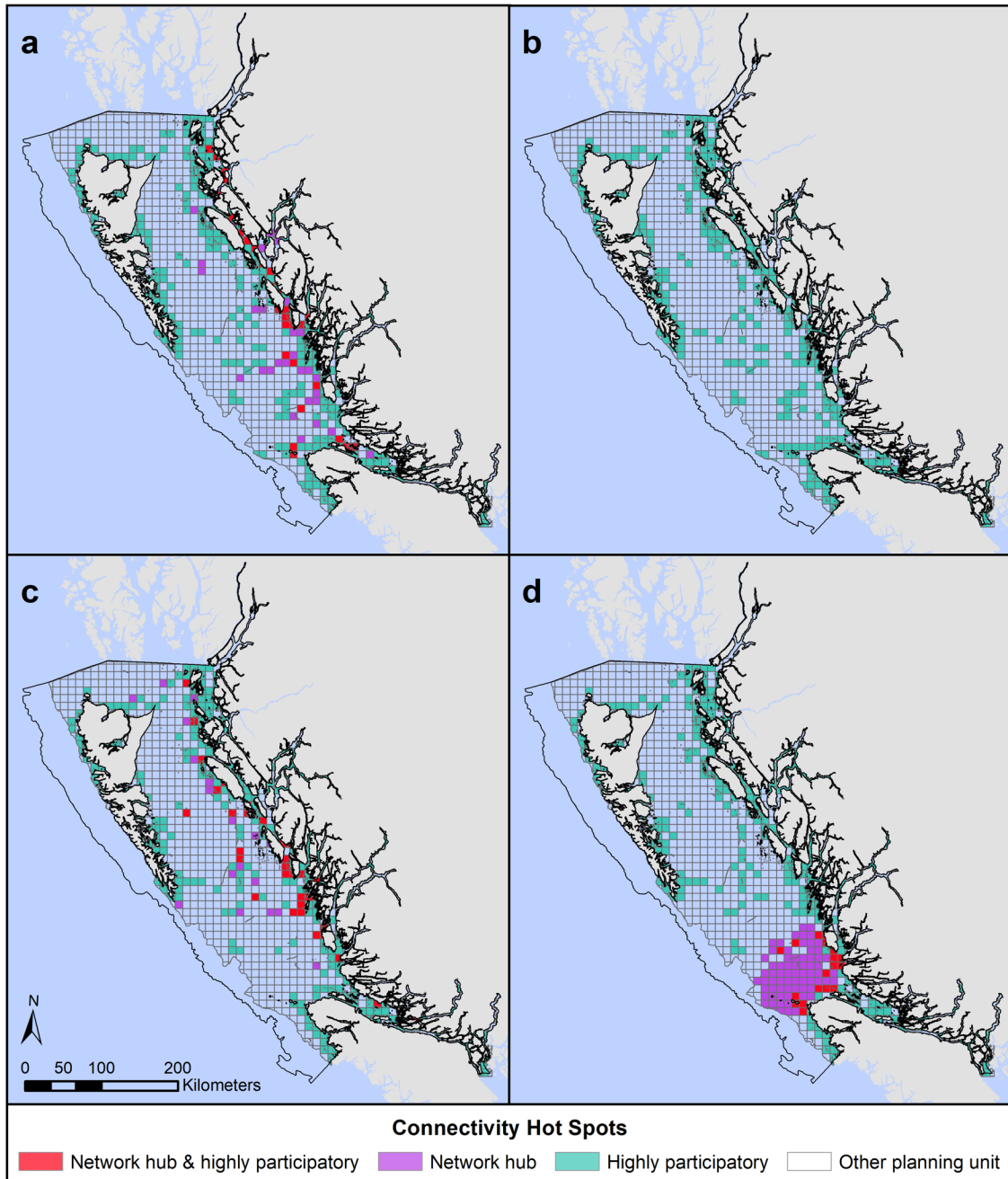


Figure 4. Inferred regional connectivity hotspots within the Northern Shelf Bioregion, as identified by planning units in the multiplex network with z -score ≥ 2 for: a) betweenness hotspots at 15 km distance threshold; b) eigenvector centrality hotspots at 15 km distance threshold; c) betweenness hotspots at 50 km distance threshold; d) eigenvector centrality hotspots at 50 km distance threshold. Highly participatory planning units are identical in a) and b), and in c) and d).

The multiplex network had little overlap between the identified network hubs ($z \geq 2$) and highly participatory ($P_i > 0.66$) planning units. The majority of highly participatory planning units were in nearshore waters along the coast, where there is higher habitat diversity. The multiplex connectivity hotspots had variable representation of the hotspots identified for each habitat category (Table 1), with moderate representation overall.

Table 1. Proportion of inferred connectivity hotspots ($z \geq 2$) identified in each habitat category, for each distance threshold and centrality metric, that are represented by the inferred connectivity hotspots identified in the multiplex network analysis.

		15 km		50 km	
		Betweenness	Eigenvector	Betweenness	Eigenvector
Rocky	0 – 20 m	0.86	0.79	1.00	0.86
	20 – 50 m	0.95	0.17	0.87	0.33
	50 – 200 m	0.58	0.25	0.78	0.34
	200 – 1000 m	0.11	0	0.50	0.00
	1000+ m	0	*	*	*
Sandy	0 – 20 m	0.14	0	0.50	*
	20 – 50 m	0.13	0	0.25	*
	50 – 200 m	1.00	0.04	0.80	1.00
	200 – 1000 m	0.23	0	0.45	0.23
Muddy	0 – 20 m	0.77	0.80	0.86	0.82
	20 – 50 m	1.00	0.80	1.00	*
	50 – 200 m	1.00	0.45	0.79	0.48
	200 – 1000 m	0.80	0.43	0.60	0.52
Kelp	0 – 20 m	1.00	0.75	1.00	1.00
Estuary	0 – 20 m	0	0.25	0.50	0.33
Eelgrass	0 – 20 m	*	*	*	*

* no inferred connectivity hotspots identified

2.3.2 MPA Analysis

There were 305 out of 435 existing and potential MPAs included in this analysis (Appendix S1: Figure S2), made up of 65 existing MPAs (52% of existing MPAs

considered) and 240 potential MPAs (77%). The other MPAs were excluded because there were no bathymetry data (3) or benthic habitat data (2) available at their location, or because they did not contain any habitat patches of a 'known' type that were greater than one square kilometre (125). 1642 habitat patches were located within MPA boundaries (Appendix S1: Table S4). Existing MPAs comprised 21% of the MPAs included in this analysis and made up 30% of the spatial area covered by existing and potential MPAs. 4-5% of the links were from one existing MPA to another, closely matching the proportion expected from the potential connections within each network (i.e. 2080 potential connections for a network of 65 MPAs vs. 46,360 for 305 MPAs).

I determined the number of regional connectivity hotspots that intersected with 1) existing MPAs, and 2) existing and potential MPAs (Table 2). On average, existing MPAs intersected 47% of all hotspots across the centrality metrics and distance thresholds considered. Within the existing MPAs, network hubs for betweenness were the least represented; the MPAs overlapped 30% and 35% of these network hubs at the 15 and 50 km distance thresholds respectively. Protecting a higher proportion of these hotspots may be prioritized in the planning process.

Table 2. Proportion of regional connectivity hotspots identified by the multiplex network analysis for all centrality metrics and distance thresholds that intersect 1) existing MPAs, and 2) existing and potential MPAs in the Northern Shelf Bioregion. The centrality metrics used were betweenness and eigenvector centrality; the distance thresholds used were 15 km and 50 km.

Existing MPAs				
Type of hotspot	15 km distance threshold		50 km distance threshold	
	Betweenness	Eigenvector	Betweenness	Eigenvector
Network Hub	0.30	*	0.35	0.61
Highly Participatory [†]		0.49		0.45
Any Hotspot	0.46	0.49	0.44	0.48
Existing and potential MPAs				
Type of hotspot	15 km distance threshold		50 km distance threshold	
	Betweenness	Eigenvector	Betweenness	Eigenvector
Network Hub	0.68	*	0.86	0.69
Highly Participatory [†]		0.81		0.80
Any Hotspot	0.79	0.81	0.79	0.78

* no inferred connectivity hotspots were identified

[†] there is one set of highly participatory planning units for each distance threshold

For both distance thresholds and both MPA scenarios, the multiplex network densities were quite low, and fairly similar to the network densities of individual habitat categories (Figure 5). The exception to this was the eelgrass habitat network, made up of only eight MPAs (two existing MPAs), with much higher network densities of 0.39 for existing and potential MPAs and 1.00 for existing MPAs, resulting from a link between the only two MPAs with eelgrass habitat patches at both distance thresholds. As expected, network density at the 50 km threshold was greater than at the 15 km distance threshold, other than in the eelgrass networks.

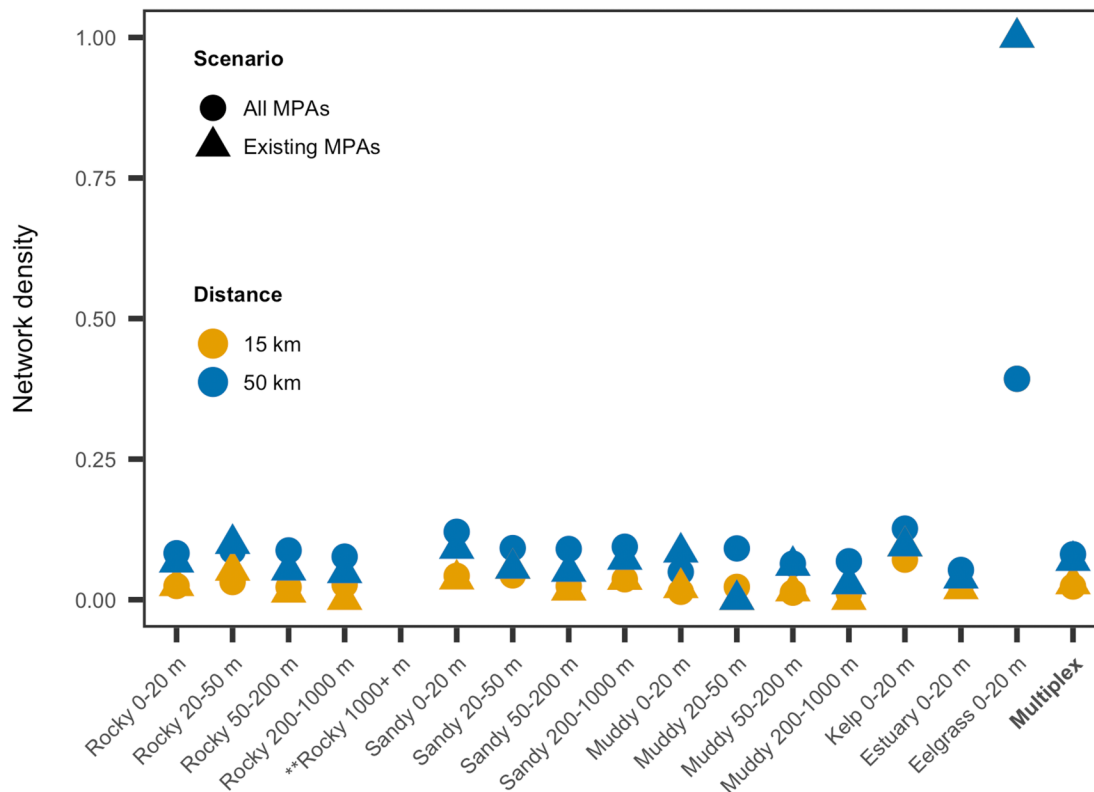


Figure 5. MPA network density for existing MPAs, as well as existing and potential MPAs, at two distance thresholds. Network density, the proportion of inferred connections to possible connections if every MPA was connected to every other MPA, was computed for 16 habitat categories and for a multiplex network. No MPAs contained rocky habitat with greater than 1000 m depth. Two habitat patches were eelgrass; eelgrass network densities at the 15 km distance threshold are identical to, and therefore obscured by, the network densities at the 50 km threshold. Figure generated using ‘ggplot2’ package in R (Wickham 2016).

All multiplex networks had moderate participation coefficients for each entire network, but the networks containing existing and potential MPAs ($P = 0.34$ at 15 km; $P = 0.44$ at 50 km) had more even participation across habitat categories than those with existing MPAs only ($P = 0.15$ at 15 km; $P = 0.25$ at 50 km). This also indicates that connections at the 50 km distance threshold were more evenly spread across habitat categories than at the 15 km threshold for both MPA configurations, despite an unequal number of MPAs containing each habitat category.

2.4 Discussion

Despite its importance for MPA effectiveness, connectivity has rarely been incorporated directly into MPA network planning (Magris et al. 2014). I developed an approach for incorporating connectivity via adult movement into MPA network planning for consideration alongside other MPA design objectives (e.g. representation), when data are limited. Connectivity via adult movement has not been as well studied as larval dispersal (Sala et al. 2002, Cowen and Sponaugle 2009, Anadón et al. 2013; but see Freiwald 2012, Pittman et al. 2014). Rather, previous studies have considered how adult movement may decrease efficacy of an MPA or affect MPA sizing (Walters et al. 2007, Moffitt et al. 2009, Grüss et al. 2011a). My approach best aligns with species that have strong benthic associations as adults, and has the potential to represent animals for which species-specific information may not be available. It is widely applicable because it can inform planning where resources and data are limited, but also contains many assumptions.

My results are being integrated into the interactive platform that MPATT is using to create and evaluate alternative MPA network configurations, enabling inferred connectivity as an additional design objective in the Northern Shelf Bioregion planning process. I received iterative guidance from MPATT in creating this method to ensure that this work remained applicable as the planning process and my research developed. Many of the planning units that emerged as inferred regional connectivity hotspots have conservation importance for other reasons. For example, many multiplex hotspots have some spatial overlap with areas previously identified as Ecologically and Biologically

Significant Areas in the planning area (Department of Fisheries and Oceans Canada 2012). Protection of these overlapped hotspots would result in progress towards multiple conservation targets. There was low interconnectedness among existing MPAs (network density), particularly at the 15 km distance threshold. To increase connectivity between existing areas in the region, planners should prioritize areas that may act as stepping stones among existing MPAs. However, planners may also want to keep MPAs disconnected intentionally, as isolation contributes to uniqueness and resistance to disease transmission between MPAs (Dakos et al. 2015, Hermoso et al. 2015), and it is unclear what the threshold for adequate MPA interconnectedness would be. In addition, network density is likely to be affected by the number of nodes and the spatial extent of the planning region, so it may be more useful to compare the network density of multiple potential MPA network configurations to determine that which is most interconnected, rather than evaluating a single network configuration against a target density.

My approach can also be used to prioritize MPAs for upgraded protection, if it is not possible to increase protection in all MPAs. Potential MPAs could be assessed individually to determine their overlap with inferred regional connectivity hotspots and contribution to network density, identifying those that would best complement the existing MPA network (with respect to inferred connectivity only). An important result from my study was that the centrality metrics and distance thresholds I explored highlighted different planning units as regional connectivity hotspots, and therefore which MPAs were identified as contributing to inferred regional connectivity. This finding aligns with other studies, such as those that have investigated larval dispersal with

multiple planktonic larval duration times or connectivity metrics (Trembl et al. 2008, Magris et al. 2016, D'Aloia et al. 2017). Thus it is important to consider multiple approaches when evaluating connectivity, and ensure they align with priorities identified for the particular MPA planning process.

My analysis incorporated multiple ways in which connectivity can be used in MPA planning: (1) identifying areas that were important for inferred connectivity within the study region, and (2) evaluating existing and potential MPA networks with respect to regional inferred connectivity and interconnectedness. Other studies have identified regional connectivity hotspots through modeling (e.g. larval dispersal by oceanic currents), then used Marxan to produce an optimal or near-optimal configuration of planning units based on connectivity (D'Aloia et al. 2017, Krueck et al. 2017, Magris et al. 2016). This is valuable for determining priority sites to consider as MPA candidates in planning processes, as well as evaluating the performance of existing or proposed networks in protecting these hotspots. However, these methods do not assess the extent to which MPAs within the resulting network are connected to each other. Evaluating inferred connectivity between existing and potential MPAs can be used to explore and enhance network interconnectedness, but the 'best' network configuration may or may not include regional connectivity hotspots. Objectives for connectivity in MPA design are often unclear and qualitative (Magris et al. 2014); it is important that both regional connectivity and MPA interconnectedness are incorporated into planning processes. My two approaches complement and may provide feedback to each other as a network

configuration is developed. Both can also be used to compare possible network configurations alongside other MPA design objectives.

I aggregated inferred connectivity across multiple habitat types using multiplex networks, useful for integrating multiple habitat types, as well as species, in an MPA planning process. To my knowledge, this was the first application of multiplex networks to incorporating connectivity into MPA network planning. Multiplex network hubs take into account that some areas can be important only for one habitat category, whereas others can be important for multiple habitat categories (Battiston et al. 2014, De Domenico et al. 2014). For my case study, highly participatory planning units contribute to inferred regional connectivity in multiple habitat categories, so planners may prioritize these planning units as highly as the network hubs with high contributions to inferred connectivity in one or a few habitat categories. Multiplex network density and participation may be useful in comparing proposed MPA network configurations, as these metrics provide an indication of how well connected the proposed MPAs are, and how evenly these connections are distributed across conservation priorities. In my results, the multiplex inferred regional connectivity hotspots and network densities were moderately representative of those identified for each habitat category, although individual habitat categories varied in level of representation. Inferred multiplex hotspots could be biased towards habitat categories with more links, resulting from greater habitat distribution throughout the region, but not necessarily with higher network density. Planners may prioritize (or deprioritize) habitats with less areal extent or fewer connections, as well as habitats that are important for threatened species or vulnerable life stages (e.g.,

Department of Fisheries and Oceans Canada 2017, Roberts et al. 2003); weighting of layers within the multiplex can be altered to reflect this. Multiplex networks may also be used for evaluating connectivity for multiple species or communities (i.e. assigning each layer to one species or community), and between different habitat or ecosystem types (Gilarranz et al. 2015, Pilosof et al. 2017). If data are available, multiplex networks can integrate connection weight and directionality for both intra- and inter-layer edges (Battiston et al. 2014, De Domenico et al. 2014, see Baggio *et al.* 2016 for an example of a directed, weighted multiplex network analysis in a socio-ecological context).

2.4.1 Limitations

My study had several limitations and assumptions that should guide the use and interpretation of both the methods and results. First, my study was constrained by limited data about connectivity (but see e.g., Robinson et al. 2005, Fong and Dunham 2007), leading us to use habitat data as the best available spatial data at the scale of the region. However, these data also have limitations, as they came from multiple sources with different survey methodologies and may not have not been ground-truthed.

Second, there was limited information about adult movement to inform my modelling efforts. Ideally, I could incorporate information about species-specific movement barriers (e.g. unsuitable substrate or depth range, freshwater influence, thermal or pH tolerance threshold, habitat degradation), habitat preferences, and behaviors (e.g. foraging) (Caldwell and Gergel 2013, Engelhard et al. 2017), but such data were too limited or incomplete in the study region for my analysis. Species-specific movement patterns may also be influenced by many other factors including oceanic currents, density

dependence, species interactions, site fidelity, seasonality, and fishing mortality between MPAs (Moffitt et al. 2009, Grüss et al. 2011a, Botsford et al. 2014, Daigle et al. 2015, Green et al. 2015), but again such data were not available for the study region.

Finally, the data and information limitations lead us to use simplifying assumptions. In particular, I assumed that all nodes were effective sources and sinks, although I excluded habitat patches $<1 \text{ km}^2$ (because of computational feasibility); however, the minimum patch size necessary to support a viable population is species-dependent. Population viability is an important consideration as some of the connections identified may not exist if there are no or small source populations (Cowen and Sponaugle 2009, Pe'er et al. 2014, D'Aloia et al. 2017). I also assumed that all connections were bidirectional and had the same strength, and that animals traveled to the nearest MPA using the shortest path. The shortest path may cross multiple habitat categories, and is thus relevant for habitat generalist species like *Sebastes alascanus* or *Metacarcinus magister*. Habitat specialist species may not be able to travel through unsuitable habitat. In addition, individual habitat patches vary in their suitability, attractiveness, quality, and carrying capacity so their contributions as population sources and sinks would also vary (i.e. actual links could be stronger or weaker than assumed by analysis), but I lacked this information. Because of this, some of the nodes that I identified as inferred connectivity hotspots may not contribute very much to network connectivity, while other nodes may have more important contributions than assumed. Overall, actual connectivity patterns may differ from what I have inferred through this analysis, as is expected with many modeling approaches (Fulton et al. 2015). These limitations (and resulting uncertainty) should be considered when interpreting this study,

particularly in a management context (Fulton et al. 2015). As more data become available, they can be easily integrated into my approaches to gain a better understanding of connectivity. Ongoing monitoring of the MPA network, once established, is important for assessing actual connectivity, as is adaptive management if different connectivity patterns are detected (Lubchenco and Grorud-Colvert 2015, Carr et al. 2017).

Given data and information limitations, and the assumptions I used, my results likely represent the best possible case for inferred connectivity via adult movement. While there was some buffering capacity in my analysis because I calculated path distance between habitat patch centroids, rather than patch edges, these distances are still likely lower than what would occur in reality because of my assumption that individuals traveled along the shortest path from one MPA to the next. If movement barriers exist, I may have identified connections that do not exist in nature. This is particularly important for areas identified as betweenness hotspots; if crucial 'bridging' links between otherwise disconnected regions do not exist, the associated nodes may have only marginal importance for network connectivity. It is also possible that there are links present (perhaps unidirectional) that were not identified by my modeling efforts (e.g. individuals moving downstream with currents may be able to traverse greater distances because of lower energetic cost), so some nodes may have higher importance for network connectivity than concluded by this analysis. However, reliable understanding of most species' movement patterns is still needed (Pe'er et al. 2014). In regions where this information is available, my approach could be modified by calculating distance between habitat patches using least cost path analysis instead of visibility graphing (Galpern et al. 2011, Caldwell and Gergel 2013, Pittman et al. 2014).

The approaches that I developed can be expanded upon in future work. Adult movement is an important aspect of ecological connectivity to be considered in marine planning, whether through single- or multiple-species assessments (Frisk et al. 2014). It would be valuable to incorporate fishing mortality and larval dispersal into future analyses, as each has significant impacts on population persistence and connectivity (Shanks et al. 2003, Grüss et al. 2011b). In addition, connectivity measurements through tagging, surveys, and genetic analyses would help ground truth my inferred connectivity work (e.g. Buonomo et al. 2017, Zemeckis et al. 2017). After determining connections between nodes through connectivity models or measurements, there may be more appropriate network analysis metrics to use than betweenness and eigenvector centrality, depending on the specific conservation planning objectives. Planning processes should include social-political considerations, particularly where multiple jurisdictions exist, as these influence the MPA network's effectiveness and potential for monitoring and enforcement (Schill et al. 2015, Dehens and Fanning 2018). Future research should also assess shifting connectivity patterns with climate change (Magris et al. 2014, Andrello et al. 2015). Data on present and predicted future ocean conditions (e.g. temperature, pH, and current shifts) or species distributions can be integrated into my approaches to explore how regional connectivity hotspots and MPA network interconnectedness may change over time. Most importantly, these approaches can be applied to other MPA planning processes, even when data are limited.

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Chapter 3 – Effects of changing ocean temperatures on ecological connectivity among marine protected areas: A case study of Dungeness crab and Shortspine thornyhead in northern British Columbia²

3.1 Introduction

Climate change has impacted and will continue to impact marine ecosystems despite marine conservation efforts, including the establishment of marine protected areas (MPAs) (Burrows et al. 2011, Poloczanska et al. 2013, Stuart-Smith et al. 2015, Scheffers et al. 2016, Coleman et al. 2017, Henson et al. 2017, Bruno et al. 2018). The climate-related change with the most documented impacts to date is ocean temperature, affecting species abundance, life histories, distributions, and connectivity (Munday et al. 2008, Magris et al. 2014, Deutsch et al. 2015). Temperature influences species across different life stages based on thermal physiological tolerance (Huey and Kingsolver 1989, Neill et al. 1994). As ocean temperatures change, conditions within individual MPAs may become more or less suitable for species (Bruno et al. 2018), with implications for population connectivity and effectiveness of MPA networks. A key question for future viability of MPA networks is how climate change may affect species targeted for protection by MPAs and their regional ecological connectivity patterns.

Ecological connectivity is important for the stability and resilience of populations, and is thus a fundamental attribute in the design and evaluation of MPAs and MPA networks (Carr et al. 2017, Magris et al. 2018a). Marine population connectivity studies

² This chapter is in preparation for publication with co-authors Natalie C. Ban, Emily Rubidge, Rebecca Martone, and Karen Hunter.

have focused mostly on larval dispersal (e.g. Treml et al. 2008, Andrello et al. 2015, Magris et al. 2016), with less emphasis on the adult stage (but see Friesen et al. 2019). Yet movement of adults is important for the persistence of populations (Frisk et al. 2014, Bryan-Brown et al. 2017), and adults are at risk of fishing mortality outside of MPAs. Species with moderate adult movement distances are most relevant for evaluating connectivity via adult movement between MPAs, as the movement of far-ranging species (e.g. tuna) may limit MPA effectiveness as a conservation measure (Moffitt et al. 2009, Green et al. 2014), while the movement of species with short distance dispersal (e.g. <1 km) is likely to be contained within individual MPAs (Kaplan et al. 2009, Carr et al. 2017).

Information about adult movement is limited for most marine species, and thus modeling approaches can provide approximations for active movement of individuals and population connectivity. Two innovative approaches are least-cost theory (e.g. Pittman et al. 2014, Weeks 2017) and circuit theory (McRae et al. 2008). Both approaches incorporate movement through a matrix, with varying cost or resistance to movement based on species- and life stage-specific habitat preferences (McRae et al. 2008, Correa Ayram et al. 2016). As species movements are limited by the suitability and distribution of the surrounding habitat (Irlandi and Crawford 1997, Stevenson-Holt et al. 2014), resistance-based analyses are typically more realistic of animal movements compared to patch-based network analysis (Carroll et al. 2012). Least-cost path analysis determines the single route between two areas with the lowest accumulated cost, with the inherent assumption that individuals have knowledge of the landscape and associated costs in

order to select the lowest-cost path (Adriaensen et al. 2003, McClure et al. 2016). Least-cost corridor analysis is an extension of least-cost path analysis, through which the accumulated cost gradient is determined across the entire landscape, providing a more realistic representation of potential dispersal pathways than least-cost paths alone (Rudnick et al. 2012, Correa Ayram et al. 2016). In contrast, circuit theory incorporates random walk theory and is therefore akin to random exploratory movements by individuals without prior knowledge of the landscape (McRae et al. 2008). Circuit theory methods assess the probabilistic contributions of all possible pathways through the landscape, enabling evaluation of path redundancy and bottlenecks to movement (Carroll et al. 2012). Novel methods have been developed that incorporate least-cost and circuit theory into terrestrial connectivity studies (McRae et al. 2008); to my knowledge, these methods have not yet been applied in marine systems.

The objective of this research was to incorporate projected ocean temperature changes into evaluating ecological connectivity between MPAs in the Northern Shelf Bioregion in British Columbia, Canada. To demonstrate this, I evaluated federally-designated MPAs that were established individually, to determine if they were functioning as an ecologically connected network with respect to adult movement. Further, I explored how this interconnectedness shifted with projected temperature changes. I predicted that the overall group of MPAs would become more disconnected and contain more pinch points to movement, in response to increasing projected benthic temperatures. For my case study, I used two focal commercially important species: Dungeness crab (*Metacarcinus magister*) and Shortspine thornyhead (*Sebastolobus*

alascanus). These species have quite different life histories (Burt et al. 2014b), thus I anticipate that they will exhibit distinctive connectivity patterns. My study was timely given that a recent review had highlighted the need for more research incorporating connectivity and climate change, particularly in marine systems (Correa Ayram et al. 2016), and given that active MPA network planning was occurring in the study region.

3.2 Methods

3.2.1 Literature review for focal species' preferences

Shortspine thornyhead and Dungeness crab were selected because they have demersal adult stages, intermediate adult movement distances (Burt et al. 2014b), and were identified as conservation priorities in the Northern Shelf Bioregion MPA network planning process (DFO 2017, Gale et al. 2018). I conducted a literature review (search terms and more information in Appendix S2) to determine substrate and depth preferences, thermal tolerance ranges, and adult movement distances for each species (Table 3; details in Appendix S2: Table S1). For upper and lower thermal tolerance, I considered both pejus and critical limits, defined respectively as the threshold at which physiological function begins declining significantly, and the threshold at which mortality occurs rapidly (Pörtner and Peck 2010). For thermal tolerance thresholds that were not described in the literature, I used values reported in a physiological limits database developed by Fisheries and Oceans Canada (Steiner et al. 2018) or derived from previous species distribution modeling (Lecomte et al., in preparation). I located 4 temperature threshold values in the literature, plus relied on database values for 2 values and model outputs for 2 values (Table 3).

Table 3. Substrate and depth preferences, thermal tolerance ranges, and adult movement distance parameters identified for two focal species, as determined through a literature review. The focal species were: Shortspine thornyhead (*Sebastolobus alascanus*), and Dungeness crab (*Metacarcinus magister*). References and further details in Appendix S2: Table S2.

	Shortspine thornyhead	Dungeness crab
Suitable substrate	Sand, mud, hard	Estuary, mud, sand
Depth range (m)	134-1032	0-229
Upper critical temperature (°C)	-	25
Upper temperature where modeled probability of presence is zero (°C)	8.0*	-
Upper pejus temperature (°C)	-	17
Upper temperature where modeled probability of presence is 50% (°C)	6.1**	-
Lower pejus temperature (°C)	1.2	7
Lower critical temperature (°C)	NA***	1.6
Mean adult movement distance (km)	85	18.6

* Threshold value was determined from the application of a species distribution model to multi-annual, coupled population and environmental survey data. The value reflected the temperature at which probability of presence was 0%. Though the species may be able to survive higher temperatures, the model predicts individuals will not be found at temperatures exceeding this threshold value. See Lecomte et al. (in preparation) for model details.

** Threshold value was determined from the application of a species distribution model to multi-annual, coupled population and environmental survey data. The value reflects the temperature where probability of presence was 50%. In the absence of a pejus limit, I use the normal distribution limit as a proxy (Pörtner 2012). See Lecomte *et al.* (in preparation) for model details.

*** Lacking a reported value, I did not include a lower critical limit for these species. However, this had no impact on the analysis because there was no spatial overlap between species' suitable habitat and benthic temperature values below the lower pejus limit.

Using these species-specific parameters (Table 3), I generated maps of suitable habitat and used these maps as proxies for species distributions in the bioregion. I did not consider biogenic habitat types as their distributions may shift as climate change progresses, and probable future distributions were not known. At the time of analysis, suitability distributions for the focal species had not been conducted; the data I used are similar to other data-limited regions. The bioregion's entirety had been broadly classified into sandy, muddy, hard, and 'unknown' substrate types (Province of British Columbia 2002). I incorporated bathymetry data (obtained from SciTech Environmental Consulting) and the distribution of estuaries (obtained from the Pacific Estuary Conservation Program) to form a single contiguous substrate map. Although I used the best available data, these substrate datasets had some associated uncertainty (e.g. positional accuracy, and variation in data resolution). Using this contiguous substrate map, I determined the distribution of suitable substrate for each focal species.

3.2.2 MPA exposure to projected benthic temperature changes

I considered the three MPAs under federal jurisdiction that are within the Northern Shelf Bioregion for this case study: 1 National Marine Conservation Area, 1 Oceans Act MPA, and 1 marine National Wildlife Area (mNWA). I focused only on highly protected zones within these areas because these have been shown to provide the most conservation benefits (Lester and Halpern 2008, Sciberras et al. 2015); adaptive management zones and multiple use zones were excluded. The Scott Islands mNWA was included in its entirety because the management plan was being developed and protection

levels had not yet been finalized. I considered each spatially distinct highly protected zone as a unique polygon in my analysis (25 polygons totaling 14,470 km² in area).

For this analysis, I used biweekly mean benthic temperature outputs from an ocean circulation model developed by Masson and Fine (2012), as an application of the Regional Ocean Modeling System (Haidvogel et al. 2008), and the most recent downscaled model available for the study region at the time of analysis. This model had 0.025 decimal degree horizontal resolution and 30 vertical sigma layers, and had been used to hindcast ocean conditions for 1995-2008 (for details, see Masson and Fine (2012)). Many of the inlets and nearshore areas in the Northern Shelf Bioregion were outside the extent of the model output (Appendix S2: Figure S1). Based on the A2 emissions scenario described in the Intergovernmental Panel on Climate Change's (IPCC) Special Report on Emissions Scenarios (IPCC 2000), this model had also been forced to project future ocean conditions for 2065-2078 (for details, see Foreman *et al.* (2014) and Morrison *et al.* (2014)). The A2 emissions scenario is commonly considered a 'business-as-usual' approach and assumes no leveling off of atmospheric greenhouse gas concentrations (IPCC 2000). I used biweekly benthic temperature raster outputs for a 'hindcast' time period (1995-2008; Masson and Fine 2012) and 'projected' time period (2065-2078; Foreman *et al.* 2014, Morrison *et al.* 2014), limiting my study to the extent of the model output within the Northern Shelf Bioregion.

Using these temperature outputs, I calculated mean projected benthic temperature change for the MPA polygons. Within each time period, I calculated the mean of the

temperatures in each pixel by season (Winter: December-February, Spring: March-May, Summer: June-August, and Fall: September-November), following seasonal delineations that Morrison *et al.* (2014) defined based on the timing of upwelling and transition periods. I then determined mean benthic temperature anomalies (2065-2078 minus 1997-2011) for each season, using zonal statistics to average the anomaly values of pixels intersecting each MPA polygon in ArcGIS (ESRI Inc. 2016). MPA area outside of the extent of the model outputs was excluded; 6 MPA polygons were completely excluded because there was no overlap with the model output extent. Bruno *et al.* (2018) similarly used means (although mean rates) to compare temperature changes within MPAs to each other and to surrounding regions. While acute thermal stress events and thermal variability may be more important in determining individual survival (Mumby *et al.* 2011, Pinsky *et al.* 2019), mean temperature change can provide an indication of overall broad, long term patterns and is a more appropriate metric given the temporal and spatial resolution of my data.

3.2.3 Analysis of connectivity between MPA polygons

The suitable substrate distribution maps for each species were converted to rasters with the same extent and resolution as the benthic temperature outputs, where pixels were identified as suitable if suitable substrate occupied more than half of the ocean area present (ocean may not cover the entirety of nearshore pixels). For each season within each time period, I identified the pixels with temperatures between the lower and upper pejus temperature threshold, then overlapped these with the suitable substrate distribution rasters to determine suitable habitat (consisting of suitable substrate, depth, and

temperature) for each species. The pejus limits should roughly equate to normal distribution limits for a given species (Pörtner 2012). The suitable habitat maps were used as proxies for species distributions within each season and time period; other factors that contribute to realized species distributions, such as population dynamics, habitat quality, and biotic interactions were not considered here. However, in a visual comparison, my maps lined up well with fishery data for each species, providing qualitative support that my habitat suitability maps accurately delineated where these species are found.

I generated a set of network nodes and resistance surfaces for each species within each time period, producing the inputs needed for the connectivity analyses. To identify the network nodes that would be used for the connectivity analyses, I determined the distribution of species' suitable habitat for each time period within the 19 MPA polygons, restricting the network node area to only the suitable habitat area. Because my focus was on physiological tolerance, I based resistance to movement on species' substrate associations, depth ranges, and thermal tolerance ranges. While there are other contributing factors to seascape resistance such as habitat quality and species interactions, these were outside the scope of my analysis. To generate resistance surfaces for the connectivity analyses, I rescaled the seasonal mean temperature rasters for each time period based on each species' thermal tolerance range. Pixels with temperatures between the lower and upper pejus temperatures were assigned a value of 1; temperatures exceeding this were rescaled 1-100 from the upper pejus temperature to the upper critical limit using an exponential transformation function; I used the same approach for temperatures below the lower pejus temperature to the lower critical limit. I assigned

higher resistance to temperatures beyond the pejus temperature range because they are associated with lower physiological function (Pörtner and Peck 2010). Pixels with temperatures beyond the critical limits were considered complete barriers to movement (assigned a value of NoData). For each focal species, I combined the rescaled seasonal mean temperature rasters for each time period with the corresponding suitable substrate maps to produce resistance surfaces.

I mapped connectivity between polygons containing suitable habitat for each combination of species, season, and time period using Linkage Mapper (McRae and Kavanagh 2011, 2017), using the corresponding network nodes (polygons containing suitable habitat) and resistance surfaces. This tool determined neighbouring polygons and calculated linkages between them using cost-weighted distance across the resistance surface (McRae and Kavanagh 2011). Cost-weighted distance was calculated by adding together the resistance values of each pixel traversed in the path; the path with lowest accumulated cost for each linkage was identified as the least-cost path (McRae and Kavanagh 2011). Because Linkage Mapper integrates least-cost path approaches with circuit theory, resistance to movement is identical in both directions of a linkage (i.e. movement cost of 'A' to 'B' equals cost of 'B' to 'A') so the directionality of ocean currents could not be incorporated (McRae et al. 2008). I calculated the length of each least-cost path and excluded all linkages whose Euclidean distance exceeded the focal species' mean adult movement distance (Table 3). Each pixel's contribution to individual least-cost corridors was normalized against the least-cost path, then all least-cost corridors were mosaicked to create a least-cost corridor heat map using Linkage Mapper

(McRae and Kavanagh 2011). These heat maps showed the relative value of individual pixels to maintaining connectivity via adult movement across the MPA network (McRae and Kavanagh 2017). Given that the least-cost corridor values have been normalized, the corridors could only be qualitatively compared within and between time periods.

I used three metrics to compare polygon interconnectedness between the two time periods: change in corridor quality, network density, and pinch points. Corridor quality was calculated by Linkage Mapper as the ratio of cost-weighted distance to path length for each least-cost path (McRae and Kavanagh 2017), enabling us to identify average resistance values encountered along the path, plus examine changes within individual linkages between the two time periods. I averaged the corridor quality values of all linkages within the network, then compared average corridor quality between the two time periods. Network density was calculated as the proportion of identified linkages to possible connections in the network (i.e., if every polygon containing suitable habitat was connected to every other polygon containing suitable habitat), enabling determination of changes in overall network connectivity between the two time periods. I calculated pinch points within the network, or areas that dispersers are forced to pass through due to substrate or temperature restrictions in the surrounding area, using Pinchpoint Mapper (McRae et al. 2008, McRae 2017). Because this tool uses circuit theory, movement is restricted to random walks, which can be thought of as random exploratory movements by individuals between habitat patches (McRae et al. 2008, Dutta et al. 2016). I conducted a seascape-level analysis where Pinchpoint Mapper injected simulated electric current into a source MPA and allowed it to flow through the network to all other MPAs,

iterating through all MPAs (McRae 2017). In my movement ecology application, electrons within the current were analogous to dispersing individuals, while electric current density was analogous to probability of passage by those dispersers (McRae et al. 2008). This allowed us to examine the relative importance of linkages and pinch points for maintaining connectivity across the entire network (McRae 2017). Pinch points have high probability of movement by dispersers because there are few to no alternative dispersal pathways between two habitat patches, thus areas with high electric current density were identified as pinch points (McRae et al. 2008). Because pinch points may be critical to movement between patches, negative impacts on these areas are likely to have a disproportionate impact on network connectivity (McRae et al. 2008, McRae 2017). Higher current density does not indicate an area with higher individual movement rates or higher quality to dispersing individuals, only that there are fewer alternative dispersal pathways available (McRae et al. 2008, Dutta et al. 2016).

3.3 Results

Similar connectivity patterns were observed across seasons; therefore I have presented only results pertaining to the summer season, which reported the most extreme changes (for other seasons, refer to Appendix S2). Shallower areas generally had higher summer benthic temperatures in both time periods, plus were projected to undergo greater temperature changes (Figure 6). There was a significant negative relationship between the mean depth of an MPA and its mean projected summer benthic temperature change (GLM with Gamma distribution: $p < 0.0000001$). On average, summer benthic temperatures were projected to increase more quickly in MPA polygons (mean change =

+1.17 °C) than for the overall bioregion (+0.99 °C), although this difference may have been heavily influenced by relatively stable temperatures along the continental slope rather than less change across the bioregion as a whole (Figure 6).

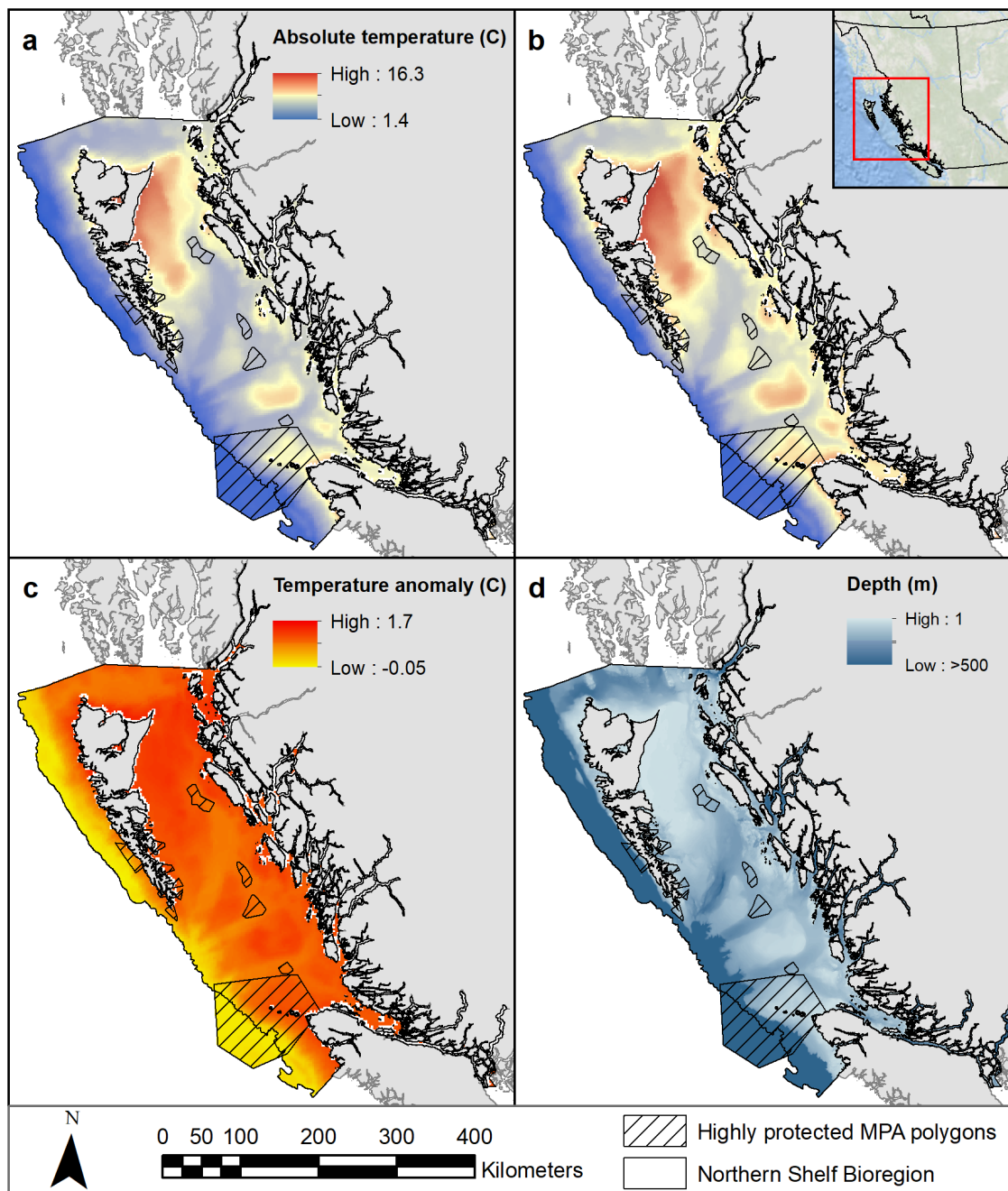


Figure 6. Mean summer benthic temperature projected for the Northern Shelf Bioregion in the (a) hindcast time period (1995-2008) and (b) projected time period (2065-2078). (c) Mean summer benthic temperature anomalies (projected – hindcast time period) across the bioregion. (d) Bathymetry of the bioregion. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Appendix S2: Figure S1).

Dungeness crab and Shortspine thornyhead exhibited opposite trends in habitat availability between the two time periods (Figure 7). For both species, summer habitat was present with mean benthic temperature between the pejus and critical temperature limits in both time periods. Increased resistance values were associated with temperatures below the lower pejus limit for Dungeness crab, whereas they corresponded to temperatures above the upper pejus limit for Shortspine thornyhead. As a result of warming benthic temperatures, there was 58% more suitable summer habitat area available for Dungeness crab within the study region in the projected compared to the hindcast time period (30,505.81 km² vs. 19,296.31 km² respectively; Figure 7). Conversely, only approximately one third of the total hindcast suitable habitat area for Shortspine thornyhead was available in the projected summer season as additional areas were pushed above the upper pejus temperature limit (23,634.70 km² vs. 7,908.03 km² respectively; Figure 7).

Relative to the hindcast time period, my model predicted an increase in MPA polygon suitability and interconnectedness for Dungeness crab in the projected period, but a decrease for Shortspine thornyhead (Figure 8). In the hindcast summer season, there were 10 MPA polygons that contained suitable habitat for Dungeness crab and one linkage between these polygons. This increased to 14 MPA polygons and three linkages in the projected summer season. Despite this increase, interconnectedness was still quite low as all three linkages were between isolated pairs. For Shortspine thornyhead, there were 10 MPA polygons with suitable habitat and eight linkages connecting most of the polygons as one graph component, but this decreased to three MPA polygons and one

linkage in the projected summer season. Two of the other seasons exhibited no change in interconnectedness, however this was already minimal in the hindcast time period (1 linkage).

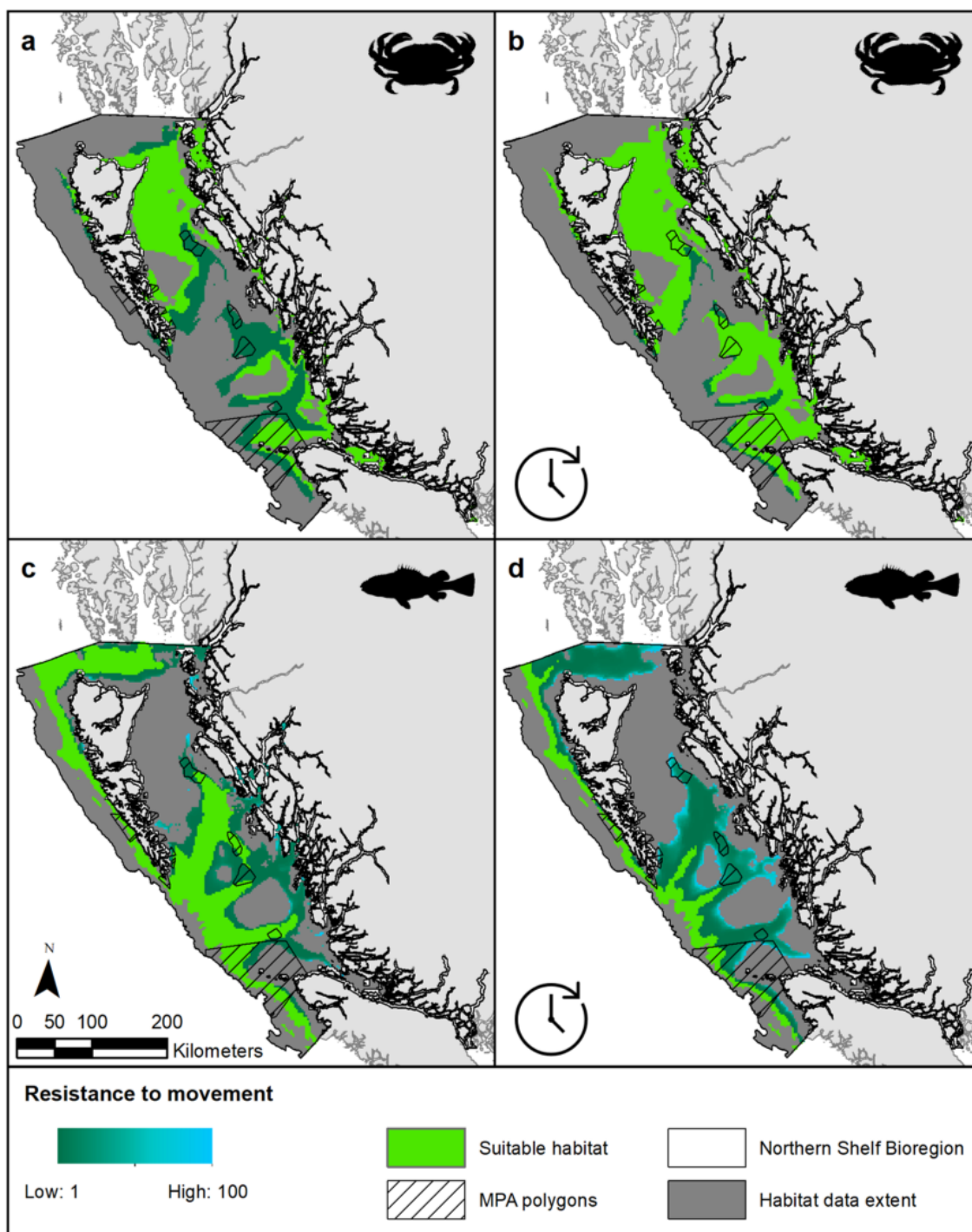


Figure 7. Resistance to movement within the Northern Shelf Bioregion for (a)(b) Dungeness crab and (c)(d) Shortspine thornyhead in two time periods: (a)(c) hindcast (1995-2008) and (b)(d) projected (2065-2078). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits; resistance to movement within suitable habitat is 1. Resistance to movement is scaled exponentially between species' pejus and critical limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Appendix S2: Figure S1).

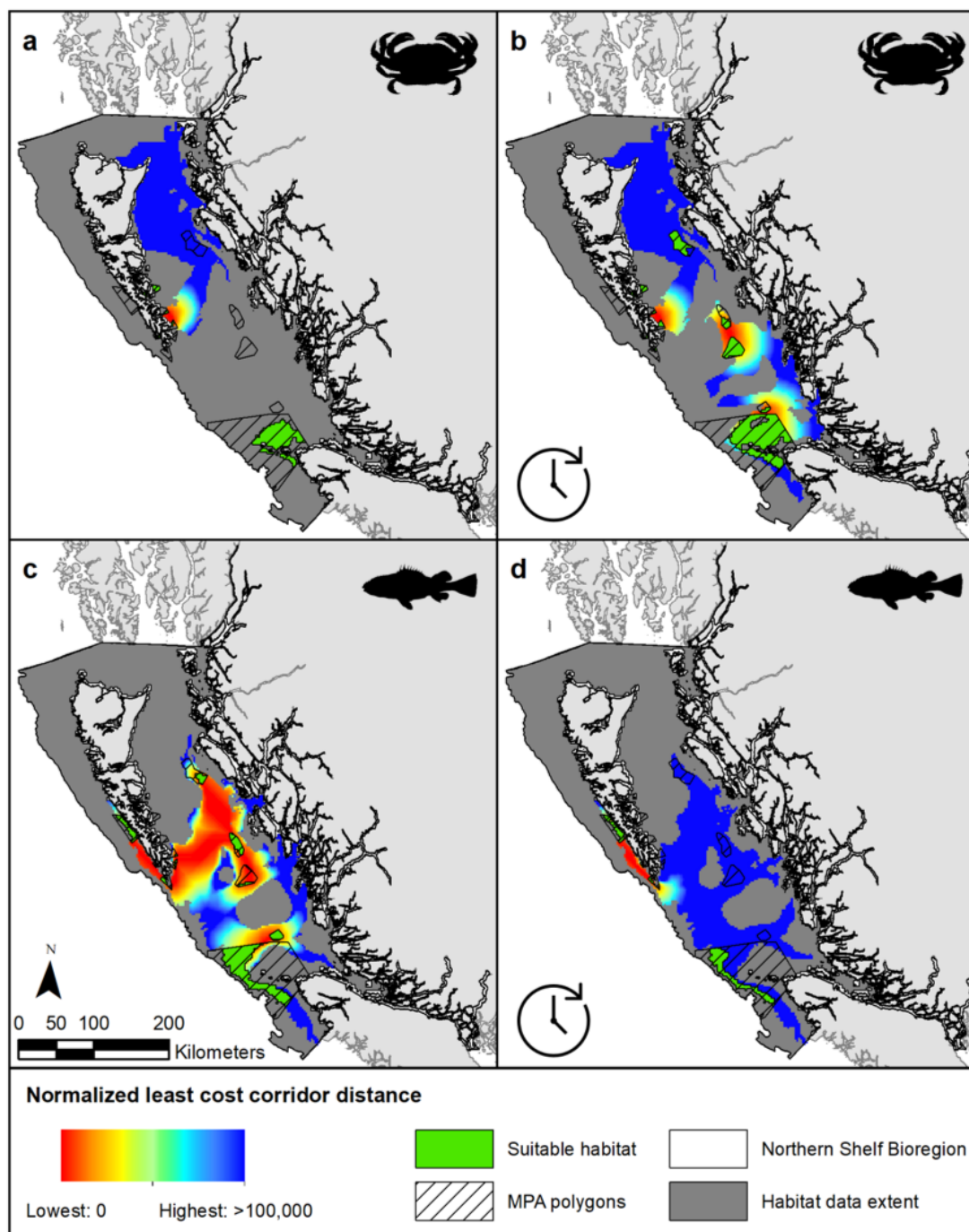


Figure 8. Least-cost corridors between highly protected marine protected area polygons containing suitable habitat for (a)(b) Dungeness crab and (c)(d) Shortspine thornyhead in two time periods: (a)(c) hindcast (1995-2008) and (b)(d) projected (2065-2078). Least-cost paths are shown in red; colours indicate how much more costly the route passing through each pixel is relative to the least-cost path. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Appendix S2: Figure S1).

Average corridor quality was very high (i.e. average ratio value close to 1) and stable between the time periods, while network density exhibited more change. It was 1.00 for the Dungeness crab network in both time periods, indicating that the least-cost path was almost exclusively situated through suitable habitat (Figure 9). For the Shortspine thornyhead network, average corridor quality was 1.01 in the hindcast because a small portion of several least-cost paths passed through temperatures below the lower pejus temperature limit (Figure 9). A single high quality linkage (1.00) was retained in the projected network. Note that this metric did not allow conclusions about other definitions of corridor quality, such as habitat degradation or fishing pressure. Network density increased from 0.022 to 0.033 in the projected time period for Dungeness crab, and from 0.178 to 0.333 for Shortspine thornyhead. However, these changes may not be meaningful because the number of MPA polygons and linkages were so small.

The electrical current density maps generated by the Pinchpoint Mapper analyses identified wide corridors, indicating that movement was fairly unrestricted (Figure 10). The maps suggested high probabilities of movement between habitat patches that were close together. However, there did not appear to be pinch points to movement between MPA polygons for the focal species in either time period; the highest electrical current densities were seen in areas adjacent to the suitable habitat patches acting as sources. In addition, because all core areas were set to supply the same amperage of electrical current, areas adjacent to small core areas showed the highest densities because the current was divided across less area. In the hindcast period, the pinch point maps were useful for demonstrating that Shortspine thornyhead movement across Hecate Strait is

likely to be more diffuse than between MPA polygons on the western side of Haida Gwaii, where suitable habitat area on the continental slope was more narrow (Figure 10c). The analysis also identified a potential alternative linkage across Hecate Strait that was not reported by my least-cost corridor analysis, likely because it exceeded the distance threshold for Shortspine thornyhead (Figure 10c). Since I used mean adult movement distance, this may be a potential corridor for those individuals that disperse farther than average.

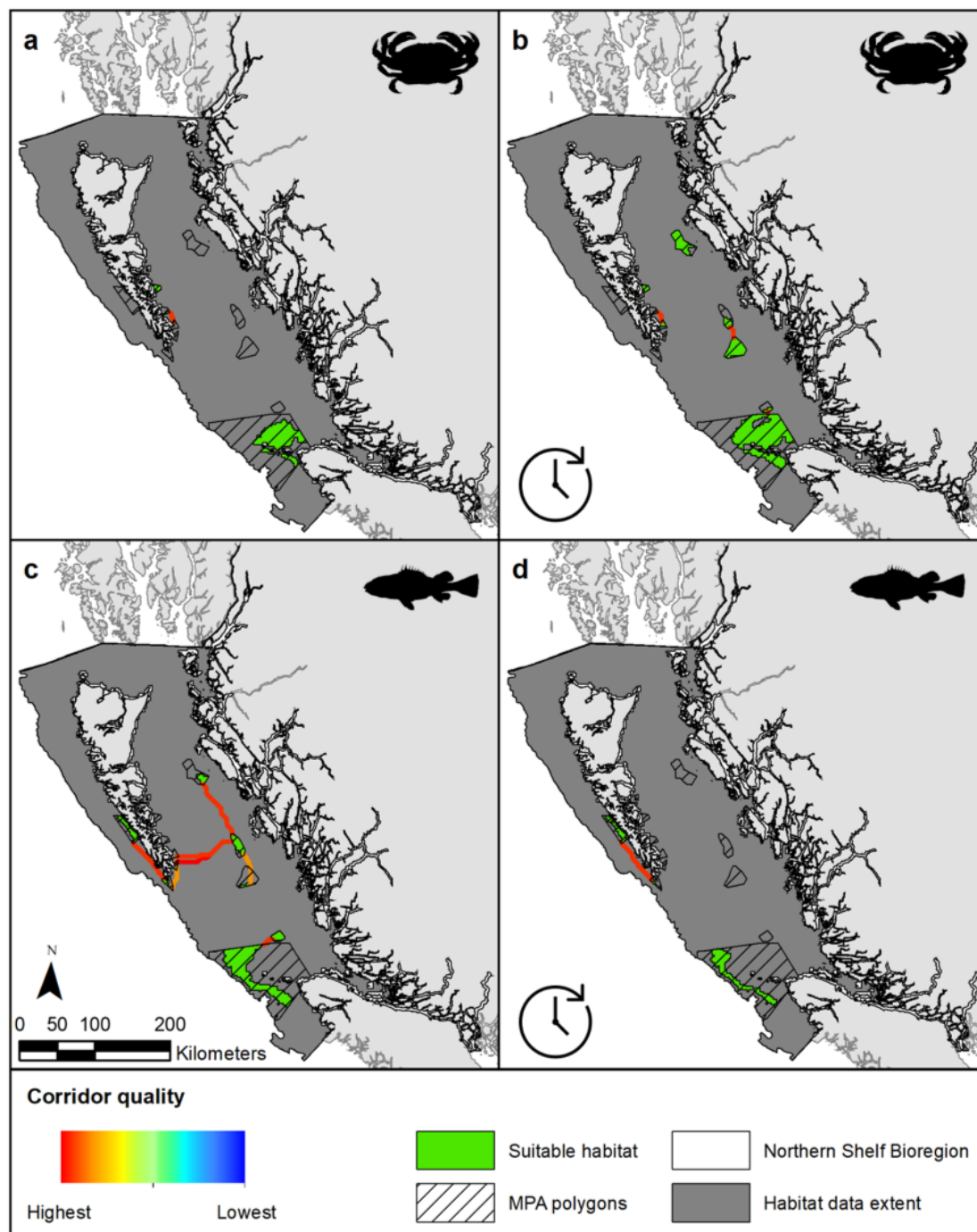


Figure 9. Corridor quality between highly protected marine protected area polygons containing suitable habitat for (a)(b) Dungeness crab and (c)(d) Shortspine thornyhead in two time periods: (a)(c) hindcast (1995-2008) and (b)(d) projected (2065-2078). Corridor quality was calculated as the ratio of cost-weighted distance to path length for each least-cost path; corridors with highest quality are shown in red. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Appendix S2: Figure S1).

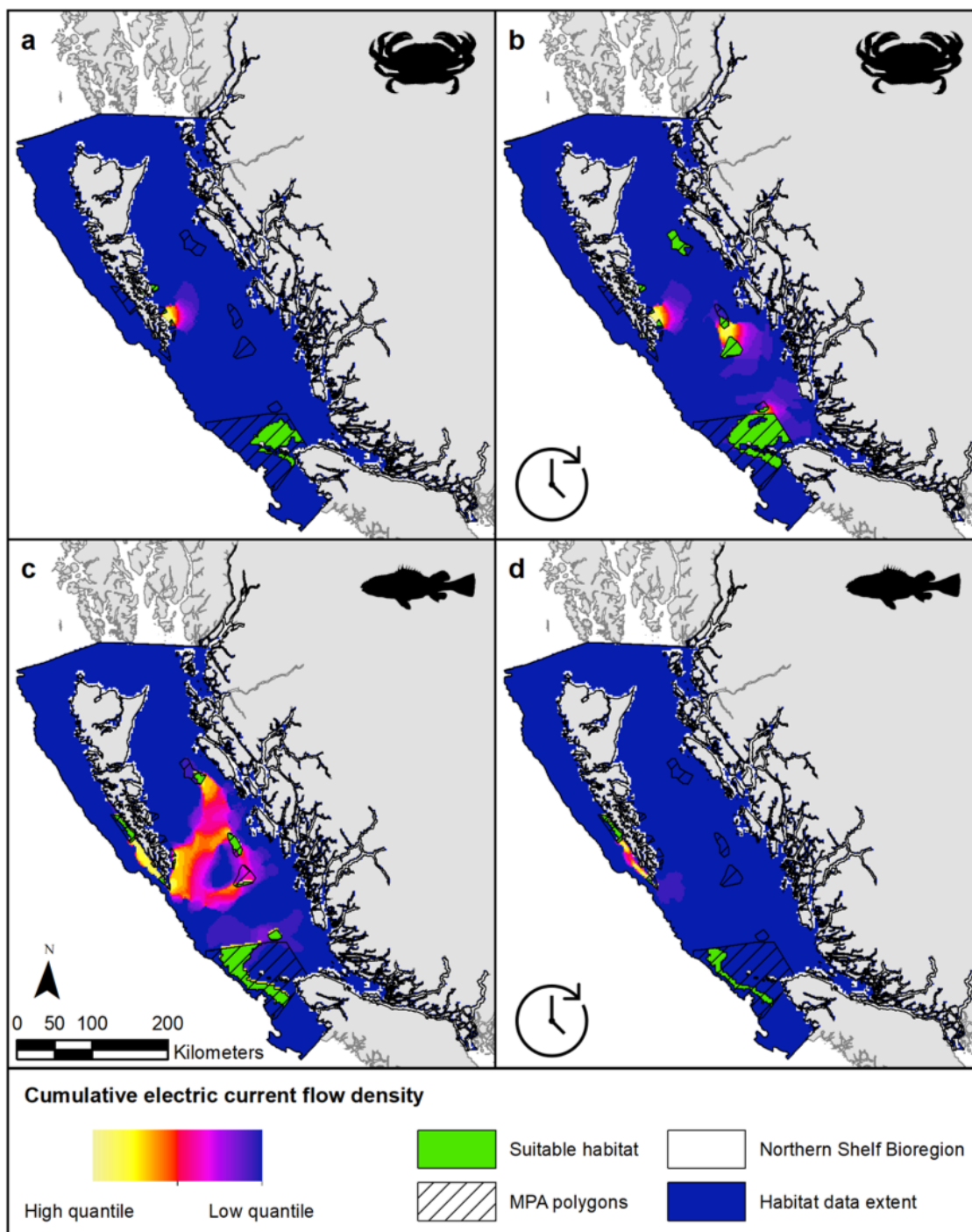


Figure 10. Seascape-level pinch points between all pairs of highly protected marine protected area polygons containing suitable habitat for (a)(b) Dungeness crab and (c)(d) Shortspine thornyhead in two time periods: (a)(c) hindcast (1995-2008) and (b)(d) projected (2065-2078). High current flow density (yellow) indicates areas where flow is more restricted relative to other areas (note quantile symbology). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Appendix S2: Figure S1).

3.4 Discussion

I found that projected warming benthic temperatures impacted MPA interconnectedness oppositely for my two focal species. I had predicted that the MPA network would become more disconnected with respect to adult movement in the projected time period, which was true for Shortspine thornyhead. This is in line with larval dispersal studies that have forecasted lower connectivity as climate change progresses (Kendall et al. 2016, Young et al. 2018). However, Dungeness crab exhibited the reverse trend, showing greater interconnectedness in the projected time period compared to minimal MPA polygon interconnectedness in the hindcast period. Although this result was contrary to my prediction, it makes sense based on the species' thermal tolerance ranges; warm-adapted species are expected to expand distribution ranges as climate change progresses (Poloczanska et al. 2016, Morley et al. 2018), and there is evidence that this is already occurring (Solmundsson et al. 2009, Cure et al. 2014). Andrello *et al.* (2015) also reported higher MPA network connectivity in the future for a species limited by low temperatures, although via larval dispersal. It is possible that my results are representative of other species provided that they have similar life histories.

I assumed that species' spatial niche and movement were constrained exclusively by substrate, depth, and temperature but there are other contributing factors such as biogenic habitat distributions, local population dynamics, and biotic interactions with competitors, prey, and predators (Pulliam 2000, Carr et al. 2017). These factors, as well as other physical environmental parameters, will shape the extent to which species distribution ranges expand or contract. Despite my predictions that more pinch points

would be present in the projected period, I did not determine any clear pinch points in either time period for either species. While my analysis identified areas with high electric current density, most were adjacent to core areas which more likely reflects the way in which simulated current is introduced to the system than ecologically-meaningful pinch points. For my focal species, changes in MPA interconnectedness appeared to be driven primarily by changes in MPA suitability rather than the emergence of pinch points or complete barriers to movement between MPAs, so MPA placement is a key factor.

My results suggest a “loser” and a “winner” as climate change progresses, but there are also other factors that will influence the outcome for each of these species. For example, previous work on Dungeness crabs found that reproductive output (egg production and hatching success) was already greatly reduced as temperatures reached the upper pejus limit (Wild and Tasto 1983). In addition, catch per unit effort of both species was observed to decline in hypoxic areas (Keller et al. 2010, Keller et al. 2017), plus demersal adult stages have highest exposure to ocean acidification because pH decreases with depth (Hodgson et al. 2016). In general, demersal species are more vulnerable to warming temperatures because they have less access to thermal refugia, whereas pelagic species may move to deeper, colder waters (Pinsky et al. 2019). These climate change effects may interact additively, antagonistically, or synergistically depending on species traits (Harley et al. 2006), so my predictions based on a single environmental stressor have high uncertainty.

Climate change is predicted to impact MPAs and marine ecological connectivity patterns significantly (Harley et al. 2006, Andrello et al. 2015, Bruno et al. 2018). My study found that projected benthic temperature change was higher in shallow areas within the Northern Shelf Bioregion. This means that MPAs, which are typically in shallow nearshore waters, are likely to have greater exposure to temperature changes; indeed, my study found that MPA polygons had higher average temperature anomalies than the bioregion overall. For thermally sensitive species, this means that they may move out of MPAs as climate change progresses (as was the case for Shortspine thornyhead), while other species may move in (as I found with Dungeness crab), taking advantage of warmer habitats, with probable implications for ecological community composition (Poloczanska et al. 2013, Okey et al. 2014). Because demersal species may be shifting to deeper areas to reduce thermal stress (Dulvy et al. 2008), planners may want to establish new MPAs in these areas, particularly as they are projected to be more thermally stable. Identifying and protecting climate refugia, if they exist, can help safeguard sensitive ecosystems (Brito-Morales et al. 2018). For many species (especially in the larval stage), connectivity is expected to decrease as temperatures increase (O'Connor et al. 2007). This may have implications for maintaining population resilience and replenishing fished areas. Conversely, decreased connectivity between regions may allow for local adaptation to changing environmental conditions (Young et al. 2018). It is important that climate change impacts are considered during planning processes, particularly for MPA networks, and that our conservation tools remain adaptable as changes are observed (Groves et al. 2012). This work shows the importance of implementing a replicated and representative network, as it would be difficult to model potential climate change impacts

and prioritize sites for multiple species without high uncertainty. In particular, representation of deeper areas within the Northern Shelf Bioregion MPA network is important because of their potential to buffer climate change impacts.

To my knowledge, this study is the first integration of both least-cost theory and circuit theory to evaluating marine ecological connectivity (for integration of one, see Pittman *et al.* 2014, Dambach *et al.* 2016). The analysis tools developed by McRae *et al.* (2008) can identify probabilistic flow and alternative dispersal pathways across the seascape, which may not be possible in passive particle-tracking or patch-based network models (Tremblay and Kool 2018). It is important to consider probabilistic flow and alternative paths, as redundancy can help increase MPA network resiliency to stressors like climate change (McRae *et al.* 2008, Rayfield *et al.* 2011). In addition, electric current flow methods do not assume that dispersers have any prior knowledge of the best path to follow (Carroll *et al.* 2012), so they may be more representative for non-migratory species. This approach may be particularly beneficial to specialist species, as there are more likely to be key pinch points to their movement that are important for maintaining overall network connectivity. Resistance is identical in both directions of a linkage (i.e. Patch A to B = B to A) so ocean currents cannot be incorporated despite their influence on animal movements (McRae *et al.* 2008). Terrestrial systems (for which these tools were developed) typically have more data available, such as species distributions, habitat quality, and spatial influence of anthropogenic pressures which could contribute to movement pinch points (e.g. Carroll *et al.* 2012, Dutta *et al.* 2016). Enough species-specific data are necessary to parameterize the analysis and generate the resistance

surface, which are not available for all species or life stages; my literature review yielded sparse information, even though both species are of commercial and conservation importance (DFO 2017). For data-limited species, it may not be possible to parameterize the resistance surface without introducing a lot of uncertainty, thus it may be more appropriate to use simplistic or habitat proxy models (e.g. Friesen et al. 2019). Overall, the analysis tools elucidate potential connectivity patterns and climate change effects in other marine contexts. However, it is important to note that, as with other modeling approaches, these may not represent true individual movement rates or gene flow. In particular, these patterns should be reconsidered once the Scott Islands mNWA management plan has been finalized; if benthic habitat is not highly protected, the associated ecological connections may not exist. Conversely, it is likely that other areas also contribute to regional connectivity patterns, particularly if those areas have some level of protection (such as within adaptive management zones). In this case, highly protected MPA zones may actually be more connected than my results suggest, provided that there are areas to act as stepping stones and facilitate movement between these zones.

My study had several limitations and assumptions that should be considered in interpreting my results, particularly with respect to the ocean circulation model. While I used the only ocean circulation model available for this region (and the only downscaled forecast), it necessarily constrained the analysis. Hindcast data were only available for 1995-2008, approximately two decades before the time of this study. Regional ocean temperatures have increased during this time (Okey et al. 2014), alongside other global

climate change impacts such as decreased pH and deoxygenation (Okey et al. 2014, Henson et al. 2017). Because of this, it is likely that contemporary MPA suitability and connectivity patterns are somewhere between those represented by each of the study's time periods. While electrical current flow analysis is reasonably robust to changes in scale (McRae et al. 2008), the fairly coarse resolution of the model (0.025 decimal degree) may have also affected observed patterns. Naturally, there is also uncertainty inherent in any projections of the future, but these are valuable in allowing predictions and planning for potential climate change impacts (Clark et al. 2001). By projecting future environmental conditions under the IPCC A2 'business as usual' emissions scenario (Foreman et al. 2014, Morrison et al. 2014), the circulation model incorporated a precautionary approach, so my analysis is likely to overpredict rather than underpredict changes in MPA suitability and connectivity. Other than temperature, I assumed that physical conditions remained constant between the time periods; as ocean circulation patterns shift, there may be changes in the timing or strength of upwelling, with the potential to affect the temporal delineation of seasons (Harley et al. 2006, Foreman et al. 2011). Habitat distributions may also shift, especially biotic habitats (Tanaka et al. 2012), which will in turn affect the distribution and connectivity patterns of dependent species.

I focused on temperature as a single potential stressor, yet these biological changes are also driven by other climate change impacts such as deoxygenation, acidification, and changes in ocean circulation, as well as further anthropogenic impacts like fishing (Harley et al. 2006, Okey et al. 2014). The species' environmental preferences were extracted from the literature, but studies were sparse and predominantly

lab-based so the thresholds that I used may differ from complex wild conditions. Expanding this approach to other species of conservation interest might be limited by the availability of physiological data. I focused only on the exposure component of a temperature vulnerability assessment, but species' sensitivity and adaptive capacity will also shape responses to climate change (IPCC 2001). I assumed that species' preferences remained constant between the two time periods, but this does not consider potential acclimatization or adaptation (Somero 2010). For example, there is some evidence to suggest that some marine species' depth preferences are shifting deeper, presumably to remain within suitable temperature limits (Dulvy et al. 2008, Nye et al. 2009). Climate change studies should seek to incorporate species' potential for acclimatization and adaptation, although much more data are needed to enable such predictions. Physical habitat suitability is determined by temperature preferences, but also by species' pH and dissolved oxygen preferences, among others (Deutsch et al. 2015). In addition, multiple environmental stressors (e.g. acidification) may have additive or multiplicative effects (Ainsworth et al. 2011). The integration of these additional variables, including their interactions, would likely alter my results. I also only focused on the demersal adult stage of my two focal species, but different life stages are expected to vary in their exposure and sensitivity to climate change impacts (Munday et al. 2008). Future studies could incorporate this added complexity, as well as species' capacity for acclimatization or adaptation.

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Chapter 4 – Conclusion

4.1 Thesis Overview

The goal of this thesis was to evaluate ecological connectivity through the mechanism of adult movement, focusing on the Northern Shelf Bioregion as a data-limited case study. I used four research objectives to meet this goal. I successfully achieved all of the objectives as follows.

Objective 1: Evaluate potential connectivity via adult movement for the entire bioregion, using habitat proxies for distinct ecological communities

I developed an approach that can be applied in data-limited marine systems, using novel multiplex network methods. With this approach, I evaluated inferred connectivity within multiple benthic habitat categories for two moderate distance thresholds, then identified regional connectivity hotspots using two network centrality metrics. By using habitat proxies, I was able to infer connectivity patterns for species and communities for which data are unavailable or extremely limited. Regional connectivity hotspots differed depending on the distance threshold and centrality metric considered; for an MPA context, this highlights the importance of tailoring connectivity analyses to the specific objectives and conservation priorities of individual MPA planning processes. Overall, my approach is valuable because it enables multiple entities (such as habitats, species, life stages, time periods, or interaction types) to be considered simultaneously in MPA planning processes (Pilosof et al. 2017), which are typically tasked with multiple conservation objectives. In addition, the approach is general and therefore could easily incorporate additional data when available. For instance, with additional data, instead of

using visibility graphing, connectivity patterns could be more realistically represented through least cost modeling, circuit theory methods, particle tracking simulations, tagging studies, and genetic analyses (Urban and Keitt 2001, Galpern et al. 2011, Correa Ayram et al. 2016, Treml and Kool 2018). Once network linkages have been identified (perhaps including link strength and direction), they can still be evaluated using my multiplex network analysis methods. Because of this, the approach could also be extended to freshwater or terrestrial systems.

Objective 2: Assess potential connectivity via adult movement among existing and potential MPAs, using the same habitat proxies

With the approach developed for Objective 1, I evaluated inferred connectivity among existing and potential MPAs in the bioregion, as well as the extent to which these MPAs overlapped with the regional connectivity hotspots. I found that existing MPAs intersected a moderate proportion of regional connectivity hotspots, which was increased by the addition of potential MPAs. Although ecological connectivity is a key attribute of MPA design, connectivity among MPAs has not been well studied. For population persistence within MPAs, there must be sufficient self-recruitment or immigration of individuals from other areas; in heavily fished regions where commercially-harvested species may be in low abundance outside of protected areas, movement of individuals between MPAs may be critical for long term population viability (Botsford et al. 2001, Green et al. 2014, Carr et al. 2017). My study found that interconnectedness among existing MPAs was quite low, suggesting that MPA network resilience could be enhanced by the addition of strategically-placed stepping stone MPAs.

*Objective 3: Model potential connectivity via adult movement among MPAs for two focal species (*Metacarcinus magister* and *Sebastolobus alascanus*) and predict how this interconnectedness may shift based on projected ocean temperature changes*

In my third chapter, I applied least cost and circuit theory to model patterns of MPA interconnectedness for *M. magister* and *S. alascanus*. Using benthic temperature outputs from an ocean circulation model, I compared MPA suitability and interconnectedness between a hindcast and projected time period. MPA suitability and interconnectedness for *M. magister* increased with warming temperatures, but decreased for *S. alascanus*. This highlights the importance of modeling potential climate change impacts on multiple species of conservation interest (Magris et al. 2016). Moving beyond my study, it is important to consider multiple perspectives in conservation planning; actions to benefit one species (or stakeholder) may hinder another. I also found that MPAs were projected to undergo greater temperature changes than average in the bioregion. My analysis suggested that deeper areas may have the potential to act as temperature refugia as benthic temperatures in these areas were more stable across the time periods. If species can acclimatize or adapt to deeper distributions, this may ameliorate temperature impacts (Dulvy et al. 2008). However, other studies have found that pH decreases with depth so species distributions may become squeezed rather than shift (Harley et al. 2006, Okey et al. 2014, Hodgson et al. 2016).

Objective 4: Contribute the results of these analyses to the Marine Protected Area Technical Team's (MPATT's) ongoing planning process so that connectivity may be considered in the implementation of a new MPA network in the bioregion

This thesis has had direct application to MPATT's planning process for a new MPA network in the bioregion, enabling ecological connectivity to be considered alongside other MPA design elements such as representation and replication. Committee members Emily Rubidge and Rebecca Martone are part of the technical team; their guidance, as well as that of other MPATT members, ensured that my thesis remained pertinent to the planning process as it developed. The results of Chapter 2, plus results from additional habitat-specific analyses, were delivered to MPATT in 2018 and incorporated into the team's marine spatial planning tool. It is possible that Chapter 3 results may also be integrated into the planning process, but data constraints limit applicability of the climate change analysis. Because many of the inlets and nearshore areas in the bioregion were outside the spatial extent of the ocean circulation model outputs, most existing provincial MPAs would have been excluded from any analysis. However, the effects of climate change impacts on MPA interconnectedness and the identification of deeper areas as potential climate refugia may be valuable considerations in the Northern Shelf MPA network planning process.

4.2 Contributions of research

My thesis has contributions to the literature and practical applications beyond MPATT's planning process. Under the Convention on Biological Diversity's Strategic Plan for 2011-2020, Canada has committed to establishing well-connected MPAs in 10%

of its oceans by 2020 (Convention on Biological Diversity 2010); my thesis enabled the connectivity component of this to be considered in the Northern Shelf Bioregion.

Previous connectivity studies have primarily focused on larval dispersal (Sala et al. 2002, Cowen and Sponaugle 2009, Anadón et al. 2013), so my focus on adult movement is complementary to the existing literature. Previous adult movement studies have considered how adult movement may affect individual MPA efficacy (Walters et al. 2007, Moffitt et al. 2009, Grüss et al. 2011a), while I have investigated how adult movement may contribute to connectivity patterns (also examined for the Caribbean region by Pittman *et al.* 2014). My research is the first application of multiplex network theory, as well as of circuit theory, to incorporating ecological connectivity into MPA network planning, advancing these theories to new contexts and providing new strategies for connectivity modeling. Both of my studies have developed methods that can be used in data-limited contexts where other modeling methods may not be possible (such as Bode et al. 2016, Castorani et al. 2017), yet are easily adapted to incorporate more data as the scientific understanding of animal movement increases, or as regional information become available. This thesis has provided practical methods that may be applied to other data-limited planning processes, as well as evaluation of MPA networks after implementation. The analytical methods that I developed for the climate change study can also help with adaptive management to ensure that MPAs continue to be connected, even as the species contained therein may change with climate change.

4.3 Limitations and areas for future research

Because my goal was ‘to evaluate ecological connectivity through the mechanism of adult movement, focusing on the Northern Shelf Bioregion as a data-limited case study’, the scope of my thesis was necessarily limited by the data available, plus some strategic decisions to make the research tractable. The first limitation is that I only considered the contributions of adult movement to connectivity patterns, yet other life stages are also important for connectivity (Carr et al. 2017). Life stages may have different dispersal abilities; larvae are typically transported by oceanic currents, so may be able to travel much farther than motile adults (Roberts 1997). Overall, this region may have much higher connectivity for various species due to egg or larval dispersal, than my results suggest. However, the available oceanic circulation model did not include many of the nearshore areas and inlets, so I would not have been able to assess larval connectivity for the whole study region. Different life stages may also exhibit unique habitat preferences, thus ontogenetic shifts between habitat types may also influence connectivity patterns (Gillanders et al. 2003). Early life stages tend to have greater sensitivity to increased ocean temperatures, plus are found closer to the surface where temperatures are higher than those experienced by benthic adults (Pörtner and Peck 2010, Poloczanska et al. 2016). Thus these life stages may be more vulnerable to warming temperatures associated with climate change and may be excluded from areas that would be suitable for adults (Pörtner and Peck 2010). In this case, the lack of recruits is likely to inhibit persistence of adults in these areas, so my connectivity patterns may overestimate suitable habitat areas and the connectivity patterns between them. While this was beyond

the scope of my thesis, future studies should integrate all life stages to more realistically model ecological connectivity patterns and climate change impacts for a given species.

Another limitation is that species distributions were assumed to be determined exclusively by habitat type and depth range (plus benthic ocean temperature in Chapter 3), yet there are many factors that contribute to a species' realized spatial niche (Deutsch et al. 2015, Carr et al. 2017). These include physical environmental conditions such as pH and dissolved oxygen (Deutsch et al. 2015); because these parameters are also shifting with climate change, they may greatly influence species' responses to climate change (e.g. low pH or oxygen at depth may limit species' ability to avoid warm shallow areas) but this was outside my thesis scope, in part due to the lack of understanding of how these variables will shift with climate change in this region. The results of my climate change analysis, which are based on a single environmental stressor, provide a simplified prediction of future conditions. Species distributions are also constrained by population recruitment dynamics, intra- and inter-species competition, resource availability, predation risk, biogenic habitat distributions, habitat quality, and anthropogenic impacts (Pulliam 2000, Puritz and Toonen 2011, Carr et al. 2017, de Oliveira Soares 2018). Developing a species distribution model that integrates these additional factors, including how each may be affected by a changing climate, would have comprised an entire thesis in and of itself. It is probable that some species may acclimate or adapt to novel environmental conditions over time (IPCC 2001, Somero 2010), so parameterization of a species distribution model may vary under climate change conditions. In addition, we assumed that movements were restricted to within species' preferred habitat type and

depth range, yet it is possible that species may move through more marginal areas in order to reach suitable habitat. Building a better understanding of species responses, species distributions, and movement behaviour is important for filling these data gaps.

Future studies should seek to incorporate oceanic currents and anthropogenic impacts into ecological connectivity analyses. While currents have been integrated into passive larval dispersal studies (e.g. Treml et al. 2008), it is still unclear how interactions between currents and active movement may influence connectivity patterns (Caldwell and Gergel 2013). Genetic analyses in some regions have shown that recruitment is much more localized than predicted by passive larval dispersal modeling, indicating that larval behaviour is exerting some control over dispersal distance (Gerlach et al. 2007, Hoffman et al. 2012). The extent to which oceanic currents facilitate or inhibit the active movements of motile juveniles and adults, thereby contributing to connectivity patterns, is species-specific and data were not available for my focal species. Future knowledge on this would be invaluable for calculating effective resistance to movement across a seascape. In addition to climate change, other anthropogenic impacts will also influence connectivity patterns (Puritz and Toonen 2011, de Oliveira Soares 2018). Habitat destruction, high fishing mortality, or pollution may disrupt a connection between two protected areas or make core areas unsuitable (Puritz and Toonen 2011). However, data were not available for the entire study region.

While my results allow connectivity to be considered in the Northern Shelf Bioregion planning process where it otherwise would not have been possible, the most

important limitation of this thesis is that it is based on modeling exercises. In order to ensure the validity of my study assumptions and accuracy of my modeling results, it is essential that they are ground truthed through tagging, tracking, or genetic sequencing studies. At the time, there were no existing data for the region to which I could compare my modeling results. Genetic analyses in particular would be valuable as they could elucidate connectivity patterns across all life stages of a species, however they would not identify key dispersal routes to the same extent as a tracking study. Fine-scale tracking studies could help determine the effective resistance to movement of various habitat types, depth ranges, temperature, and other environmental parameters. As more data become available, my models could incorporate these data to provide a more realistic representation. Alternatively, the realized connections determined through tracking, tagging, or genetic studies could be analyzed using the network analysis methods that I have developed, in order to prioritize areas for protection.

Future research should seek to fill the data gaps that I have outlined here. Of particular importance is the need to integrate all life stages into connectivity analyses and ground truth modeling exercises. Another potential area for research is the expansion of multiplex network analyses to other MPA connectivity contexts. For example, layers within the multiplex network could correspond to different life stages, species, seasons, temporal periods, types of dispersal events, or disease transmission. Multiplex networks could also be used to represent and evaluate the relationships between different stakeholders involved in an MPA planning process, or the multiple institutions responsible for managing an MPA. Future studies would facilitate the integration of

connectivity into adaptive management or future planning processes, as well as further our understanding of marine ecological connectivity for different species and life stages. Ultimately, this will contribute to the efficacy of MPAs and biodiversity conservation in the future.

4.4 Literature Cited

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Appendix S1 – Supplementary information for Chapter 2

Table S1. Adult movement ranges and habitat preferences of some benthic-associated MPATT Conservation Priority species for the Northern Shelf Bioregion. Moderate movement ranges are shaded grey.

Habitat	Adult movement range		
	<0.05 km	0.05 – 1 km	1 – 10 km
Rocky	Wolf Eel, China Rockfish, Redstripe Rockfish, Yelloweye Rockfish, Green Urchin, Spiny Scallop, Pink Scallop, Gooseneck Barnacle, Purple-hinged Rock Scallop, California Mussel	Rougeye Rockfish, Copper Rockfish, Greenstriped Rockfish, Widow Rockfish, Quillback Rockfish, Black Rockfish, Red Urchin, Northern Abalone	Prawn, Giant Pacific Octopus
Sandy	Redstripe Rockfish, Cockles, Littleneck Clam, Manila Clam, Butter Clam, Horse Clam	Greenstriped Rockfish, Black Rockfish	Shortspine Thornyhead, Dungeness Crab, Prawn
Muddy	Cockles, Littleneck Clam, Manila Clam, Butter Clam, Horse Clam	Darkblotched Rockfish	Shortspine Thornyhead, Dungeness Crab, Prawn
Kelp		Black Rockfish, Red Urchin	
Eelgrass			Dungeness Crab
Estuary			
Habitat	Adult movement range		
	10 – 50 km	50 – 1000 km	1000+ m
Rocky	Lingcod, Bocaccio	Canary Rockfish	Walleye Pollock
Sandy	Inshore Tanner Crab, Deepwater Tanner Crab	Arrowtooth Flounder, Pacific Halibut, Dover Sole	Walleye Pollock
Muddy	Inshore Tanner Crab, Deepwater Tanner Crab		Walleye Pollock
Kelp	Lingcod	Yellowtail Rockfish	
Eelgrass	Lingcod		
Estuary			

(Burt et al. 2014, Department of Fisheries and Oceans Canada, 2017)

Table S2. Source of habitat and bathymetry shapefiles

Type of Data	Source	Notes About Data Uncertainty**
Bathymetry (100 m raster)*	SciTech Environmental Consulting	<p>“...depth accuracy will vary with the density of contours, and likely decreases with increasing depth. Thus, an accuracy of +/- 10% is likely a reasonable assumption.”</p> <p>“Data become sparser with increasing depth likely leading to a loss of resolution at depth.”</p> <p>“Based on the comparison with the NRCan data, the horizontal referencing could be off by several hundred metres in places. Neither source data set aligned well with the best available coastline across the entire study area suggesting minor distortions in the projection of the original contour data. However, these data, and the source data sets are self-consistent, and thus provide a suitable framework for studies at coastwide extents.”</p> <p>“Qualitative assessment of positional accuracy suggests that significant errors exist, however the sources used are self-consistent, making these data suitable as a framework for coastwide, and possibly regional analyses.”</p>
Benthic habitat (mud, sand, rock, and unknown habitat)*	Parks Canada; BC Marine Conservation Analysis	“Accuracy of benthic habitats have not been ground truthed or field tested.”
Kelp habitat*	BC Marine Conservation Analysis; Government of British Columbia (Ministry of Forests, Lands, Natural Resource Operations and Rural Development)	“This dataset is a compilation of data collected by many people, for different purposes, using different survey techniques with different methodologies within each technique and, therefore, considerable care must be taken when using the data...” (from Giant Kelp Polygons Metadata)
Estuary habitat	Pacific Estuary Conservation Program	
Eelgrass habitat*	BC Marine Conservation Analysis	“This dataset is a compilation of data collected by many people, for different purposes, using different survey techniques with different methodologies within each technique and, therefore, considerable care must be taken when using the data...”

*accessed via the BC Marine Conservation Analysis data repository (<https://bcmca.ca/maps-data/browse-or-search/>). The BCMCA has links to the data custodians for each data set, who may be contacted for the data

**quotes from the source metadata are used to provide a qualitative sense of the uncertainty associated with the data

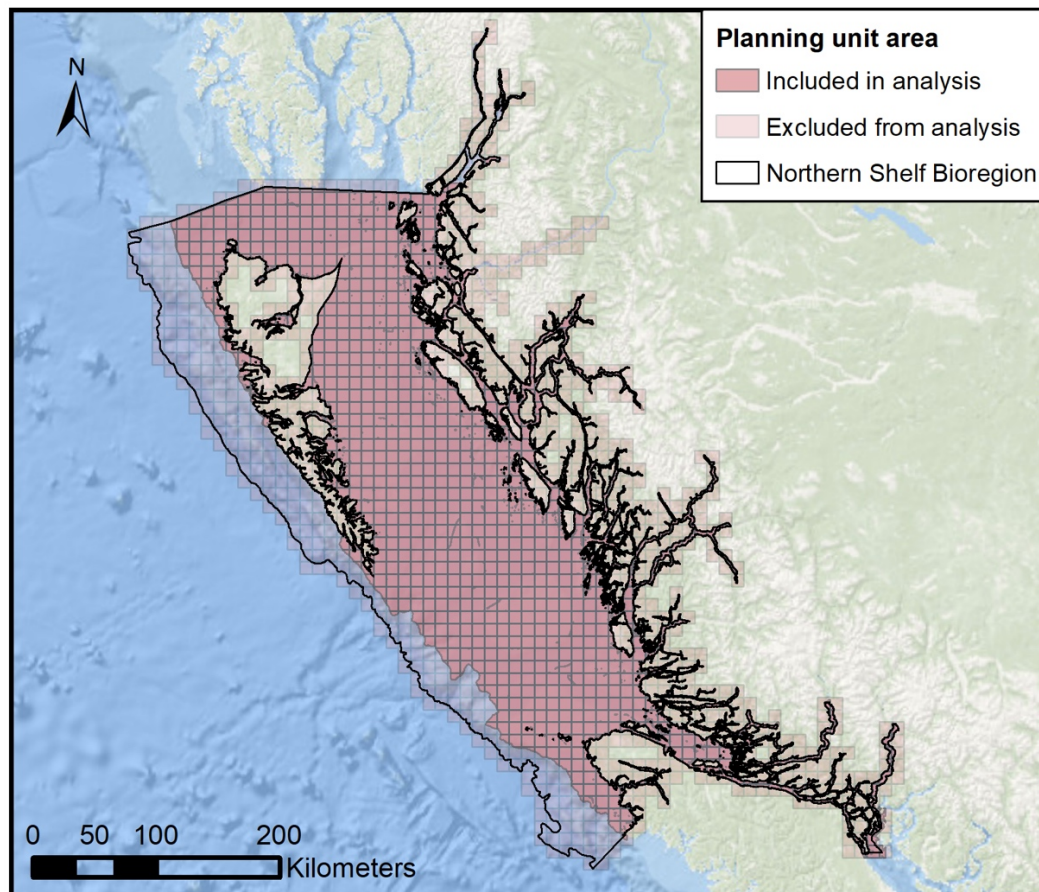


Figure S1. Planning unit area included in analysis. Areas were excluded if habitat patches were of unknown type or <1 square kilometre.

Table S3. Number of planning units containing each habitat category*

	Rocky	Sandy	Muddy	Estuary	Kelp	Eelgrass
0 – 20 m	220	114	214	38	33	5
20 – 50 m	255	162	72	1**	1**	
50 – 200 m	468	473	366			
200 – 1000 m	206	216	261			
1000+ m	6					

* Where multiple habitat patches were identified in the same location, I gave them priority in order of eelgrass, kelp, estuary, then rocky/sandy/muddy habitat. Biogenic habitats and estuaries were prioritized over the contiguous rocky/sandy/muddy habitat layer because the data are finer resolution and are more spatially restricted. The priority order for eelgrass, kelp, and estuary was determined by maximum retention of habitat patches (some patches were completely within patches of another habitat type).

** Connectivity is not relevant for one habitat patch, so these were not considered in the analysis.

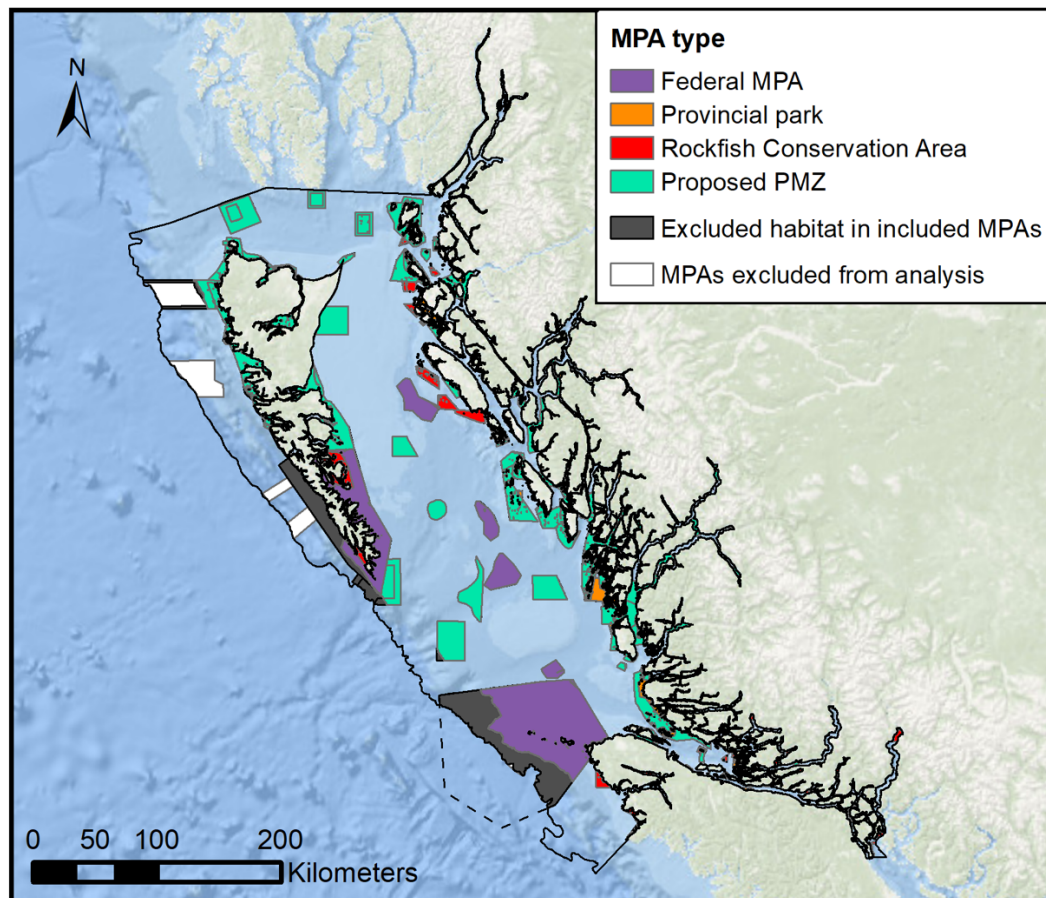


Figure S2. Habitat area within MPAs included in analysis. Areas were excluded (including entire MPAs) if habitat patches were of unknown type or <1 square kilometre. In my analysis, existing MPAs are Federal MPAs and Provincial Parks, while potential MPAs are Rockfish Conservation Areas and Proposed Protection Management Zones. Each core area of the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area was considered a distinct MPA for this analysis. Many small MPAs are not visible at the regional scale.

Table S4. Number of marine protected areas containing each habitat category*

	Rocky	Sandy	Muddy	Estuary	Kelp	Eelgrass
0 – 20 m	121	51	78	28	23	8
20 – 50 m	88	39	27	1**	1**	
50 – 200 m	122	79	96			
200 – 1000 m	34	24	59			
1000+ m	1**					

* Where multiple habitat patches were identified in the same location, I gave them priority in order of eelgrass, kelp, estuary, then rocky/sandy/muddy habitat. Biogenic habitats and estuaries were prioritized over the contiguous rocky/sandy/muddy habitat layer because the data are finer resolution and are more spatially restricted. The priority order for eelgrass, kelp, and estuary was determined by maximum retention of habitat patches (some patches were completely within patches of another habitat type).

** Connectivity between MPAs is not relevant for one habitat patch, so these were not considered in the analysis.

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Appendix S2 – Supplementary information for Chapter 3

I conducted a literature review, supplemented where necessary by technical reports. Where possible, only studies that directly measured one or more of these parameters were considered. To attain a more representative understanding, I considered studies that reported typical depth ranges rather than absolute minimum or maximum ranges, as well as mean adult movement distances. For Dungeness crab thermal tolerance thresholds that were not described in the literature, I used values reported in a physiological limits database developed by Fisheries and Oceans Canada (Steiner et al. 2018). This database was originally developed for arctic and subarctic species, but has since been expanded to the Pacific Northeast and all adult Dungeness crab studies referenced in the database are from this region. For Shortspine thornyhead thermal tolerance thresholds that were not described in the literature, I used values derived from previous species distribution modeling done by Lecomte *et al.* (in preparation) based on multi-annual, coupled population and environmental survey data.

Dungeness crab literature search terms: (("Dungeness crab" OR "Dungeness Crab" OR "Metacarcinus magister" OR "Cancer magister") AND (depth OR temperature OR habitat OR substrate OR movement OR distance OR "home range" OR physiology OR adult))

Shortspine thornyhead literature search terms: ("shortspine thornyhead" OR "Sebastolobus alascanus" OR "Sebastodes alascanus") AND (depth OR temperature OR habitat OR substrate OR movement OR distance OR "home range" OR physiology OR adult))

Table S1. Preference parameters for Dungeness crab (*Metacarcinus magister*) and Shortspine thornyhead (*Sebastolobus alascanus*), as determined through a literature review. For thermal tolerance thresholds that were not described in the literature, I used values reported in a physiological limits database developed by Fisheries and Oceans Canada (Steiner et al. 2018) or derived from previous species distribution modeling (Lecomte et al., in preparation).

<i>Dungeness crab</i>			
Parameter	Value	Source(s)	Notes
Suitable substrate	Estuary, mud, sand, (eelgrass)	(Smith and Jamieson 1991, Stone and O'Clair 2001, Stone and O'Clair 2002, Hosack et al. 2006, Curtis and McGaw 2008, 2012, Froehlich et al. 2013, Rasmuson 2013, Harding and Reynolds 2014)	Biogenic habitat (eelgrass) not considered in my analysis
Depth range (m)	0 – 229	(Pauley et al. 1989, Hildenbrand et al. 2011, Rasmuson 2013, Burt et al. 2014a)	Min and max depths are means of four secondarily reported values
Upper critical temperature (°C)	25	(Steiner et al. 2018) *	
Upper pejus temperature (°C)	17	(Steiner et al. 2018) *	
Lower pejus temperature (°C)	7	(Steiner et al. 2018) *	
Lower critical temperature (°C)	1.6	(Shirley et al. 1987)	Minimum temperature within suitable substrate and depth range is > 1.6 °C so threshold does not affect analyses
Mean adult movement distance (km)	18.6	(Hildenbrand et al. 2011)	Excluded other references based on no mean value reported, plus: spatially restricted (Stone and O'Clair 2001), temporally and spatially restricted (Froehlich et al. 2013), and binning of distances (Diamond and Hankin 1985)
<i>Shortspine thornyhead</i>			
Parameter	Value	Source(s)	Notes

Suitable substrate	Sand, mud, hard **	(Jacobson and Vetter 1996, Else and Haldorson 2002, Tissot et al. 2007, Du Preez and Tunnicliffe 2011)	
Depth range (m)	134-1032	(Starr and Haigh 2017)	The only reference that directly measured depth range
Upper temperature where modeled probability of presence is zero (°C) ***	8.0	(Lecomte et al., in preparation)	Modeled threshold used as proxy for upper critical temperature ***
Upper temperature where modeled probability of presence is 50% (°C) ****	6.1	(Lecomte et al., in preparation)	Modeled threshold used as proxy for upper pejus temperature ****
Lower pejus temperature (°C)	1.2	(Kaschner et al. 2016)	Modeled threshold. Minimum temperature within suitable substrate and depth range is > 1.2 °C so threshold does not affect analyses
Lower critical temperature (°C)	NA		Minimum temperature within suitable substrate and depth range is > 1.2 °C so threshold does not affect analyses
Mean adult movement distance (km)	85	(Echave 2017)	The only reference that directly measured home ranges

* Adult Dungeness crab studies referenced in Steiner *et al.* (2018) database: (Prentice 1971, Des Voigne 1973, Mayer 1973, Prentice and Schneider 1979, Wild and Tasto 1983, Pauley et al. 1989, Brooks 2001). Note that technical report for database is focused on arctic and subarctic species, but the database has since been expanded to the Pacific Northeast and all reference studies for Dungeness crab are from this region.

** For Shortspine thornyhead, a generalist species that may be found in sandy, muddy, and hard substrates, I also considered 'unknown' substrate to be suitable as it would be classified as one of these three substrate types if data were available.

*** No literature values were found for upper critical temperature. This threshold value was determined from the application of a species distribution model to multi-annual, coupled population and environmental survey data. The value reflected the temperature at which probability of presence was 0%. Though the species may be able to survive higher temperatures, the model predicts individuals will not be found at temperatures exceeding this threshold value. Thus I consider this threshold as a proxy for the upper critical temperature, at least in the context of spatial distribution and connectivity analyses. See Lecomte *et al.* (in preparation) for model details.

**** No literature values were found for upper pejus temperature. Threshold value was determined from the application of a species distribution model to multi-annual, coupled population and environmental survey data. The value reflects the temperature where probability of presence was 50%. In the absence of a pejus limit, I use the normal distribution limit as a proxy (Pörtner 2012). See Lecomte *et al.* (in preparation) for model details.

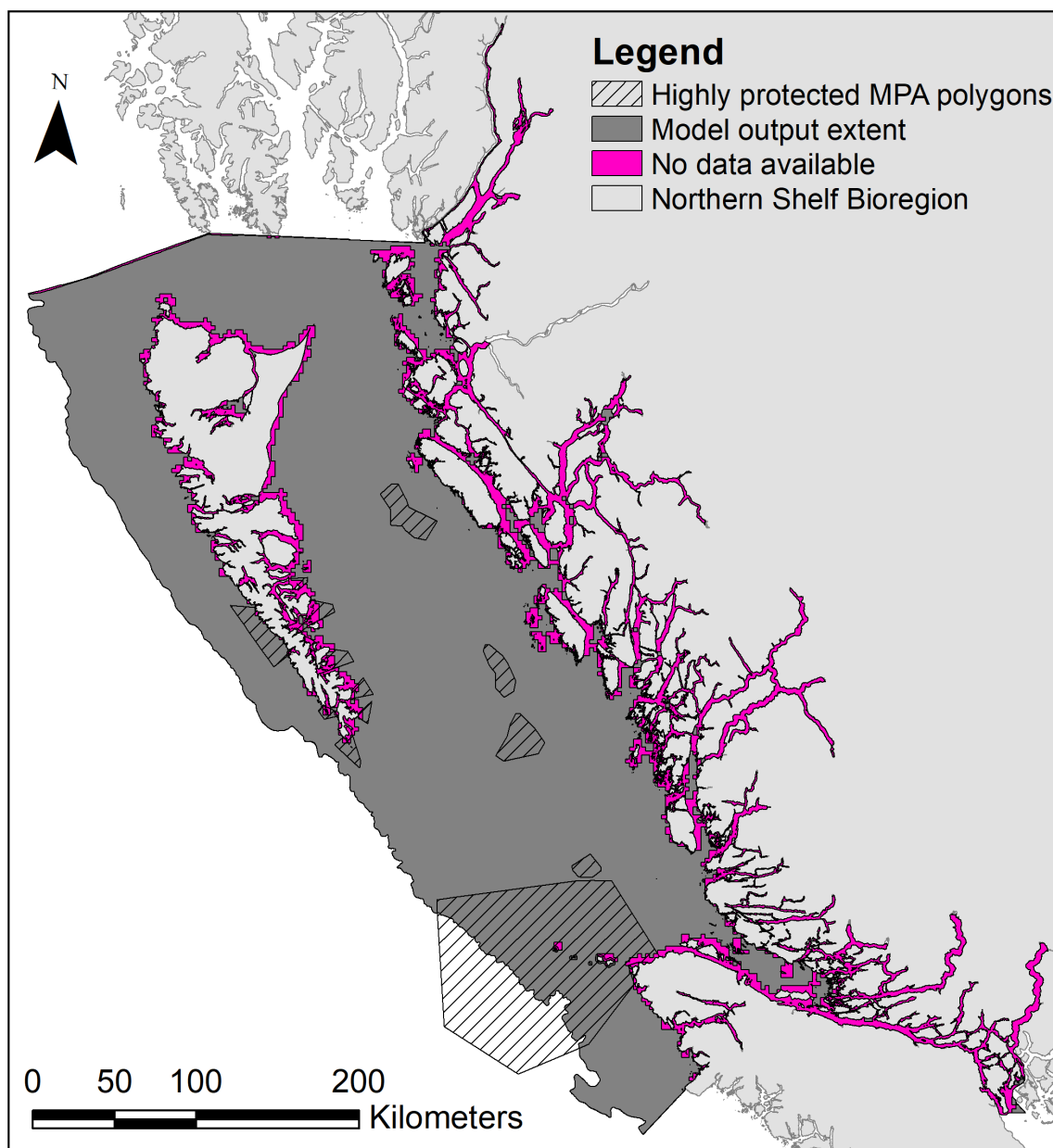


Figure S1. Spatial limitation of the oceanic circulation model outputs used in analysis; pink denotes Northern Shelf Bioregion areas that were excluded because they were outside the model output extent.

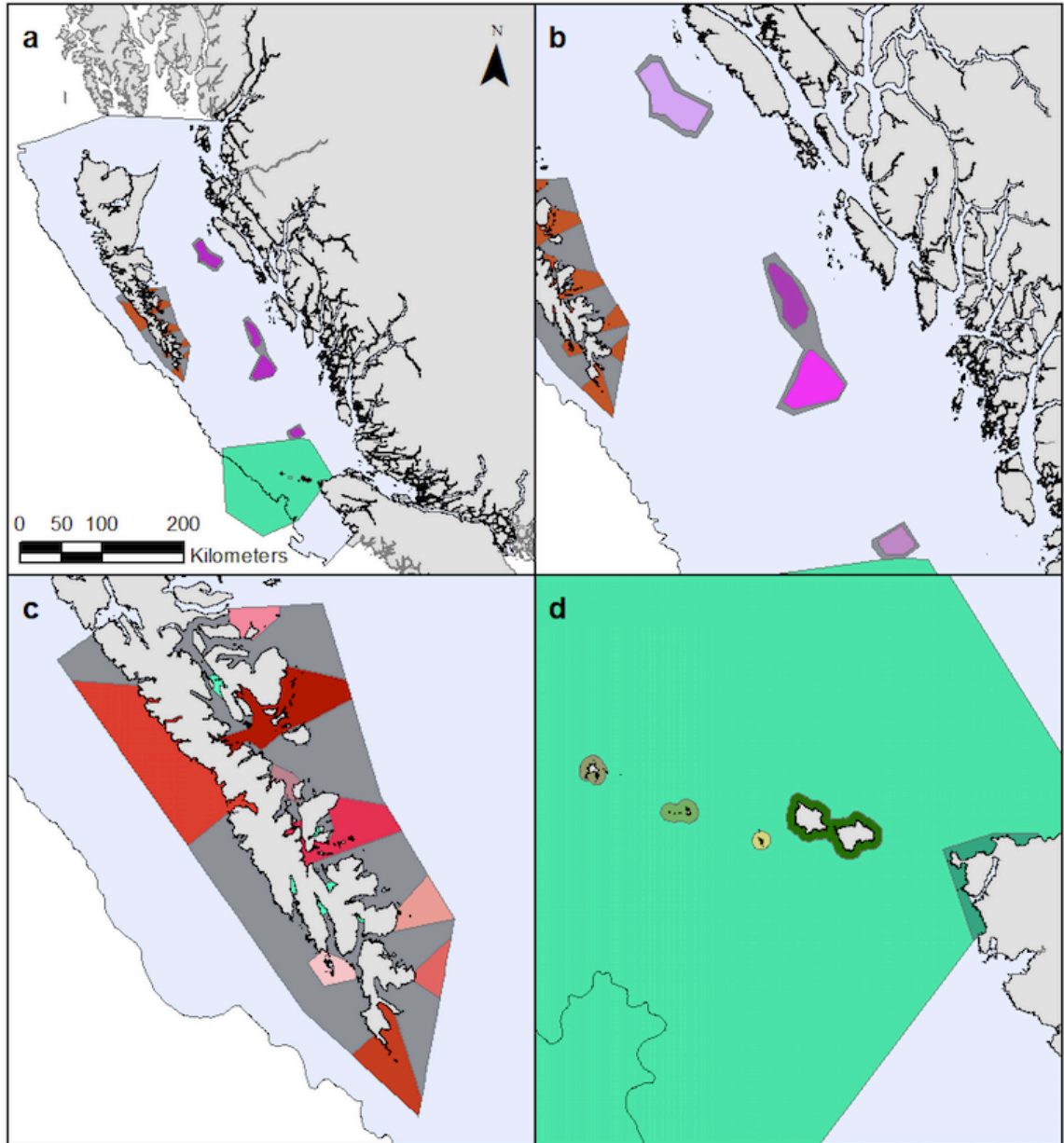


Figure S2. (a) Marine protected areas (MPAs) included in analysis; colours differentiate unique MPAs [3]. Individual highly protected MPA polygons are shown within the (b) Hecate Strait/Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area [4], (c) Gwaii Haanas National Marine Conservation Area Reserve & Haida Heritage Site [9], and (d) Scott Islands marine National Wildlife Area [6]. MPA areas with lower levels of protection (shown in gray) were excluded from analysis. Note: Turquoise in (c) indicates highly protected polygons that were excluded because of no overlap with oceanic circulation model output extent [6].

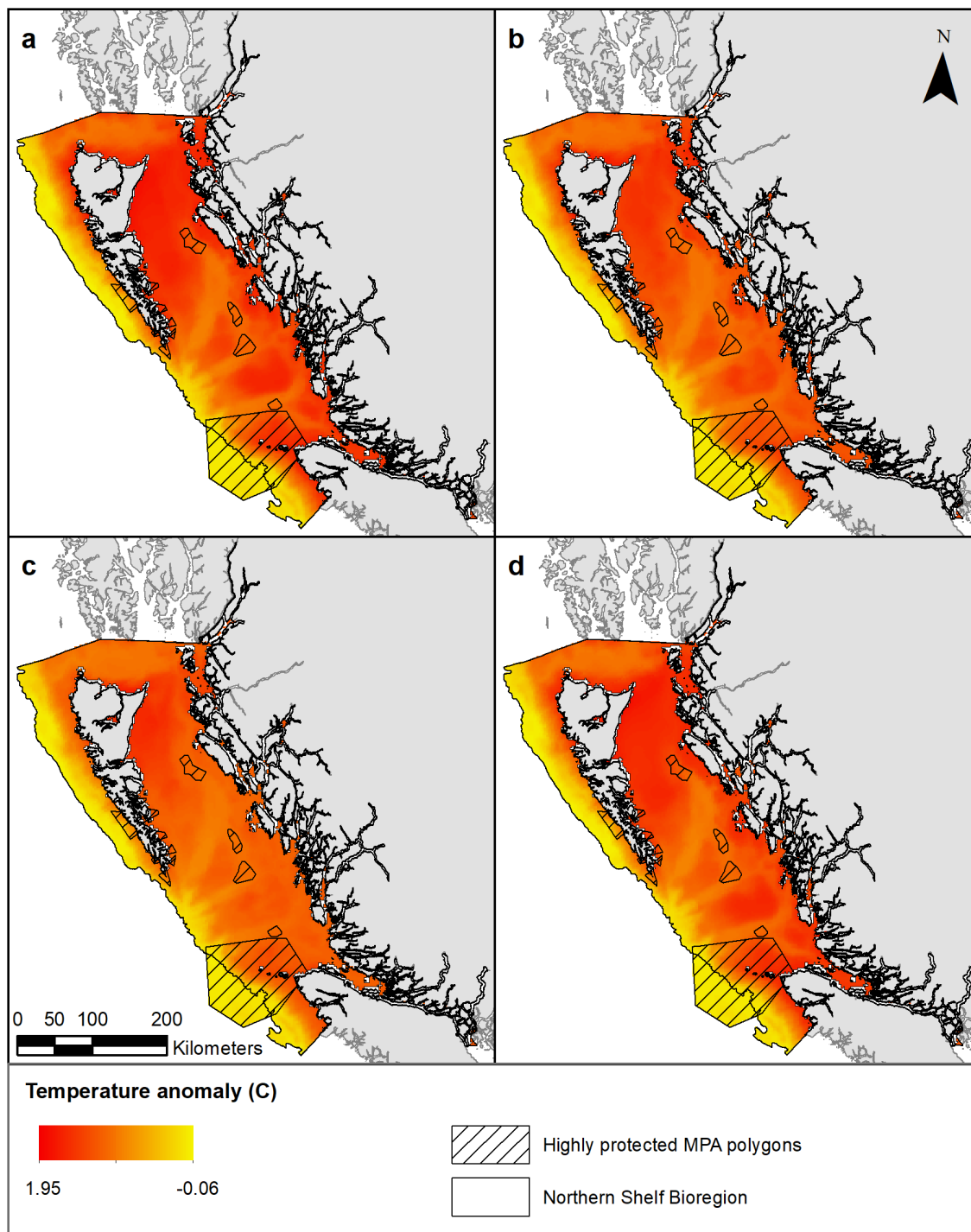


Figure S3. Mean projected benthic temperature anomalies (2065-2078 minus 1995-2008) by season for the Northern Shelf Bioregion. Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: a) spring (Mar-May), b) summer (Jun-Aug), c) fall (Sep-Nov), and d) winter (Dec-Feb).

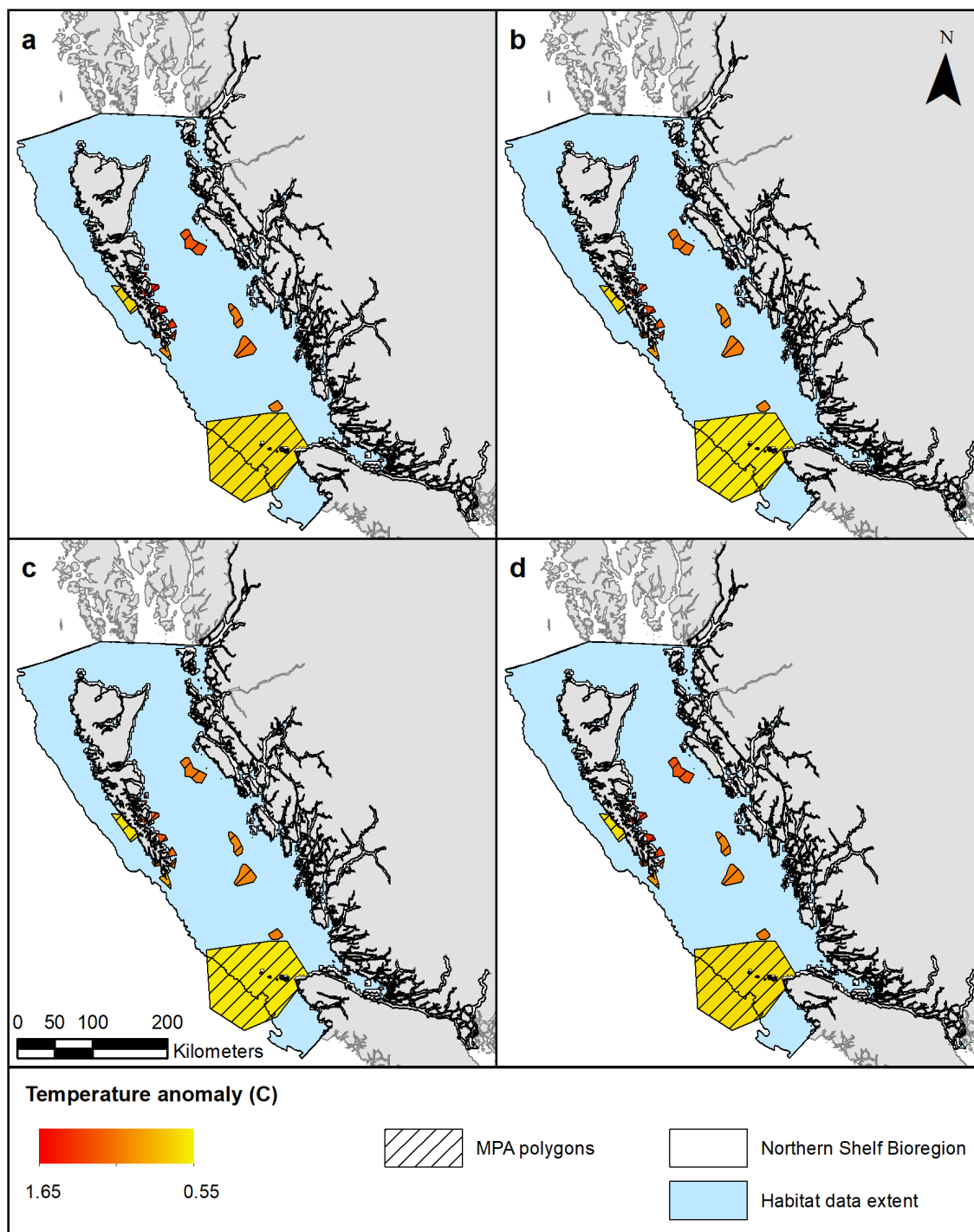


Figure S4. Mean projected benthic temperature anomalies (2065-2078 minus 1995-2008) by season, averaged across highly protected marine protected area polygons in the Northern Shelf Bioregion. Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: a) spring (Mar-May), b) summer (Jun-Aug), c) fall (Sep-Nov), and d) winter (Dec-Feb).

The relationship between mean depth of an MPA and its mean projected benthic temperature change within each season was investigated using a generalized linear model with a Gamma distribution and inverse link function. For all seasons, there was a significant negative relationship between the mean depth of an MPA and its mean projected benthic temperature change ($p < 0.000001$, 18 degrees of freedom). The standard error range of the generalized linear model's parameter estimate for all seasons did not cross zero for any season.

Table S2. Projected benthic temperature anomalies (2065-2078 minus 1995-2008) by season averaged across the Northern Shelf Bioregion, as well as across highly protected marine protected area polygons in the bioregion. Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb).

Season	Average projected benthic temperature change across bioregion (°C)	Average projected benthic temperature change for MPAs (°C)
Spring	+1.08	+1.30
Summer	+0.99	+1.17
Fall	+0.93	+1.11
Winter	+1.05	+1.26

Table S3. Total area of suitable habitat available each season within the entire Northern Shelf Bioregion for Dungeness crab (*Metacarcinus magister*) and Shortspine thornyhead (*Sebastolobus alascanus*) in two time periods: hindcast (1995-2008) and projected future (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb). Area reported in square kilometres.

Season	Dungeness crab			Shortspine thornyhead		
	Hindcast	Projected	Change in area	Hindcast	Projected	Change in area
Spring	24,975.55	32,847.82	+32%	15,291.64	6,108.31	-60%
Summer	19,296.31	30,505.81	+58%	23,634.70	7,908.03	-67%
Fall	22,430.92	31,626.16	+41%	21,203.29	6,817.47	-68%
Winter	27,728.76	33,002.77	+19%	11,459.79	5,530.26	-52%

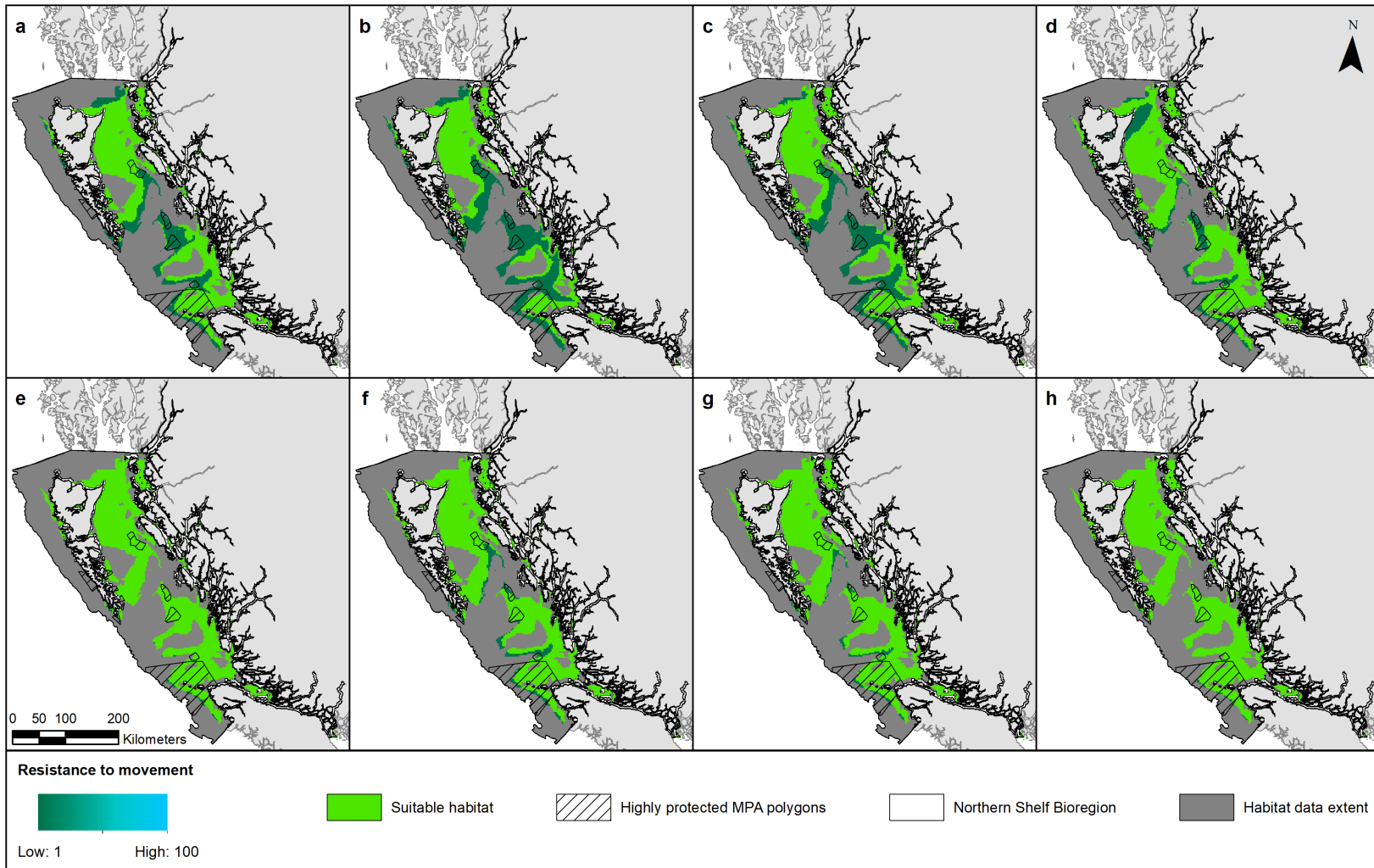


Figure S5. Resistance to movement within the Northern Shelf Bioregion for Dungeness crab (*Metacarcinus magister*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits; resistance to movement within suitable habitat is 1. Resistance to movement is scaled exponentially between species' pejus and critical limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

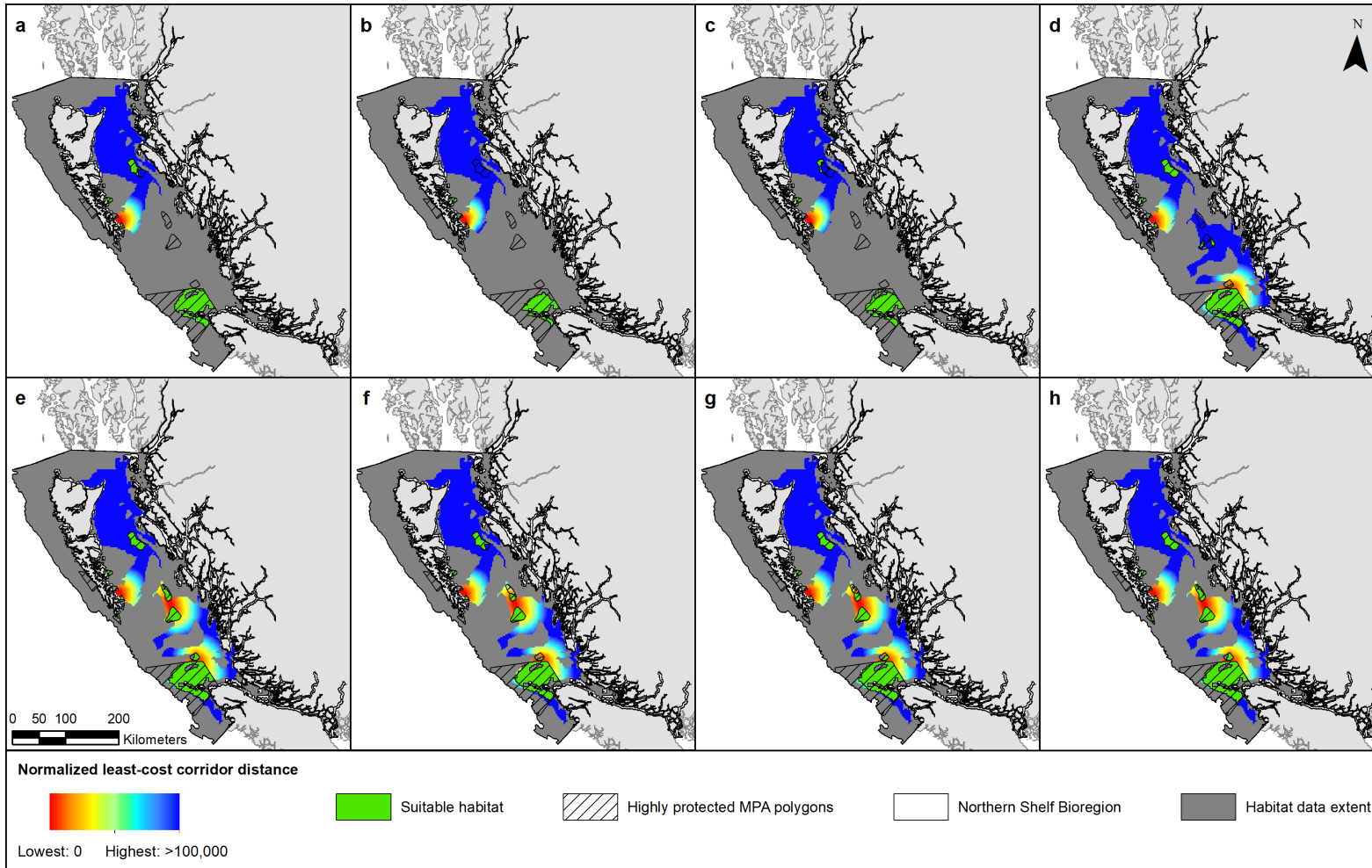


Figure S6. Least-cost corridors between highly protected marine protected area polygons containing suitable habitat for Dungeness crab (*Metacarcinus magister*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Least-cost paths are shown in red; colours indicate how much more costly the route passing through each pixel is relative to the least-cost path. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

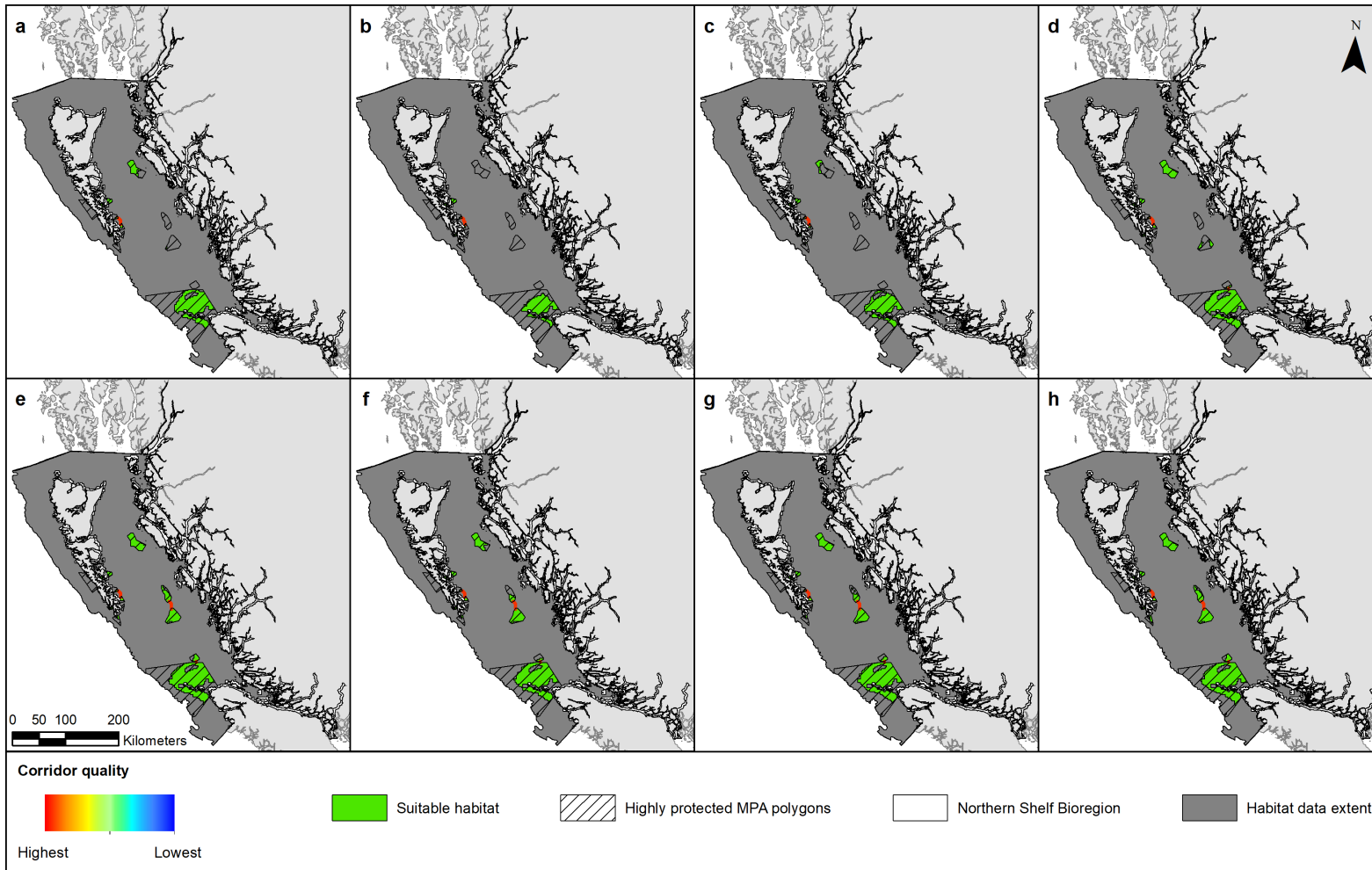


Figure S7. Corridor quality between highly protected marine protected area polygons containing suitable habitat for Dungeness crab (*Metacarcinus magister*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Corridor quality was calculated as the ratio of cost-weighted distance to path length for each least-cost path; corridors with highest quality are shown in red. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

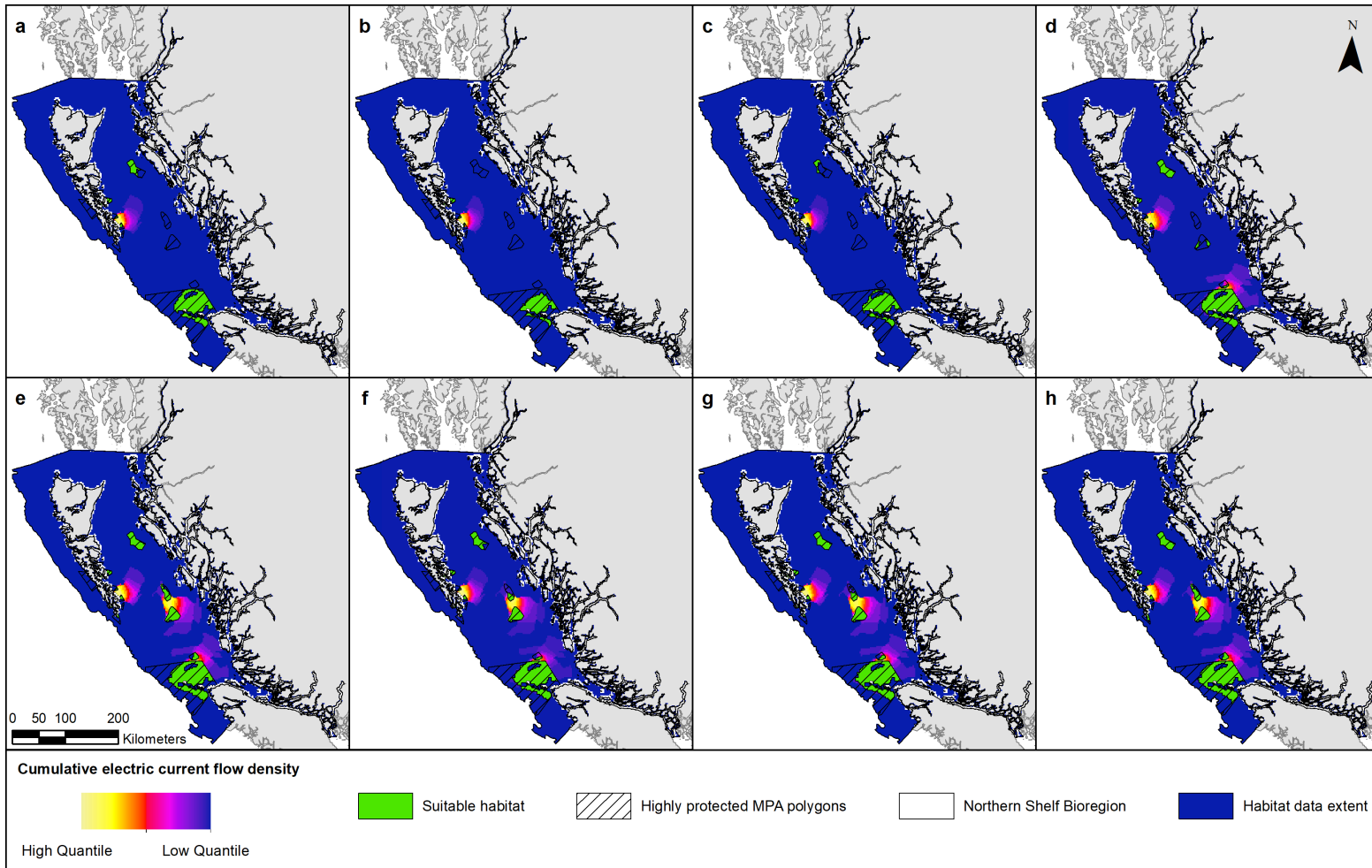


Figure S8. Seascapes-level pinch points between all pairs of highly protected marine protected area polygons containing suitable habitat for Dungeness crab (*Metacarcinus magister*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). High current flow density (yellow) indicates areas where flow is more restricted relative to other areas (note quantile symbology). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

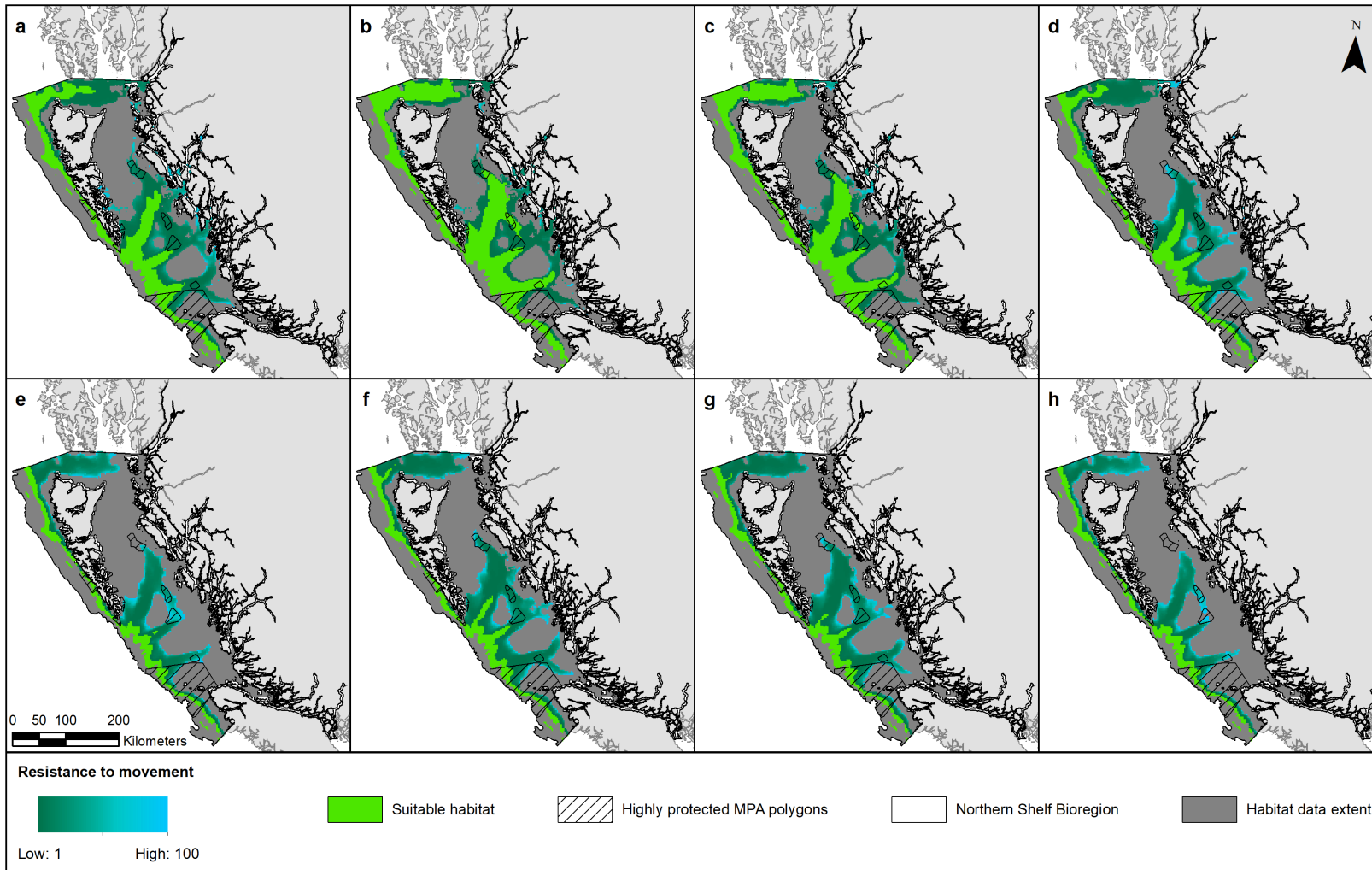


Figure S9. Resistance to movement within the Northern Shelf Bioregion for Shortspine thornyhead (*Sebastolobus alascanus*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits; resistance to movement within suitable habitat is 1. Resistance to movement is scaled exponentially between species' pejus and critical limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

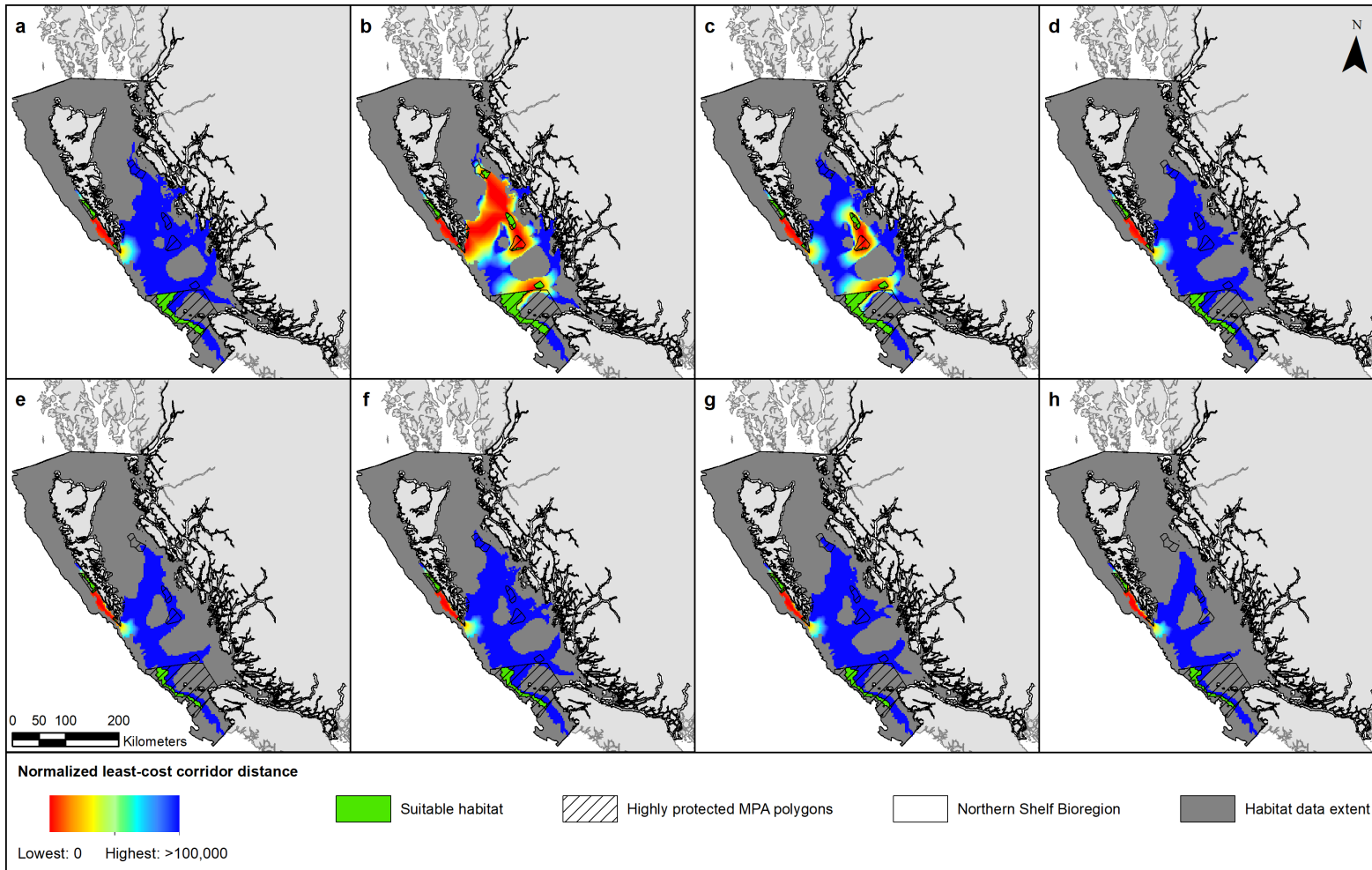


Figure S10. Least-cost corridors between highly protected marine protected area polygons containing suitable habitat for Shortspine thornyhead (*Sebastolobus alascanus*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Least-cost paths are shown in red; colours indicate how much more costly the route passing through each pixel is relative to the least-cost path. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

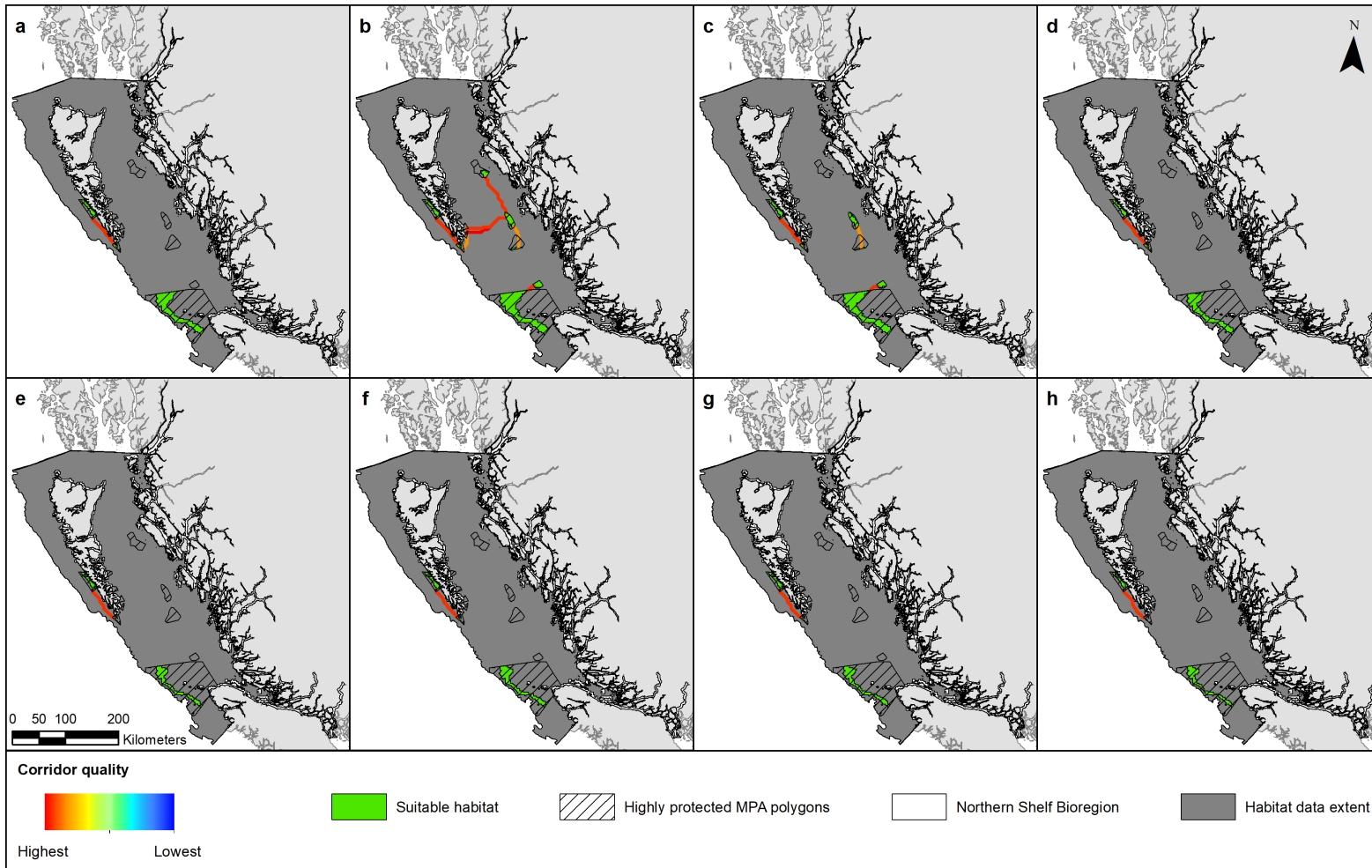


Figure S11. Corridor quality between highly protected marine protected area polygons containing suitable habitat for Shortspine thornyhead (*Sebastolobus alascanus*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). Corridor quality was calculated as the ratio of cost-weighted distance to path length for each least-cost path; corridors with highest quality are shown in red. Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

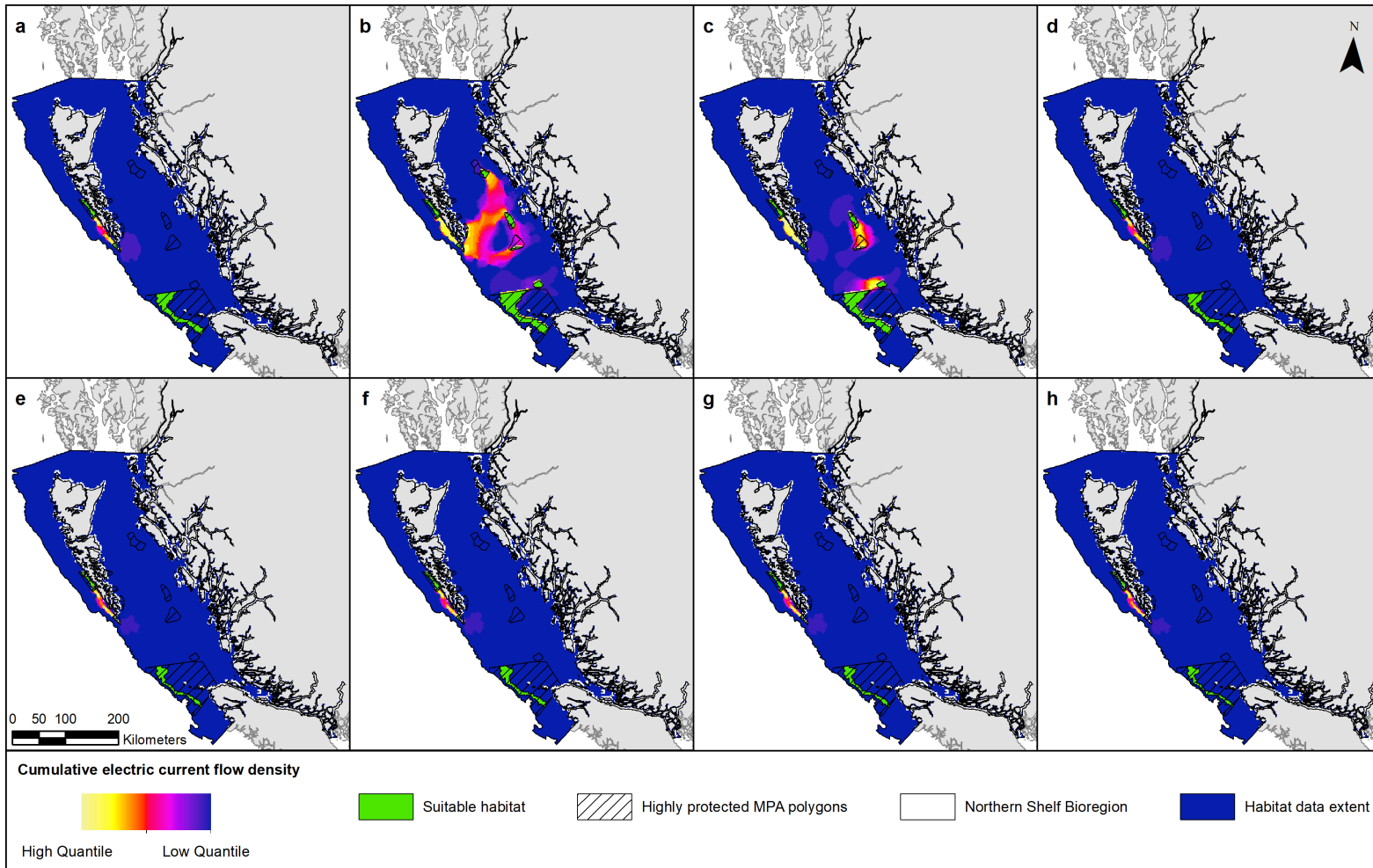


Figure S12. Seascape-level pinch points between all pairs of highly protected marine protected area polygons containing suitable habitat for Shortspine thornyhead (*Sebastolobus alascanus*) across seasons and two time periods: (a-d) hindcast (1995-2008) and (e-h) projected (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: (a)(e) spring (Mar-May), (b)(f) summer (Jun-Aug), (c)(g) fall (Sep-Nov), and (d)(h) winter (Dec-Feb). High current flow density (yellow) indicates areas where flow is more restricted relative to other areas (note quantile symbology). Suitable habitat (green) refers to area within species' substrate and depth preferences, as well as pejus temperature limits. Note that the model outputs do not extend to the inlets and nearshore (no data areas in white; Figure S1).

Table S4. Number of highly protected marine protected area polygons containing suitable habitat, number of linkages between highly protected polygons, and network density for Dungeness crab (*Metacarcinus magister*) and Shortspine thornyhead (*Sebastolobus alascanus*) across seasons in two time periods: hindcast (1995-2008) and projected future (2065-2078). Seasons were delineated by Morrison *et al.* (2014) based on the timing of upwelling and transition periods as follows: spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb).

Time period	Season	Dungeness crab			Shortspine thornyhead		
		Polygons	Linkages	Network density	Polygons	Linkages	Network density
Hindcast	Spring	11	1	0.018	5	1	0.100
	Summer	10	1	0.022	10	8	0.178
	Fall	11	1	0.018	9	3	0.083
	Winter	14	2	0.022	3	1	0.333
Projected	Spring	14	3	0.033	3	1	0.333
	Summer	14	3	0.033	3	1	0.333
	Fall	14	3	0.033	3	1	0.333
	Winter	14	3	0.033	3	1	0.333

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