Fisheries and Oceans Canada
Pêches et Océans Canada

Ecosystems and Oceans Science
Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2020/050

National Capital Region

Approaches for Assessing and Monitoring Representation, Replication, and Connectivity in Marine Conservation Networks

Arieanna C. Balbar[1], Remi M. Daigle[2,3], Susan G. Heaslip[2], Nicholas W. Jeffery[2], Beatrice Proudfoot[4], Carolyn K. Robb[5], Emily Rubidge[6], Ryan Stanley[2]

[1] Department of Oceanography
Dalhousie University
1355 Oxford Street
Halifax, NS B3H 4R2

[2] Bedford Institute of Oceanography
Fisheries and Oceans Canada
1 Challenger Drive
Dartmouth, NS B2Y 4A2

[3] Département de biologie
Université Laval
1045, av. de la Médecine
Québec, QC G1V 0A6

[4] Comox Valley Project Watershed Society
2356A Rosewall Crescent
Courtenay, BC V9N 8R9

[5] Pacific Regional Headquarters
Fisheries and Oceans Canada
200 – 401 Burrard Street
Vancouver, BC V6C 3S4

[6] Institute of Ocean Sciences
Fisheries and Oceans Canada
PO Box 6000
Sidney, BC V8L 4B2

September 2020

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Balbar, A.C, Daigle, R.M., Heaslip, S.G., Jeffery, N.W., Proudfoot, B., Robb, C.K., Rubidge, E. and Stanley R. 2020. Approaches for Assessing and Monitoring Representation, Replication, and Connectivity in Marine Conservation Networks. DFO Can. Sci. Advis. Sec. Res. Doc. 2020/050. vii + 57 p.

Aussi disponible en français :

Balbar, A.C, Daigle, R.M., Heaslip, S.G., Jeffery, N.W., Proudfoot, B., Robb, C.K., Rubidge, E. et Stanley R. 2020. Approches pour évaluer et surveiller la représentation, la réplication et la connectivité dans les réseaux de conservation marine. Secr. can. de consult. sci. du MPO, Doc. de rech. 2020/050. vii + 62 p.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Canada has committed to developing effective and representative marine conservation networks. Guidance for the development of these networks focuses on core design features, including the incorporation of ecologically and biologically significant areas, ecological representation, replication, connectivity, and adequacy/viability. Network planning using these design features is currently underway in five priority bioregions: the Gulf of St. Lawrence, the Scotian Shelf, the Newfoundland-Labrador Shelves, the Western Arctic, and the Pacific Northern Shelf. To ensure these networks achieve their biodiversity protection goals and objectives, the extent to which the design features are being achieved must be evaluated and monitored over time. Practical advice on how to monitor and evaluate Marine Protected Area (MPA) networks is critical for identifying the key elements of (future) successful management plans. This paper focuses on approaches for evaluating and monitoring the core design features of the Canadian MPA Network. We describe the importance of these design features and detail tools and approaches relevant for evaluation and monitoring at the network level. We then present a detailed case study to show how marine conservation network planning in the Northern Shelf Bioregion (NSB) has incorporated the design features in evaluations of draft network designs and how those methods can direct future monitoring within the NSB and more broadly in the Canadian MPA Network.

ACRONYMS

BLM	Boundary Length Modifier
CBD	Convention on Biological Diversity
CGA	Conservation Gaps Analysis
CSAS	Canadian Science Advisory Secretariat
CSM	Connectivity Strength Modifier
DFO	Fisheries and Oceans Canada
EBSA	Ecologically and Biologically Significant Area
GIS	Geographic Information System
GPS	Global Positioning System
IBD	Isolation-By-Distance Relationship
MPA	Marine Protected Area
MPATT	Marine Protected Area Network Technical Team
MSE	Management Strategy Evaluation
MSP	Marine Spatial Planning
NSB	Northern Shelf Bioregion
OECM	Other Effective Area-based Conservation Measures
PLD	Pelagic Larval Duration
PM	Performance Measure
PMECS	Pacific Marine Ecological Classification System
RAD-Seq	Restriction site Associated DNA Sequencing
SCP	Systematic Conservation Planning
SDM	Structured Decision Making
SNP	Single Nucleotide Polymorphism

1. INTRODUCTION: REVIEW OF MPA NETWORK DESIGN FEATURES IN CANADA

Monitoring programs are an essential component of Marine Protected Area (MPA) and MPA network management, providing requisite information on the state of, and changes in, protected ecosystems. Monitoring is required to gauge the efficacy of MPA networks in achieving their conservation objectives and provides information needed to demonstrate that restricted access has provided benefits to biodiversity. Moreover, where MPA network restrictions are distributed across activities, monitoring will facilitate validation of management decisions, to ensure continued access does not undermine the conservation objectives of the MPA (Kenchington 2013).

Canada has committed to developing MPA networks in all 13 of its bioregions, and planning is currently underway in five priority regions (Figure 1). The Canadian MPA network, also referred to as a marine conservation network, is composed of bioregional subnetworks, and several regulatory conservation mechanisms including *Oceans Act* MPAs, *Fisheries Act* Closures (or Marine Refuges), Parks Canada conservation areas, and other effective area-based conservation measures (OECMs; as outlined by CBD 2018)[1]. Bioregional planning has been guided by National Science Advice processes including guidance on developing MPA networks (DFO 2010), developing conservation objectives, indicators, monitoring protocols and strategies (DFO 2013a), and achieving representativity (DFO 2013b). In 2011, federal, provincial, and territorial governments released the National Framework for Canada's Network of MPAs (Government of Canada 2011), which has provided strategic direction and overarching goals for each of the bioregional MPA network processes. Design features highlighted in the national framework include the incorporation of Ecologically and Biologically Significant Areas (EBSAs), Ecological Representation, Connectivity, Replication, and Adequacy/Viability.

---

[1] For the purposes of this working paper, we use "MPA Network" as a synonym to the "Marine Conservation Network" expression recently adopted in Canada. The use of "MPA Network" aligns with previous documentation and international literature.

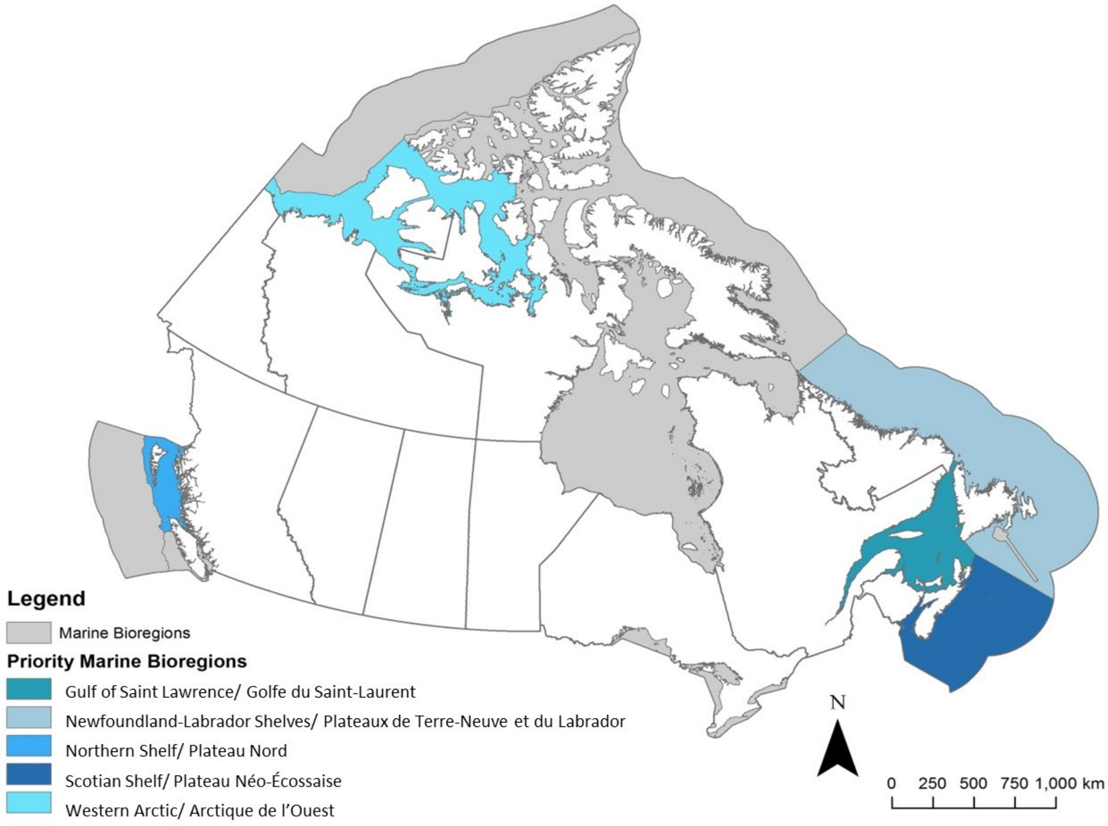

Figure 1. Priority marine bioregions for MPA network planning in Canada. Canada's marine protected areas network is being advanced in five of thirteen priority bioregions. Non-priority marine bioregions are shaded gray.

Network planning in each of the priority bioregions is led or co-led by regional DFO Oceans Management, and uses regional strategy documents (e.g., Canada – British Columbia Marine Protected Area Network Strategy 2014) and Science Advice on selecting conservation priorities and the development of design strategies specific to each bioregion (DFO 2015a, 2017a, b, 2018a, 2019). Ecological conservation priorities focus on the species and habitats to be protected in each network. Design strategies identify the areas or features to be conserved within the network and their related conservation targets. For example, based on conservation goals, an ecologically important species of fish could be identified as a conservation priority. The design strategies help identify a relevant spatial feature for that fish (e.g., nursery habitat), and recommend a conservation target (e.g., 20-40% of nursery habitat) to be included in the MPA network scenario. In general, conservation priorities and design strategies are used as inputs into MPA network site selection analyses, often using the spatial planning tool Marxan (Ball et al. 2009). The design strategies also provide recommendations on other network design features, such as connectivity, replication, size and spacing, and protection levels.

Scientific monitoring for MPA networks is required for adaptive management, with a focus that goes '*above and beyond monitoring that takes place at a site level*' (Government of Canada 2011). Regular reporting to the Canadian public on the effectiveness of bioregional MPAs and MPA networks (including OECMs) in achieving their stated goals and objectives is required. Monitoring will be particularly important as protected areas and OECMs are by definition static

(DFO 2016), yet the ecological and physical attributes of the area by which they are applied are inherently dynamic, particularly in light of climate change (see Section 5 MPA Network Monitoring and Climate Change). This contrast necessitates a continuous evaluation of protected areas and, in particular, MPA networks. Theoretical insight into the design of MPA networks is well established in the literature (e.g., Botsford et al. 2003; Gaines et al. 2010) and in practice (Table 1); however, empirical evidence supporting their predicted outcomes is often missing (Grorud-Colvert et al. 2014) and current perspectives on how best to monitor MPA networks remains largely conceptual.

The objective of this working paper is to provide practical advice on approaches for assessing and monitoring design features (replication, representativity, connectivity, and EBSAs) in Canada’s MPA networks. Previous Science guidance (DFO 2013a) highlighted the importance of ensuring design features are adequately incorporated to ensure regional MPA networks meet their respective conservation objectives. To better understand how and if these features were considered when designing Canada’s networks, we conducted a review of the network planning processes in each of the five priority bioregions (Figure 1). We found that implementation of design features varied among bioregions, and this variability was primarily related to some design features not being incorporated explicitly into the network configuration (Table 1) due to data availability and/or differing design strategies. Ultimately, monitoring programs must reflect how these features were incorporated into design.

Table 1. Summary of MPA network design features in each of the priority bioregions and indication of whether approaches for incorporation were recommended by regional advice. Information on the bioregional processes was gathered from published and in some cases, unpublished[2], documents (DFO 2015a, 2017b, 2018a, 2019). "Post-Marxan" indicates that the design feature was assessed after site selection analysis (i.e., not set as a parameter in the analysis) but prior to network implementation.

Design Feature	Northern Shelf	Scotian Shelf	Newfoundland & Labrador Shelves	Estuary and Gulf of St. Lawrence	Western Arctic
Representation (spatial targets including targets for EBSAs)	Yes	Yes	Yes	Yes	Yes
Replication	Yes	Yes	Not explicitly addressed	Yes	Yes
Connectivity	Post-Marxan	Post-Marxan	Not explicitly addressed	Not explicitly addressed	Partial consideration
Size and Spacing (Adequacy/ Viability)	Yes	Not explicitly addressed	Not explicitly addressed	Not explicitly addressed	Yes
Protection Levels (Adequacy/ Viability)	Yes	No	No	No	No

Network planning in each of the priority bioregions has incorporated key characteristics of a systematic conservation planning approach (SCP; Margules and Pressey 2000) by defining explicit goals, identifying conservation priorities and quantitative representation targets, and using repeatable methods to delineate a potential network of MPAs. The benefits of regional protected area networks should go above and beyond the benefits of individual conservation areas because of three key concepts built into networks through an SCP approach: connectivity, complementarity, and irreplaceability (Margules and Pressey 2000). Connectivity benefits the configuration of MPA networks by facilitating functional linkages between individual MPAs, including movement between larval production areas and habitats encompassing other life-history stages (Government of Canada 2011). When established, these linkages should lead to a net effect of the networks that exceeds the sum of the individual component effects. In other words, connected networks are assumed to have a synergistic interaction among protected areas that result in outcomes '$\boldsymbol{O}$' (e.g., increased biomass, productivity or resiliency), such that:

Equation 1.

$$\boldsymbol{O}_{\text{network}} = \sum \boldsymbol{O}_{\text{component}} + \boldsymbol{O}_{\text{network interaction}}$$

where $\boldsymbol{O}_{component}$ is the summed response (e.g., magnitudes of change) within individual component MPAs and $\boldsymbol{O}_{network\ interaction}$ is the magnitude of the interactive effect for reserves,

---

[2] Faille, G., Dorion, D., and Pereira, S. unpublished. Methodology for the Development of the Marine Protected Area Network. Draft Document November 2014 for the Technical Committee on the Marine Protected Area Network.

which is assumed to be >0 if connectivity has been integrated into the reserve network (Grorud-Colvert et al. 2011).

Elements of connectivity are also relevant to the adequacy and viability of the network through the size and spacing of individual MPAs. MPAs should be designed to have the size and proximity necessary to support ecological processes important for maintaining biodiversity, such as food-web interactions or nutrient flow and spacing to permit connectivity between individual MPAs (Government of Canada 2011). Both complementarity and irreplaceability are addressed in network design through the representation and replication design features. Complementarity is also achieved through coordination among proposed MPA sites, such that the ensemble protection provided by the network meets the broader conservation objectives. Irreplaceable MPAs contribute to the targets of ecological features that cannot be met elsewhere in the study area. The resilience of an MPA network (e.g., to disturbance such as climate change) should relate to whether representation, replication, and connectivity are adequately achieved in the final configuration (McLeod et al. 2009). Most assessments of MPA networks to date have focused on implementation but not quantified these synergistic network effects (Proudfoot and Rubidge, in prep.[3]).

In the following sections, we describe approaches to assess representation, replication, and connectivity, and highlight the importance of monitoring these features in an adaptive management framework to ensure the network is fulfilling long-term biodiversity protection objectives. Particular detail is provided for the tools and approaches that can be used to assess connectivity, given this design feature has had less focus in past bioregion-specific Science Advice and, to date, remains largely conceptual in MPA design and monitoring (Balbar and Metaxas 2019). We then present a detailed case study to show how MPA network planning in the Northern Shelf Bioregion (NSB) has incorporated and assessed the design features using a structured decision-making approach, and how this approach could be adapted to a monitoring framework.

2. REPRESENTATION

Representation and replication are key design features of Canada's MPA network framework, which recommends that Canada's network be "*ecologically comprehensive, resilient, and representative…*" in order to protect biodiversity and ensure ecosystem integrity for present and future generations (Government of Canada 2011). This approach aligns with the Convention on Biological Diversity's (CBD) advice for "ecologically representative" networks of MPAs (CBD 2010). Striving for ecological representation in a systematic fashion also helps ensure that MPA networks meet international targets (e.g., the protection of 10% of marine and coastal areas (CBD 2011)) in an ecologically meaningful way, as opposed to focusing on areas with lower opportunity costs (Margules and Pressey 2000; Devillers et al. 2015; House et al. 2017). At a broad scale, an ecologically representative network includes the full range and diversity of habitats found within the focal area, which in turn will help protect finer-scale natural features and areas of importance for the species found within. The representation of identified EBSAs in particular is highlighted in Canada's MPA network framework (Government of Canada 2011), and national guidance recommends incorporating representation in an iterative fashion that optimizes the other network design features, including EBSAs, replication, and connectivity (DFO 2013b).

---

[3] Proudfoot, B., and Rubidge, E. In prep. Approaches for evaluating the ecological benefits of Marine Protected Area networks.

Regional science advice related to the representation and replication of species, habitats, and natural features selected as conservation priorities was similar among the five priority bioregions and is provided in the design strategies documents for the bioregional network design processes (DFO 2015a, 2017b, 2018a, 2019). MPA network design that follows a SCP approach can incorporate representation using feature-specific targets as inputs into site selection analyses using decision-support software (e.g., Marxan). In all bioregions, features were identified from broad-scale habitat classifications, referred to as coarse-filter or representative features, and priority species or natural features, sometimes referred to as fine-filter features[4]. Both coarse- and fine-filter features were assigned a range of spatial conservation targets that varied based on the ecological characteristics of the species or habitats (DFO 2015a, 2017a, b, 2018a, 2019). In four of the five bioregions, Marxan spatial optimization analyses were used to provide options for meeting conservation targets, while the Western Arctic bioregion used ‘moving-window’ and overlay analyses (DFO 2015a). All approaches used available spatial data on the conservation priorities to characterize the planning landscape. In all bioregions, EBSAs were identified as conservation priorities to be captured within network designs, were assigned explicit targets, and were included in spatial prioritizations. For example, in coastal areas within the Scotian Shelf bioregion (<100 m depth), EBSAs that overlapped multiple fine- or coarse-filter features were prioritized for network inclusion (DFO 2018a). In the Newfoundland and Labrador Shelves bioregion, the inclusion of EBSAs was not done through Marxan analyses but, instead, were evaluated through GIS overlays because it was anticipated that spatial protection wouldn’t benefit all EBSAs equally (DFO 2017b).

Representation is also a commonly used metric in MPA network evaluation, often tied to international targets (e.g., Evans et al. 2015; Jantke et al. 2018; Fischer et al. 2019). Representativity-related assessment and monitoring activities can also incorporate the spatial conservation targets established within each bioregion for MPA network design, in particular for species that are identified as indicators. When aligned with operational objectives, representation analyses can provide an evaluation of whether conservation targets are maintained over time and as network sites are added to the network. In addition, if conducted in tandem with monitoring efforts that facilitate improved spatial information through the collection of new data, repeat assessments of representation can detect changes in species diversity, species distribution, and habitat quality. This information can be integrated into an adaptive management framework, help refine EBSAs and spatial datasets on conservation priorities, and re-evaluate their contribution towards network conservation objectives (also see Section 5). Monitoring areas of importance for species or functional groups can also help identify species range extensions or re-establishments, which can demonstrate the added value of an MPA network when compared to *ad hoc* collections of MPAs (Roff 2014). Additionally, monitoring changes in representation of sensitive benthic habitats within a network is important not only for informing adaptive management but also for monitoring the potential recovery of conservation priorities in response to network implementation.

Assessments of representation can be used to compare proposed or existing MPA networks to the broader marine region. Common methods found in the literature include analyses of similarity based on sampling of fish communities inside and outside networked MPAs to isolate changes in fish biomass, density, or diversity in MPAs compared to surrounding areas (e.g.,

---

[4] Fine-filter features represent priority species or spatially discrete natural features (e.g., estuaries). Coarse-filter features are broad-scale features of which smaller scale features were nested (e.g., oceanographic units).

Hamilton et al. 2010; Grorud-Colvert et al. 2014; Soykan and Lewison 2015) and GIS overlays to determine how well proposed or finalized MPA networks capture conservation priorities and their conservation targets (e.g., seabed geomorphic features and habitat classes; Young and Carr 2015; Jantke et al. 2018; Fischer et al. 2019; Martone et al. in prep.[5]) or areas of high conservation value identified through site selection analyses (e.g., Evans et al. 2015; House et al. 2017; Virtanen et al. 2018). These analyses have reported on representation for individual ecological features (Young and Carr 2015; Martone et al. in prep.[5]) or using compiled metrics, such as species richness (Soykan and Lewison 2015) and mean target achievement, i.e., the degree to which conservation targets are attained for the identified conservation priorities (Jantke et al. 2018). Examples of representativity-related monitoring tools include eDNA (e.g., Sawaya et al. 2019), remote sensing imagery collected using satellites, planes, or drones (e.g., Nijland et al. 2019; Schroeder et al. 2019), bathymetric data collected using multi-beam sensors (e.g., Haggarty and Yamanaka 2018), or multispecies and habitat surveys conducted using divers or remotely operated vehicles (e.g., Haggarty 2015; Frid et al. 2018).

The appropriateness of a monitoring tool will depend on the indicator that is being monitored, the expected spatial-temporal scales of response, and the stressors and natural disturbance at the individual sites. Those factors will in turn dictate the frequency and spatial extent of monitoring surveys to ensure monitoring resources are used efficiently. For example, a conservation target for deep-water sponge reef with very slow recovery times may be monitored on a different time frame than a conservation target for canopy-forming kelp forests that have rapid growth rates, respond to disturbance on much shorter time scales, and die off annually. For sponge reefs in Pacific Canada, Dunham et al. (2018) suggest a general monitoring time frame of 3-10 years, with a focus on routine broad-scale surveys and less frequent intensive surveys, recommending that the time frame be refined in an adaptive framework as trends become clearer as monitoring progresses.

3. REPLICATION

Replication, another key design feature and a measure of a network's resilience and adaptive capacity, has been assessed less frequently in the literature in comparison to connectivity and representation (Proudfoot and Rubidge, in prep.[3]). Similar to assessments of representation, studies have often used GIS overlays to determine how well seabed features, habitat classes, and areas of importance for priority species are replicated throughout a proposed or final MPA network (e.g., Ban et al. 2014; Young and Carr 2015; Foster et al. 2017). Integral to these analyses are considerations of adequacy/viability and efforts to define a "replicate" or the amount of a specific habitat type that must be captured within an MPA in order to qualify as a replicate, sometimes referred to as a habitat's minimum patch size. Assessments of the MPA network in California have used species-area curves developed locally to determine the minimum area required to capture 90% of the species known to use a habitat, using that information to define which habitat patches within the network qualify as a replicate (Saarman et al. 2013; Young and Carr 2015). Ideally, habitat-specific species-area curves would be available in the Canadian context and a similar threshold could be applied. However, these data are often unavailable and, therefore, the "replicate" definition must be derived from other information such as patch size. Monitoring efforts can help identify the biodiversity associated with habitat patches at varying scales, informing the patch sizes appropriate for replication and the efficacy of MPA networks in protecting those habitats.

---

[5] Martone, R.G., Robb, C.K., Gale, K.S.P., Frid, A., McDougall, C., and Rubidge, E. In prep. Design strategies for the Northern Shelf Bioregional Marine Protected Area Network. DFO Working Paper.

Another key component of a “replicate” definition is habitat quality. Most MPA network assessments rely on GIS layers of habitat types, some of which are dated with known data gaps. These datasets are often used in MPA network site selection analyses assuming uniform habitat quality across the planning area. An MPA network monitoring program designed to monitor replication can provide information to update spatial datasets and integrate habitat quality indices into the habitat type maps. Information on habitat quality can then be incorporated into the “replicate” definition, further improving the ability to assess whether the network is meeting its replication objectives. The resulting definition of what constitutes a “replicate” in an MPA network would have a minimum area (defined by species-area curves) and associated habitat quality index (e.g., blade density). An alternative index of habitat quality could be developed using human impact scores and proximity to human-derived stressors, to identify areas that are more pristine and, therefore, likely to have lower degradation. This approach can be used in a GIS framework using cumulative impacts maps (e.g., Clarke Murray et al. 2015). Monitoring efforts that result in the collection of new data could also feed back into this type of assessment, improving our understanding of cumulative effects.

Once a definition of what constitutes a replicate of the various habitat types is determined, the next step is to assign the number of replicates needed. Less information is available to guide the appropriate number of replicates for a given habitat type, though many studies have recommended at least three spatial replicates be included in MPA networks (e.g., IUCN-WCPA 2008; Fernandes et al. 2012). However, it is unlikely that there is a uniformly appropriate number of replicates for each habitat type, and the suitable number of replicates should be informed by risk, sensitivity, and considerations of habitat quality and be assessed at a bioregional (or finer) scale. When features are mapped across the planning landscape, replicate monitoring can form a basis for adaptive management. For example, replication thresholds (e.g., three replicates of each feature at a defined spatial scale) could be used to gauge network performance and trigger management intervention in situations where the replication is insufficient or decreasing.

Regional Science Advice on replication varies among the five priority bioregions. For example, for the NSB, the number of replicates was recommended to be based on patch size and rarity, in addition to being stratified by a broad-scale physical habitat classification system or by planning areas with similar ecological characteristics (DFO 2019). For the Scotian Shelf, Science Advice recommended at least two spatial replicates for coarse-filter features and at least one spatial example of adequate size for most fine-filter features (which are nested within the coarse-filter features), such as biogenic habitats, representing the conservation priorities (DFO 2018a). The Newfoundland & Labrador and the Western Arctic MPA network processes did not include specific advice on the number of replicates to include in the network (DFO 2015a, 2017b), while the Gulf regional process[6] recommended at least three replicates, based on recommendations from the literature.

Given the differences in the approaches to setting the number of replicates across the bioregions, assessment and monitoring advice will be specific to each planning area. However, all assessments will have to consider a few key components to assess and eventually monitor replicates. These steps include: 1) explicitly define what constitutes a “replicate” in terms of patch size and quality of habitats or areas of importance for species; 2) understand the replication goals for the network (i.e., how many replicates were recommended and

---

[6] Faille, G., Dorion, D., and Pereira, S. unpublished. Methodology for the Development of the Marine Protected Area Network. Draft Document November 2014 for the Technical Committee on the Marine Protected Area Network.

implemented into the final design); and 3) incorporate iterative feedback of newly collected data on habitat use, patch size, and quality (e.g., percent cover, species diversity in patch, stipe/shoot density) into the description and accounting of replicates. Monitoring the quantity of replicates is important because, over time, some habitat patches may be lost or degraded (e.g., via climate change (Section 5) or interaction with extractive activities), while others may be gained (e.g., via natural recovery or restoration) within the network. Additionally, the appropriate number of replicates should be periodically reassessed to reflect changes in risk and/or impacts from climate change. Finally, it is important to acknowledge that design features within the network interact synergistically to achieve an overall functioning network. In the case of replication, this is particularly true with respect to metapopulation[7] structure and connectivity. A network with adequate replication (or number of metapopulations) will also be inherently more connected and, therefore, more viable.

4. CONNECTIVITY

Addressing connectivity aligns with Canada's commitment to the international target set by the CBD to protect "*10 percent of coastal and marine areas [through] ecologically representative and well-connected systems of protected areas*" by 2020 (CBD 2010). Ecological spatial connectivity refers to the movement of organisms, genes, energy, chemicals, or materials among habitats, populations, communities, or ecosystems (Carr et al. 2017; Table 2). Even though connectivity is a design feature, it has only been considered comparatively, partially, or *post-hoc* in the five priority bioregions in Canada (Table 1). Grorud-Colvert et al. (2014) identify five types of MPA networks, including ad-hoc, conservation, management, social, and connectivity. Canada's bioregional MPA networks currently fall under the ad-hoc or conservation categories because connectivity was not explicitly incorporated or evaluated within their designs. To meet the expectation to develop connected networks of MPAs within the larger Canadian MPA network, regionally specific Science Advice on connectivity will be required to inform design and ultimately assessment.

---

[7] A metapopulation is an assemblage of semi-discrete spatial subpopulations connected through dispersal.

Table 2. Definition of the types of ecological spatial connectivity and considerations for MPA network monitoring. The movement of organisms refers to spores, eggs/larvae, juveniles, or adults. Each metric is explained in more detail in the following sections.

Type of connectivity	Definition	Considerations for MPA network monitoring
Landscape connectivity	The degree to which the landscape facilitates or impedes movement among habitats, populations, communities or ecosystems.	· Lowest data requirements · Can address multispecies questions · Gives information about network-scale connectivity patterns · Species-specific models require field validated resistance values
Population – genetic connectivity	Movement of genes among distinct populations through the movement of organisms of a single species among distinct populations.	· Detects changes over multiple generations · Detects realized connectivity patterns · Spatial resolution is an issue and limited/defined by sampling
Population – demographic connectivity	Movement of organisms of a single species among patchy or discontinuous subpopulations or habitats.	· In-situ measurement tools can provide real-time dispersal information (e.g. satellite tags) · Models provide network scale connectivity patterns · Models can predict changes to connectivity patterns under future climate conditions · Validating models can be challenging
Ecosystem connectivity	Movement of energy and nutrients through the movement of organisms, as well as chemicals and materials among ecosystems.	· Logistically challenging · May be suitable in specific cases (e.g., movement of detritus)

Measuring the extent of connectivity between network components and within the larger planning/assessment area can aid evaluation of MPA network outcomes. In a true network, individual MPAs interact with each other such that the magnitude of change in the network is greater than the sum of the individual components ($O_{network\ interaction} > 0$, see equation 1). To design a connected network, managers should first identify which conservation priorities should consider connectivity, the role that each MPA plays in supporting connectivity, and the appropriate spatial and temporal scale for each conservation priority (Balbar and Metaxas 2019). In particular, conservation priorities whose persistence depends on spatial linkages within the planning region (e.g., links between juvenile abundance and spawning grounds) should be given focus when considering connectivity in design. Assessing the connectivity of a network at multiple points in time improves the efficiency of future network design, especially when networks are designed in a stepwise fashion, by improving their ability to adapt to a changing landscape and environmental conditions (see Section 5). Monitoring connectivity patterns can be a key consideration to guide the placement, size, and spacing of future MPAs in a growing network.

The international literature provides only two notable examples of MPA networks that have considered connectivity in their design and monitoring: Western Hawaii and the coastline of California. In Western Hawaii, Papahānaumokuākea Marine National Monument, Midway Atoll National Wildlife Refuge, and the Hawaiian Islands Humpback Whale National Marine Sanctuary are MPAs that discuss genetic connectivity and tagging studies as part of ongoing monitoring. Their management plan lists understanding the genetic structure of reef invertebrate and fish populations in the archipelago as one of the strategies to monitor the local marine ecosystem (Papahānaumokuākea Marine National Monument Management Plan 2008; Chow et al. 2015). The California North Coast MPA Network assesses the size, spacing, and siting of MPAs in the network (Department of Fish and Wildlife 2017) to evaluate fundamental connectivity questions such as the influence of inter-MPA distances on connectivity and primary mechanisms of connectivity (e.g., through larval exchange or movement of adults, source and sink dynamics of populations, and home ranges of organisms (Department of Fish and Wildlife 2017). These examples show an effort to consider ecological connections; however, we do not know of real-world examples that comprehensively measure connectivity of species or habitats at a network scale.

4.1 CONNECTIVITY IN SPACE AND TIME

The ecological processes that constitute population connectivity (including spawning, dispersal, settlement, survival to reproduction, and juvenile and adult movement) vary among species over space and time. For example, larvae from the tunicate *Molgula pacifica* have an average propagule duration (or Pelagic Larval Duration – PLD) of 36 hours and, therefore, only travel distances on the scale of metres (Shanks 2009). Alternatively, the larvae of the Dungeness crab (*Cancer magister*) have a propagule duration of three to four months and can travel up to 500 km (Shanks 2009). Variation in PLD can also be linked to environmental conditions, which vary in time and space. For example, expected duration for larval American Lobster (*Homarus americanus*) can vary considerably across the Canadian range, from the warm waters of the Scotian Shelf to the much cooler waters of Northwestern Newfoundland (Quinn et al. 2013). Seasonal variation in the spawn timing for Atlantic Cod (*Gadus morhua*) expose eggs and larvae to different thermal and oceanographic regimes (i.e., early spring and summer) that augment duration and magnitude of dispersal (Bradbury et al. 2000; Stanley et al. 2013). These differences in propagule duration and dispersal distance can have large implications for the design and assessment MPA networks (Stanley et al. 2015b). Accounting for species or conservation features with short dispersal distances can be accomplished by scaling the size of an MPA, but long distance dispersers typically require adequate spacing of MPAs, especially organisms that spend different parts of their life in different habitats, as is the case for Atlantic Cod where juveniles benefit from the availability of Eelgrass (*Zostera marina*) beds before migrating to deeper, offshore waters (Lilley and Unsworth 2014). As dispersal and connectivity are influenced by environmental change (i.e., climate change, see Section 5.2) ongoing (re)assessment of the scales of dispersal and connectivity within the network will be needed to gauge network efficacy.

The various tools available for measuring connectivity, directly and indirectly, detect patterns at different spatial and temporal scales (Figure 2). For example, it is clear that many tools overlap at a spatial resolution at 1 – 10,000 km and day – annual ranges. Tools with a finer-scale resolution, such as biophysical modelling, parentage analysis, otolith chemistry, and stable isotopes, can elucidate connectivity patterns over a single generation. Conversely, tools with a coarse-scale resolution, such as phylogenetics and population genetics, can elucidate connectivity patterns over multiple generations.

When considering the temporal and spatial scale of monitoring connectivity patterns from a management perspective, having clearly defined and measurable operational objectives with associated indicators will guide the selection of the correct monitoring tool. For example, using phylogenetics would not be a suitable tool to assess network connectivity relating to a species of interest for a particular year, and landscape-based methods would not permit sufficient temporal resolution to resolve patterns of gene flow and population structure.

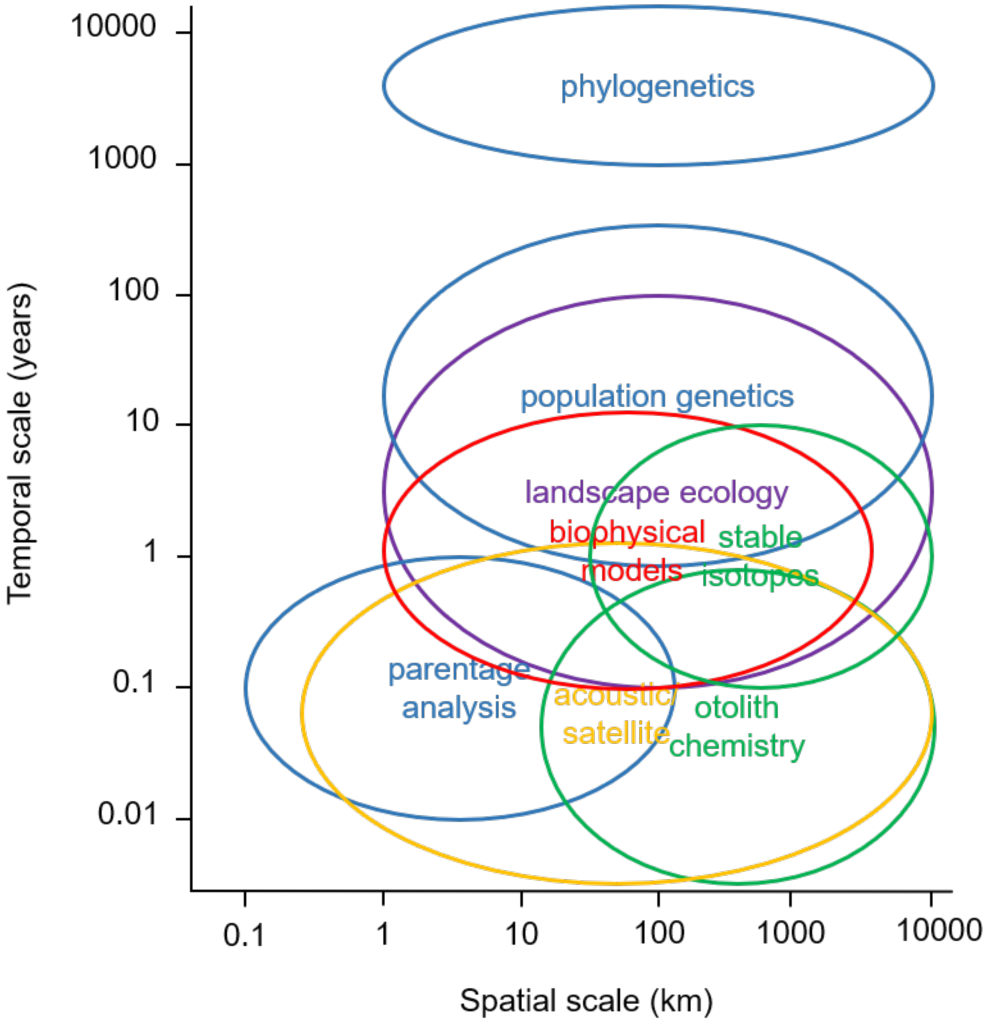

Figure 2. Spatial and temporal scales for different tools used to measure connectivity in MPA network monitoring. Blue circles indicate genetic approaches; green circles indicate chemistry tools. Note that parentage analysis can refer to mark-recapture studies, genetic, or natural (e.g., geochemistry) tagging approaches. Adapted from Jones et al. (2009).

4.2 TOOLS AND APPROACHES FOR MEASURING CONNECTIVITY

One of the barriers that complicates the inclusion of connectivity in the design and assessment of MPA networks is the myriad ways that connectivity can be measured (Figure 3) and the inherent complexity of measuring a process that varies within (e.g., populations) and among species for networks with multispecies points of focus. Here, we provide an overview of the different methods used to measure connectivity directly, and indirectly, to address a range of design and potentially conservation objectives. We also contrast these approaches with the application of implied connectivity (*“Rules of Thumb”* based on species dispersal categorization). Specifically, we focus on evaluating the spatial-temporal considerations of each tool, split into direct and indirect methods, with links to potential applications for MPA network monitoring. Described tools include: visual and molecular techniques (e.g., genetics, photo-ID, branding, and isotope ratios); passive tags (e.g., spaghetti, band, flipper, passive integrated transponder); active transmitting tags (e.g., radio, acoustic, and satellite tags); and short- (e.g., camera tags, accelerometer tags, magnetic sensor tags, internal temperature/heart rate) and long-term archival tags (e.g., pop-up archival, internal temperature/heart rate, life-history tag, daily diary tag).

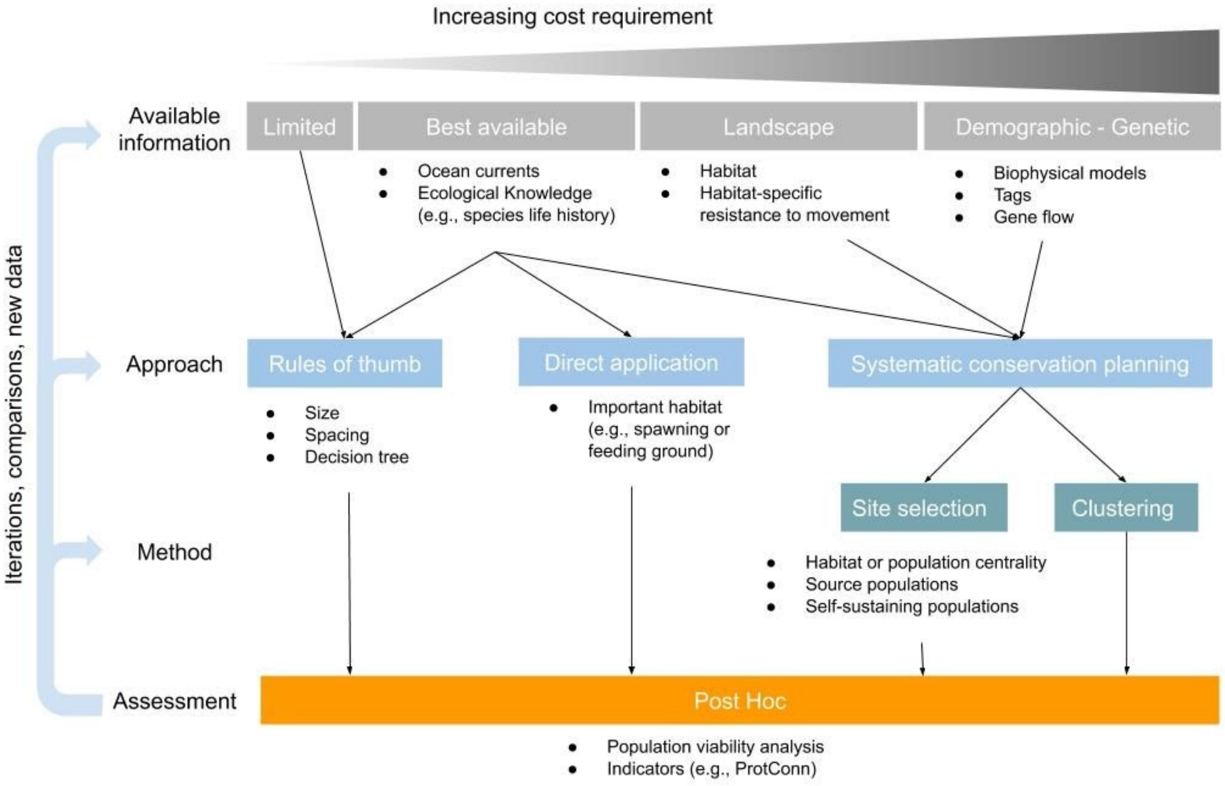

Figure 3. Potential workflows to incorporate connectivity-based knowledge into MPA network planning and monitoring with varying cost requirements.

4.2.1 Direct Methods

4.2.1.1 Genetic Tools

Integrating connectivity into MPA networks is a critical component to allow for migrant exchange, source-sink population dynamics, and gene flow (Xuereb et al. 2019). Genetic tools can be used to infer fine-scale population structure and local environmental adaptation, to understand parentage and sibship relationships, and to estimate gene flow among populations, which can provide a quantitative means of evaluating connectivity within an MPA network or network design (D'Aloia et al. 2017b; D'Aloia and Neubert 2018). Current high-throughput sequencing methods, including restriction site-associated DNA sequencing (RAD-Seq) and whole genome sequencing, have made this information more accessible than ever. Despite relatively high up-front costs, researchers now have access to thousands or millions of genetic markers (single nucleotide polymorphisms or SNPs) to assess genetic diversity and provide unprecedented information on demographic and evolutionary processes (Selkoe and Toonen 2011; Fuentes-Pardo and Ruzzante 2017; Jeffery et al. 2017; Van Wyngaarden et al. 2017b).

Many marine plants and animals have larvae that may disperse hundreds of kilometers over days or weeks, while their adult stages are sessile or less motile. This high dispersal potential coupled with (assumed) large effective population sizes historically led to the belief that geographically distinct populations would be panmictic, exhibiting weak population structure and high connectivity across vast distances (Gagnaire et al. 2015). It is becoming the norm that when using high-throughput sequencing, complex demographic histories are revealed and local adaptation to fine-scale environmental differences (e.g., surface and bottom temperatures, salinity, substrate) are being discovered (e.g., Saenz-Agudelo et al. 2015; Van Wyngaarden et al. 2017a; Stanley et al. 2018). In the Northwest Atlantic, genomics have been explored for a growing number of fishes and invertebrates, including Atlantic Cod (Bradbury et al. 2014; Kess et al. 2019), Atlantic Herring (Kerr et al. 2019), Atlantic Salmon (Sylvester et al. 2018; Lehnert et al. 2019), and Sea Scallop (Van Wyngaarden et al. 2017a), yet a greater variety of species with varying life histories warrant investigation to provide data for MPA network design and evaluation.

An advantage to large SNP panels aside from increased statistical power is that while most SNPs (≥90%) will be effectively neutrally evolving (similar to microsatellites), a minority may be ‘adaptive’ or ‘outliers’ because they reside within a gene region that in turn leads to local adaptation despite high levels of gene flow among populations. Although neutral markers evolve under genetic drift, outlier SNPs may evolve under selective pressures that can combat the effects of strong, homogenizing gene flow. Both types of markers can be useful in conservation area network design and monitoring (Xuereb et al. 2019). Adaptive markers may reveal genetically unique populations that warrant protection, either because they are rare or contribute heavily to overall genetic diversity and adaptive potential of the species, while neutral markers can provide information on connectivity among conservation areas (Xuereb et al. 2019).

Estimating dispersal using neutral genetic markers can broadly be categorized into indirect proxy methods, such as calculating the isolation-by-distance relationship (IBD) or F_{ST} (fixation index) among populations, or direct methods such as parentage assignment and clustering methods to understand limits to dispersal or self-recruitment (Gagnaire et al. 2015). Under the IBD model, populations become more genetically divergent the farther apart (geographically) they are, so the assumption is made that dispersal becomes weaker with increased geographic distance. By analyzing the slope of the IBD relationship, it is possible to generate dispersal kernels for the species of interest in order to estimate the spatial scales of genetic connectivity, which in turn can inform the spatial scale of monitoring.

Direct methods make fewer assumptions on demographic parameters than indirect models, but require far more data to provide realistic estimates of dispersal. For example, parentage analysis requires genetic sampling of both parents and potentially thousands of offspring, which can realistically only take place over a small spatial scale (D'Aloia et al. 2013; D'Aloia et al. 2018). D’Aloia et al. (2015) estimated a dispersal kernel of 1.7 km for a tropical reef fish based on parentage analysis and concluded that in order for a network of marine reserves to be effective at protecting fish communities, reserves must be <10 km apart to protect short-distance dispersers. More importantly, these methods may only yield quantifications of movement, rather than gene flow, as migrants may not successfully reproduce following dispersal (Gagnaire et al. 2015). For both indirect and direct estimates of gene flow, continuous sampling of individuals along the geographic range of interest is preferred over discrete sampling of individuals.

Population genetics has a wide variety of applications in network monitoring. These applications include monitoring genetic connectivity, detecting new migrants, and examining recruitment through parentage and sibship analyses. Once baseline genetics work has been completed, smaller, more cost-effective subsets of informative SNPs can be developed from the larger panels derived from RAD-Seq or genome sequencing. These smaller SNP panels, ranked usually by their ability to distinguish between genetically or geographically distinct populations (i.e., by F_{ST} or allele frequency differences), can provide the same information as a larger SNP panel if designed appropriately (Wringe et al. 2018). This is especially useful if a marine conservation area contains mixed stocks of a species, as these diagnostic SNPs can then determine regions of origin across regular time intervals (e.g., Jeffery et al. 2018; Sinclair-Waters et al. 2018). SNPs or new methods used to sequence hundreds of microsatellites through direct sequencing (e.g., Bradbury et al. 2018) can be used to monitor self-recruitment within MPAs and reveal spillover beyond reserve boundaries (Pelc et al. 2010). Traditional microsatellites have successfully been used in combination with biophysical modeling to study recruitment of Australasian Snapper (*Chrysophrys auratus*) in a small (5.2 km^2), coastal MPA in New Zealand. Le Port et al. (2017) revealed that adult snapper within the MPA contributed 10.6% of juveniles to a surrounding area of 400 km^2, suggesting this small reserve makes a disproportionate contribution to larvae in the broader area. Baetscher et al. (2019) genotyped nearly 15,000 individual rockfish (*Sebastes* spp.) in temperate California at 96 genetic markers and were able to identify parents and full-sibling individuals within and outside of a network of marine reserves, providing evidence of both self-recruitment within a marine reserve, and spillover into non-protected areas, providing subsidies for fished populations. These genetic markers generated via high-throughput sequencing and powerful bioinformatics analyses can be used to monitor connectivity in MPA networks through detecting migration, genetic stock identification, and parentage analyses over broad geographic and temporal scales.

4.2.1.2 Visual identification

Tracking the movements and distribution of individual marine animals is a challenging task; however, visual identification methods such as photo-identification techniques have proven to be a useful tool for estimating the abundance, distribution, population structure, and movement for well-studied populations of marine mammals (Hammond et al. 1990), sea turtles (Gatto et al. 2018), whale sharks (McCoy et al. 2018), and seabirds. Repeated documentation of animals with uniquely identifiable features (e.g., pigmentation patterns, natural scars) or passive tags (e.g., banding, branding, PIT tags) can be used in a similar way to tracking data from telemetry units (e.g., Section 4.2.1.3).

Visual identification programs have been used to estimate abundance, distribution, population structure, and movement for relatively well-studied populations of cetaceans (e.g., George et al. 2004; Wimmer and Whitehead 2004). Known behaviour(s) and individually identifiable markers can be used to track an individual through space and time (Hammond et al. 1990; Urian et al. 2015) and, in combination with digital photography and image analysis, an individual can be identified with a high degree of certainty. Photo-identification can provide an assessment of connectivity and spatial-temporal use of habitat, which is valuable information for monitoring MPAs (Hastie et al. 2003; Gormley et al. 2012). For example, mark-recapture analyses using photo identification in the Gully MPA have been used to monitor the abundance and movement patterns (among the MPA and adjacent canyons) of the endangered Northern Bottlenose Whale (*Hyperoodon ampullatus*) (Wimmer and Whitehead 2004; O'Brien and Whitehead 2013). Surveys that collect sightings data offer an advantage to telemetry methods that require relatively closer vessel approaches to deploy tags and often direct handling (Section 4.2.1.3); however, potential disturbance to animals related to vessel proximity, duration, and frequency of time spent in the vicinity of animals requires consideration. The relatively non-invasive nature of photo-identification surveys may make them a preferred method for tracking the presence, abundance, and movement of marine Species at Risk that spend some time at the surface.

MPA Network monitoring programs could offer a compelling application for the development of connectivity indicators using photo-identification methods for applicable conservation objectives (e.g., marine mammals). The long-term nature of MPA monitoring provides an opportunity to develop standardized, dedicated, and longitudinal survey designs that are required to maximize the benefits of photo-identification (e.g., O'Brien and Whitehead 2013; Cheney et al. 2014) and constrain observer error that can arise when observations are integrated across programs and platforms (Urian et al. 2015). The deployment of survey vessels as part of sustained, long-term MPA network monitoring increases the feasibility of implementing visual identification programs; however, directed survey designs will still be required (e.g., long-term monitoring of Northern Bottlenose Whale populations in the Gully MPA - Whitehead et al. 1997; O'Brien and Whitehead 2013). Information detailing space use can help to evaluate the spatial overlap between protection (e.g., locations of MPAs or zoning within) and the movement/presence of focal species or populations (e.g., O'Brien and Whitehead 2013). This may be particularly relevant for species that respond strongly to prey and environmental conditions (e.g., North Atlantic Right Whale populations in the Northwest Atlantic - Simard et al. 2019; Sorochan et al. 2019), where the importance of individual habitat may shift over time. Both visual observations and animal telemetry (4.2.1.3) provide information on individual movement that indirect methods (e.g., genetics or biophysical models – Sections 4.2.1.1 and 4.2.2.1, respectively) cannot provide.

4.2.1.3 Animal telemetry

Animal telemetry tools developed for tracking aquatic animal movement can be used to better understand biodiversity dynamics and space use across spatiotemporal scales, and they can help evaluate the design and efficacy of protected areas by providing temporal and spatial information on animal abundance, distribution, and movement of individuals. Information on animal presence/absence and movement data collected using tagging methods can help elucidate patterns in residence, migration scales, and associations with foraging habitat and niches described by concurrently collected environmental covariate data (e.g., temperature and salinity). Methods of modelling animal movement are evolving towards the inclusion of environmental variables that will lead to a better understanding of spatiotemporal patterns of habitat use by populations of species, not just individuals.

In addition to visual observations and mark-recapture methods to assess animal abundance and distribution (see Section 4.2.1.2), animal telemetry can be used to estimate dispersal and migration patterns of invertebrates, fishes, birds, and marine mammals; mortality rates and abundance of resident individuals and seasonal patterns of residence; changes in distribution in response to changes in habitat (related to recovery, natural environmental variability, and climate change); and connectivity among protected areas within a network and among networks for wide-ranging species. Radio-telemetry, acoustic telemetry, bio-logging (archival) tags, ARGOS satellite-linked location tags, pop-up archival satellite transmission tags, and GPS location tags can be used to collect animal location and additional sensor data. VHF radio tags and acoustic tags are limited by the number and distribution of receivers and time spent actively tracking; however, fine-scale positioning can be supplemented with the use of autonomous mobile acoustic surveys and harvester returns of commercial species (e.g., Cote et al. 2018), as well as by leveraging existing infrastructure such as the Ocean Tracking Network (Iverson et al. 2019). Bio-logging tags can store data from multiple sensors (e.g., depth, temperature, salinity, and light level) and provide location estimates based on light level; however, these location estimates are less precise compared to locations from satellite and GPS tags. All electronic tracking tags have some level of uncertainty associated with location estimates, which vary with ambient conditions, animal behavior, study area, duty-cycling and length of deployment.

Satellite, pop-up, and GPS tags are larger and are primarily used to track movements of large pelagic fishes, marine birds, marine mammals, and sea turtles. Data from these tagging methods can be used to characterize uncertainty in the location estimates, which in turn can be incorporated into models used to analyze movement.

In addition to location error, effects of tagging, tagging bias related to deployment location, and sufficient sample sizes are considerations when developing hypothesis-driven tagging studies, particularly given the large variation in movement behavior among individuals. The costs of, and logistics required for, deploying tags and limitations of battery life are challenges for the feasibility of long-term tracking studies of species within protected areas. Despite these challenges, data from studies that overlap with existing and future protected areas are sources of baseline data that can help design future research and monitoring plans for MPAs and MPA networks. Increased acoustic tagging efforts in the vicinity of the St. Anns Bank MPA have been supported by the fishing industry, Ocean Tracking Network, and Emera, providing valuable data on the movement of Snow Crab (Choi et al. 2018). Deployment of receivers within St. Anns Bank MPA and tagging of other species of interest (e.g., Atlantic Cod, Atlantic Striped Wolffish, and Shorthorn Sculpin) within the MPA by DFO with support from the fishing industry have supplemented and leveraged the infrastructure of this multi-partner Snow Crab acoustic tracking project (Choi et al. 2018). These data can be used to estimate spatial-temporal use of the MPA by Snow Crab and other tagged species.

Connectivity research that utilizes electronic tagging methods should be management-driven to prioritize resources and maximize the potential impact that results from such studies could have on the way MPAs and networks are planned and monitored. Baseline information on the presence of species within and adjacent to existing and proposed MPAs in the five priority bioregions has been considered during the design phase, but connectivity among protected areas has not been assessed using sightings or tracking data. Data from satellite tags on marine mammals and sea turtles, and satellite and acoustic tags on large pelagic species, provide baseline information and can be utilized for monitoring the relative abundance and movement of individuals through MPAs and networks. Such data are included as data sources for monitoring Beluga in the Tarium Niryutait MPA, Arctic Region (DFO 2013c) and Leatherback Turtles and sharks in the Laurentian Channel MPA, Newfoundland Region (DFO 2015b). In Gilbert Bay MPA, Newfoundland Region, acoustic tags are an important source of fishery-independent information for the MPA that was established in 2005 with the conservation objective of protecting and conserving a unique population of Atlantic Cod and its habitat. Movement data from these tags help to identify stock mixing, mortality, and migration of both Gilbert Bay and Northern cod throughout the year (DFO 2017c). This acoustic tagging information was also used to relate declining abundance of Gilbert Bay cod to presumptive fishing mortality outside the MPA boundaries. This information suggested that the boundary modifications, or changes to adjacent fishing activities, were required to facilitate the primary conservation objective of MPA to protect Gilbert Bay cod (Morris and Green 2014).

Tracking the movement and habitat use of individuals and populations using visual identification and animal telemetry may become increasingly relevant with climate change (see Section 5), helping to inform the application of dynamic conservation measures that track changing environmental conditions (Tittensor et al. 2019).

4.2.1.4 Geochemical Methods

Environmental heterogeneity in marine systems is ubiquitous and influences organisms at various spatial, temporal, and physiological levels. This variation and physiological response can be used to identify organisms through time and space, when chronicled through a biological record or ‘tag’ reflecting ambient environmental conditions. Because these geochemical signatures develop in-situ, without the need for artificial intervention, they are increasingly being employed as a strategic tool for marine research.

Geochemical composition of the calcified structures of marine organisms is a commonly applied natural tag that can provide information on connectivity and animal movement that is otherwise difficult to obtain from direct tagging methods. This approach requires that spatial variability in ambient conditions will generate distinct signatures that are recorded in calcified structures such as otoliths, statoliths, or shells. When accumulated through an organism's life history, these tags provide an indelible chronology of ambient conditions accumulated from daily to annual increments as the organism grows (Campana 1999). These signatures can be used to reconstruct experienced environmental conditions when compositional elements are highly correlated with specific conditions (Stanley et al. 2015a). For example, elemental strontium (e.g., Bath et al. 2000) and oxygen (e.g., Hoie et al. 2004) have been used as indicators of transitions along salinity and temperature gradients, respectively, for a variety of organisms. This approach can also be used to track the dispersal of larvae (larval shell elemental composition; DiBacco and Levin 2000), the natal origins of individuals settling into juvenile habitat (e.g., juvenile otolith microchemistry; Stanley et al. 2016), track the migration and movement of later life histories (e.g., retrospective otolith chemistry; D'Avignon and Rose 2013), or to examine natal homing of spawning adults who have migrated away from the juvenile habitat (Thorrold et al. 2001), and thus can provide a powerful tool to evaluate connectivity in marine systems (Gillanders 2005).

Various applications of geochemical analyses have been conducted in Canada to elucidate patterns of connectivity. For example, the geochemical composition of Atlantic Cod otoliths has been demonstrated to have a strong response to both temperature and salinity (Stanley et al. 2015a), which vary at local (10s to 100s km; Stanley et al. 2016) and regional (100s to 1000s km; D'Avignon and Rose 2013) spatial scales. This variation has been used to differentiate between inshore and offshore populations of Atlantic Cod (Neville et al. 2018) and to differentiate putative spawning groups (D'Avignon and Rose 2013) in the Northwest Atlantic when sampled as a mixed 'stock'. Similar elemental fingerprinting studies on Pacific Halibut (Gao and Beamish 2003) and Sockeye Salmon (Gao and Beamish 1999) provided information on their spatial distribution and migration patterns. Linking spatially discrete life-history phases could provide valuable information for evaluating and monitoring source-sink patterns across the planning landscape.

When information on the species' specific physiological response to temperature and salinity is known, and the scale of spatial variation in ambient conditions matches the scale of interest for connectivity information (i.e., size and spacing of network components), geochemical analysis can provide a useful tool for understanding spatial biocomplexity (Stanley et al. 2016). In particular, geochemical signatures may provide a strong alternative to artificial tagging when physically tagging and recapturing is impractical. Often fine-scale variation in marine ecosystems is more limited than in freshwater and estuarine systems where ambient conditions are influenced by confined terrestrial inputs.

Tissue-based stable isotope analysis has been used to evaluate marine food webs, owing to predictable variation associated with primary production types (e.g., phytoplankton to seagrasses). Like geochemical analyses of otoliths, spatial variation in food web isotopic signatures, recorded in the tissue of consumers, can provide signatures of spatial-use and movement. This information can reveal patterns of connectivity across both small and broad spatial scales in the marine environment. For example, latitudinal gradients in the fractionation of isotopes of carbon during photosynthesis have been used to evaluate broad latitudinal origin of mobile marine consumers including sharks (Bird et al. 2018) and whales (Silva et al. 2019). Small-scale spatial variation in diet composition between salt marshes within an estuary were used to demonstrate strong site-fidelity of salt marsh fish species (Green et al. 2012). Using stable isotopes of sulfur, Hesslein et al. (1991) demonstrated migratory behavior of whitefish populations in the Mackenzie River Basin based on tissue growth associated with a non-local dietary composition.

The application of stable isotopes to elucidate patterns of species movement and habitat is predicated on whether the stable isotope composition of the organism reflects the prey base that varies spatially, and whether the isotopic composition of prey can be linked to any predictable spatial, oceanographic, or biogeochemical gradients, thus producing unique geographically distributed ‘iso-scapes’. Baseline studies evaluating these iso-scapes, in addition to information on tissue- and species-specific turnover rates (relationship between elemental ratios, diet and time), are crucial for the application of this approach.

For MPA network monitoring, the most pragmatic application of otolith geochemical analyses would be to provide baseline information regarding ontogenetic movement of organisms through a conserved seascape, particularly where there is spatial movement amongst life phases (e.g., Beacham et al. 2000; Bradbury et al. 2008; Bradbury et al. 2011; Stanley et al. 2016). For the most part, stable isotope analyses may be most applicable to evaluate larger-scale processes, documenting transition between distinct habitat types and associated prey fields (iso-scapes), and to generally characterize broad-scale migratory behaviours. These tools could help to identify interacting components, thus help to articulate the success or failure of individual sites and the network as a whole. In this sense, this approach can help to identify efficacy of the existing network and help to identify (spatial) modifications to the network to ensure protection extends across life histories.

Successfully implementing geochemical tagging approaches to measure connectivity requires considerable baseline research and, most often, the results are coarse in nature except in exceptional circumstances when discrete spatial variation in ambient conditions are known and environmental variation (i.e., temperature and salinity effects, prey fields) are controlled through space (Stanley et al. 2016). Existing sampling programs for otolith (i.e., groundfish otolith for size-at-age sampling collected during multispecies research surveys) could provide a valuable data source and historical baseline for network monitoring. Existing laboratory capacity and protocols such as the Otolith Research Lab[8] could be expanded or resourced to incorporate MPA monitoring and connectivity-related research. Stable isotope analysis is a well-established field of research. Tissue sampling targeted to specific species (e.g., migratory pelagics) could be used to investigate connectivity using stable isotopes but may be limited by the frequency of sampling (most research vessel surveys are limited seasonally) and the associated tissue- and species-specific turnover rates. Integration of geochemical tagging with existing and expanding genetic programs (see Section 3.2.1.1) could be used to add additional precision when genetic and geochemical data are collected contemporaneously. This approach has been used previously for mixed stock analysis (Smith and Campana 2010) and fine-scale population assignment (Barnett-Johnson et al. 2010).

4.2.2 Indirect Methods

4.2.2.1 Biophysical Modeling

Since the dispersal of many marine species is accomplished during a planktonic (i.e., drifting in ocean currents) phase, ocean circulation typically has a large influence on the connectivity of their populations (Pineda et al. 2007; Cowen and Sponaugle 2009). The life cycle of species for

---

[8] Otolith Research Lab

which this is relevant is typified by an adult phase that is either immobile (e.g., barnacles) or has limited mobility (e.g., snails) and a planktonic phase that drifts in ocean currents. Physical models of ocean circulation can be used to estimate the trajectories of thousands to billions of ‘particles’ representing the dispersal phase (i.e., larvae). However, physical models without added biological components will only predict the dispersal of passive particles (e.g., pollutants) and thus for many species have limited precision (Metaxas and Saunders 2009). Of course, these physical models are useful for other purposes (e.g., contaminant tracking, biogeochemical cycling), and the biophysical modelling of larval dispersal is but one of many value-added products.

These modelled passive particles trajectories would offer a reasonable approximation of larval dispersal if larvae were primarily passive (i.e., limited directed behaviour). However, larvae are known to swim, or otherwise behaviourally alter their vertical distribution, in response to a number of stimuli (Cronin and Forward 1979; Daigle and Metaxas 2011; Lloyd et al. 2012; Stanley et al. 2013). Larval behaviours that affect vertical distribution can influence the horizontal distributions and resultant dispersal patterns because, in many cases, current varies with depth and circulation (e.g., vertical shear). Translating these behaviours into particle tracking models can thus create a dispersal track that better approximates larval dispersal. Similarly, many larvae will perish in the planktonic phase, but this mortality term is rarely known. Planktonic larval duration, the length of time between larval release and settlement, is correlated with dispersal distance, but other biological components mentioned above interact to generate many exceptions (Shanks 2009). As with most models, the validity of biophysical models of larval dispersal will depend on their ability to resolve both the physical (e.g., coastlines, currents) and biological (e.g., behaviour, growth, and mortality) (Metaxas and Saunders 2009) processes.

Since larval behaviour, planktonic larval duration, and mortality are species-specific traits, the number of possible biophysical models could be considered infinite. It is feasible to focus on a manageable set of key species (Magris et al. 2016) or functional traits (Daigle et al. 2016). However, since dispersal is often most influenced by physical processes (Daigle et al. 2016), using primarily physical-driven passive particle tracking with no behaviour or mortality may be a useful means of quantifying connectivity at the multi-species or MPA network scale.

In terms of MPA network monitoring, biophysical modelling is particularly useful for experimentation, prediction, or environmental assessments. The physical ocean circulation models used as the basis for particle tracking can simulate various climate change scenarios, or other anthropogenic scenarios (e.g., building a new causeway or port). Assessing connectivity between network components using this modelling framework can be used for the initial design (e.g., Magris et al. 2016), but it can also periodically be repeated to evaluate whether changing environmental conditions that in turn influence dispersal (e.g., circulation and temperature variation) have influenced connectivity at the network scale. When coupled with climate and biological models (e.g., temperature-dependent mortality and/or growth), these dispersal-simulating models can provide powerful inference for how connectivity might change and how to account and monitor for that change going forward. Importantly, in lieu of comprehensive empirical measures of connectivity (e.g., seascape genetics and tagging programs), these models can provide a cost-efficient and powerful tool to understand and monitor connectivity within the planning region. However, wherever possible, biophysical models should be accompanied by empirical validation. Comparisons of connectivity using biophysical models and population genetics (estimated relatedness) is a common approach to ‘validate’ biophysical models. In cases where biological parameters (e.g., timing, behaviour, duration) are well resolved, biophysical models generally show agreement with genetic estimates of relatedness. For example, biophysical models developed for sea cucumbers on the Pacific coast (Xuereb et al. 2018) and American Lobster in the Atlantic (Benestan et al. 2016) have shown strong agreement with analyses of genetic similarity. Even at large spatial scales (e.g., Truelove et al. 2017), well parameterized biophysical models have provided useful inference for dispersal and connectivity.

4.2.2.2 Landscape Ecology

The relationship between species (demographics and diversity) and area is well established in ecological theory, whereby a larger area generally leads to more individuals, resources, and variation, which in turn leads to more opportunities for niche specialization (MacArthur and Wilson 2001). It is through this specialization that life-history stages, species, and populations occupy habitat through space and time. During movement and dispersal, marine organisms utilize resources and thus the association of species to their habitat is inextricably linked to connectivity (Crooks and Sanjayan 2006; Hodgson et al. 2009).

Facilitation of connectivity via the conservation of habitat (aptly referred to as 'conservation connectivity') is a core component of traditional conservation planning. In terrestrial settings, conservation connectivity is generally based on the conservation of habitat patches and the corridors of habitat that link them (Doerr et al. 2011; Dickson et al. 2019). This process is encapsulated in a variety of nomenclature including 'Habitat', 'Landscape', and 'Structural connectivity', all of which refer to the physical attributes of the land- or sea-scape over which an individual disperses, and thus is an intrinsic component of the habitat preferences of the life-history stage, species, or population. Structural connectivity is thus distinct from 'Functional connectivity', which describes the degree to which movement of energy (i.e., food resources), individuals (immigration/emigration), or genetic materials (gene flow) actually occurs across the physical landscape. In this working paper, we have discussed several methods of assessing functional connectivity including artificial and natural tagging (e.g., visual observation or geochemical approaches), and population genetics, in addition to a biophysical modelling approach that attempts to simulate functional connectivity using various biophysical elements of the focal area. Landscape connectivity is generally quantified using spatial structural elements that describe the spatial arrangement and quality of habitat types within a conserved seascape (i.e., physical connectedness, size, quality, aggregation, centrality). Because these metrics are habitat-focused, they are assumed to carry some multispecies inference for connectivity within design and monitoring (Calabrese and Fagan 2004; Doerr et al. 2011).

Landscape connectivity theory has been somewhat entrenched in the design and monitoring of terrestrial systems, with the application of this theory to the marine setting generally limited to research focusing on elements of dispersal and functional connectivity. Applications of landscape-based connectivity for design and monitoring of MPAs has some history at fine spatial scales within highly structured ecosystems (Dorenbosch et al. 2007). For example, the response of fish populations has been shown to strongly respond to structure (i.e., size and spacing) and connectedness (related to suitability of between-patch areas to facilitate dispersal) of habitat patches such as coral reefs (Olds et al. 2012), mangroves (Pittman et al. 2007), and seagrasses (Nagelkerken et al. 2008; Staveley et al. 2017). The configuration of habitat patches has also been demonstrated to have a strong influence on the behavior and survival of juvenile Atlantic Cod in Newfoundland, whereby the between-patch habitat had a strongly regulated connectivity (Ryan et al. 2012).

Application of landscape-based metrics of connectivity at scales amenable to networks (100s-1000s km) are a core component for design and monitoring in terrestrial analogues but are uncommon in marine systems (e.g., Riggio and Caro 2017). This disconnect might relate to the three dimensional aspect of marine habitat, whereby habitat conditions can change between pelagic and benthic systems and across depth gradients; thus, the movement, rather than the structural elements of movement (i.e., conditions of movement habitat), have been the focus. Where landscape-based connective measurements have been made, they generally focus on spatial configuration metrics (i.e., betweenness centrality; Magris et al. 2016; Daigle et al. 2018; Friesen et al. 2019) or resistance. In resistance-based studies, connectedness between MPA network components is assessed as a cumulative score of the dispersal path, where, for example, the resistance is the inverse of habitat suitability (Dickson et al. 2019). As opposed to simple Euclidean geographic distance among sites, habitat resistances may provide a more realistic approach to modeling connectivity by revealing lower resistance among patches through suitable habitat corridors.

With a variety of tools (e.g., predictive models) and data (e.g., predictive seascape features) available to assess the distribution and habitat suitability of marine species (e.g., Kenchington et al. 2019), the application of landscape connectivity as a design and monitoring feature should be possible. However resistance-based approaches have rarely been implemented in the marine realm, potentially because for many species, the primary mode of dispersal occurs during the pelagic larval stages, which is more difficult to accurately model structural resistance. Connectivity during this life-history stage is regulated by a variety of biological and physical elements that vary in time, space, and even depth (Metaxas and Saunders 2009; Daigle et al. 2015). For marine meroplankton (benthic species with pelagic larval dispersive stages), integration of ocean currents with adult habitat suitability remains the only feasible way to study resistance models among conservation areas. Correspondingly, some studies have revealed that population structure in the marine environment correlates more strongly with ocean currents than geographic distance (Dambach et al. 2016; Xuereb et al. 2018), suggesting that isolation by distance relationships alone might be unsuitable in a complex fluid environment.

When applying connectivity to the design and monitoring of MPA networks, structural connectivity offers some advantages. Functional connectivity is challenged by the uncertainty implicit in its calculation (e.g., biological attributes of dispersal - Section 4.2.2.1), particularly because it integrates movement potential with the dynamics of each life history, species and population (Doerr et al. 2011). Despite substantial support in the literature that connectivity is a central component to conservation planning to safeguard productivity and resilience of a network of protected areas, there remains sparingly few tangible examples of its application in the design, and ultimately monitoring, of MPA networks (Balbar and Metaxas 2019). This might, in part, link to the fact that SCP considers optimization of conservation features in a spatial context, thus abstracting direct measures of functional connectivity, generally, from traditional conservation planning (but see Section 3.2.3 and Daigle et al. 2018) - connectivity and representativity have different units. Measuring structural connectivity with existing or proposed network configurations offers a mechanism to measure connectivity in space (i.e., resistance-based approaches described previously), thus fitting it into the traditional conservation spatial optimization paradigms (e.g., Marxan). In a monitoring context, a reduction in structural connectivity (e.g., through loss of linking suitable habitat) among protected areas would indicate that biological connections between areas, and thus the viability and resilience of the network as a whole, may have been reduced. When represented spatially, structural connectivity could provide managers with information on areas to prioritize for network development and to evaluate how connectivity may respond, or may be responding, to changing environmental conditions associated with climate change (Section 5.2, Stanley et al. 2018).

An ongoing study by Wilcox et al. (in prep.[9]) aims to simulate landscape connectivity using circuit theory (Shah and McRae 2008) and resistance based on gene flow, habitat suitability (adults), and circulation (larvae) (e.g., Figure 4). These maps will show hotspots for dispersal and connectivity that are based on ocean currents and suitable adult habitat (inverse used as a resistance), as well as any geographic barriers to gene flow. Information generated by this approach can provide a spatial connectivity baseline that can be used to evaluate design and also monitor change when periodically reassessed.

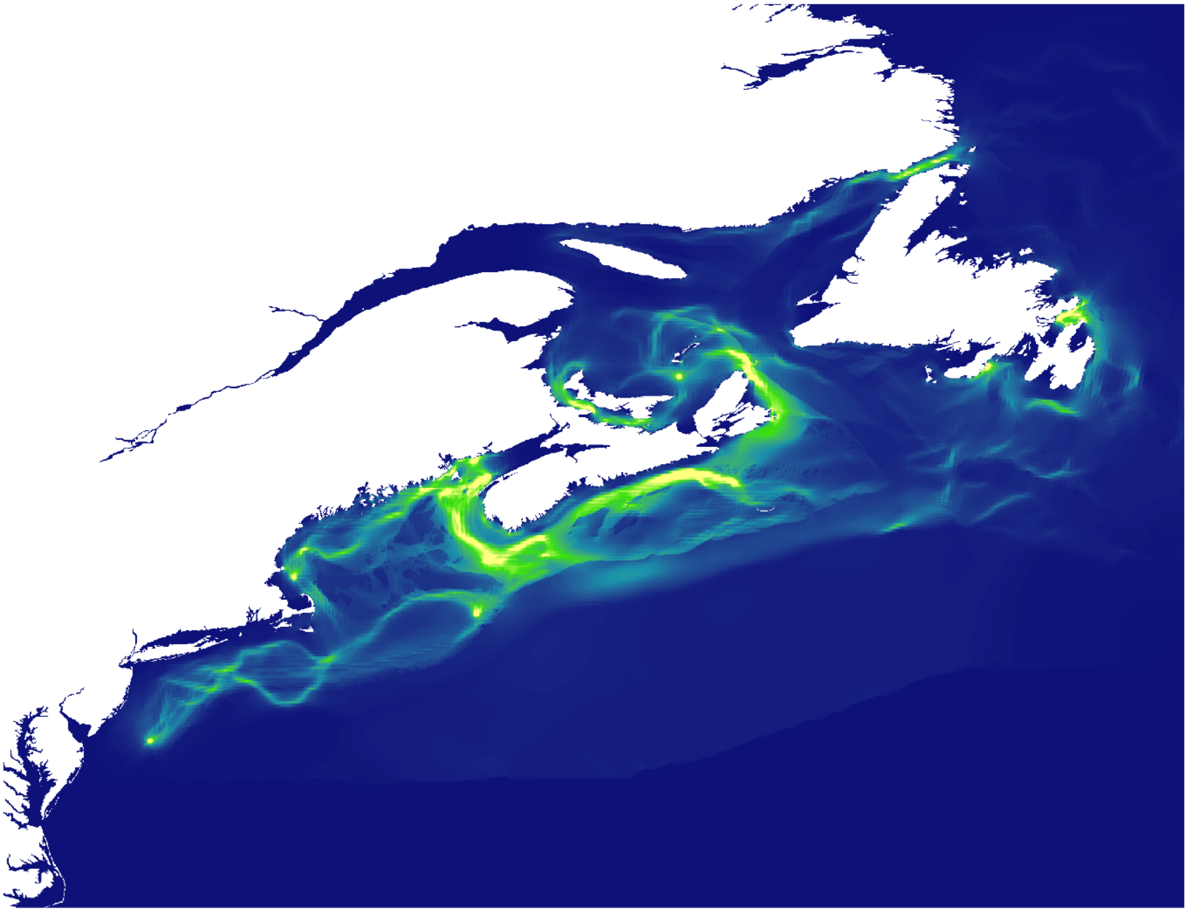

Figure 4. Resistance seascape for Atlantic Scallop based on adult habitat suitability. Bright yellow and green regions show potential corridors of low habitat resistance. These regions, especially if congruent across a wider variety of species, can highlight representative regions of potentially high connectivity that can be used in MPA network design and ongoing monitoring.

For some, the uncertainty with measuring functional connectivity abstracts it from being a tangible or practical guidepost for conservation and monitoring (e.g., Hodgson et al. 2009; Costello and Connor 2019), advocating instead that the maintenance of habitat representation and increased spatial extent of protected areas should be the primary focus. Cabral et al. (2016), for example, found habitat quality and coverage to be more useful criteria for network

---

[9] Wilcox, M., Stanley, R.R.E., Jeffery, N.W., DiBacco, C., Beiko, R., and Bradbury, I.R. In prep. Development of spatial connectivity network models in support of spatial conservation planning.

design than siting MPAs based on sources, sinks, or other centrality measures. This view assumes that connectivity conservation simply can be achieved by expanding habitat (Hodgson et al. 2009) via protected area coverage or habitat improvements. However, this ignores that the primary focus of conservation of connectivity in a planning landscape is to ensure the viability of protected metapopulation(s) across a variety of spatial scales (Worboys 2010). This objective requires that the network of protected areas both maintains and improves connections across habitats (Doerr et al. 2011), thus evaluation of structural or landscape connectivity should be an element of MPA monitoring and overall connectivity conservation (Pittman et al. 2007). Protection of habitat areas and quality alone cannot ensure metapopulation persistence.

The most pragmatic metric that could be derived from landscape-based connectivity for MPA network planning would be a summed resistance (e.g., Wilcox et al. in prep.[9]) among MPA components and conservation objectives (where appropriate). In this case, deviations from the baseline can indicate improved or decreased connectivity within the network. Resistance would be across the planning landscape and thus would imbibe spatial features both within and outside the protected network. Changes to the network configuration could be used to identify how connectivity could be improved by adding or moving network components (sensu D'Aloia et al. 2019; Tittensor et al. 2019). This approach could also be used to identify habitat types with a high ‘connective value’ that may necessitate enhanced protection (e.g., new or shifted network components). With climate change expected to have profound influences on the natural, and specifically marine, environment (IPCC 2007), monitoring changes in landscape connectivity across the protected network may be vital to integrate changes in the distribution of habitats, species, and conservation priorities within a regional planning area.

4.2.3 Connectivity and Spatial Optimization

Connectivity has mostly been considered an afterthought in MPA network planning (Table 1, Balbar and Metaxas 2019) despite being considered vital for species’ persistence and population viability. Additionally, climate change and species range shifts will undoubtedly alter connectivity in the ecosystems (Mumby et al. 2011), which may undermine the network-level benefits (e.g., population resilience, rescue effects; Section 5.2). In monitoring MPA networks, connectivity is key to understanding network level interactive effects (i.e., $\boldsymbol{O}_{\text{network interaction}} > 0$, see equation 1).

In regions where spatial optimization using Marxan was used, the most common method of including ‘connectivity’ in the design phase was the use of the Boundary Length Modifier (BLM) in conjunction with spatial dependencies (i.e., boundary definitions) that represent the shared boundary length among neighbouring planning units. The BLM is a scaling parameter in Marxan that modifies the ‘clumping’ of the selected planning units (Ardron et al. 2010). Increasing the BLM effectively reduces the edge-to-area ratio of the selected areas. Reducing this ratio is known to be associated with increasing population viability in protected areas (Woodroffe and Ginsberg 1998). If connectivity patterns are known, it is possible to use connectivity strength as the spatial dependency since connectivity is, by definition, a better indicator of movement than boundary length (e.g., Beger et al. 2010). In these cases, the scaling parameter is known as the Connectivity Strength Modifier (CSM), and increasing the CSM will create a more well-connected network and reduce the amount of emigration (i.e., spillover). This exercise can be done manually using Marxan or facilitated directly using Marxan Connect (Daigle et al. 2018).

Of course, reducing spillover is not the only goal to consider for connectivity and may not always be desirable. Connectivity can also be integrated into the Marxan process via conservation features (White et al. 2014; D'Aloia et al. 2017a; Krueck et al. 2017; Daigle et al. 2018). These connectivity-based conservation features are often based on graph theory and can be used to accomplish a wide variety of goals. Some of these conservation features are system specific, for example Krueck et al. (2017) use larval dispersal properties to identify priority areas that will promote both conservation and fisheries. Other conservation features are applicable to most systems such as 'in-degree', which indicates the number of connections coming into each planning unit. Areas with high in-degree are generally found to have higher genetic diversity, species diversity, and population resilience (Hanski 1982; Almany et al. 2009; Munguía-Vega et al. 2015). Alternatively, using PageRank, a graph theory metric that corresponds to the importance of a planning unit to the network, was associated with the highest mean metapopulation lifetime (Kininmonth et al. 2019)[10].

This variety of approaches and corresponding objectives highlights the necessity of conducting post-hoc evaluations of effectiveness for all relevant methods. Such an evaluation can take the form of population viability models or metapopulation metrics (Daigle et al. 2017; Kininmonth et al. 2019). In the absence of species-specific growth rates, fecundity, and other life-history parameters, it is also possible to set thresholds for connectivity-related indicators (e.g., ProtCon; Saura et al. 2017). It is important that evaluation methods are chosen to reflect the objectives of the network. Software like Marxan Connect could be used to evaluate network performance by incorporating new or revised connectivity information, in addition to other baseline data (i.e., information on species distribution), to evaluate network configuration(s) against an (revised) optimized baseline. These evaluations should be assessed iteratively to assure that the MPA network remains adequately connected.

4.2.4 Rules of Thumb

Connectivity has become a major research theme in marine conservation planning (e.g., Botsford et al. 2009; Balbar and Metaxas 2019). Although the inventory of tools available to evaluate connectivity is diverse and growing (reviewed above), significant investments of time, effort, and resources would be still be required to gain a comprehensive baseline of ground-truthed, spatially and taxonomically representative, measures of connectivity within an MPA network. Even for mature MPA networks (e.g., UK, California, and on the Great Barrier Reef), research on connectivity among network components continues. In Canada, information on dispersal, movement, and connectivity available within the planning regions (Figure 1) is often focused on species of commercial, recreational, conservation, or cultural importance (Burt et al. 2014), and is potentially limited in comparison to established planning regions (i.e., the Great Barrier Reef MPA Network - Balbar and Metaxas 2019). This limited range of available information on connectivity is in contrast to the overarching intent of the Canadian MPA network to safeguard a much wider array of taxa, including marine birds, marine mammals, plant and algal species, across three oceans. Capturing the complexity and diversity of information to characterize and operationalize connectivity into MPA network design and monitoring would encompass a monumental investment of time and resources, especially considering the heterogeneity in dispersal scale expected in marine species (Kinlan and Gaines 2003). Even if high-resolution ground-truthed information on connectivity within a planning region was available, the likelihood of a set of design principles serving the needs of all species and regions within the network is highly unlikely (Fernandes et al. 2012). Conversely, targeted networks developed with spatially-explicit connectivity data outperform networks developed using 'rules of

---

[10] For more information on these conservation features and more see the Marxan Connect website
Daigle, R.M., Metaxas, A., Balbar, A., McGowan, J., Treml, E.A., Kuempel, C.D., Possingham, H.P., and Beger, M. 2018. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. bioRxiv. doi:10.1101/315424.

thumb' in terms of ecological and economic outcomes for the targeted species (Rassweiler et al. 2014; Daigle et al. 2017).

Generalizing connectivity among functional groupings of species (e.g., coastal and offshore species, fish and invertebrates, spring and fall spawners, short and long pelagic larval durations) based on available information is a practical approach that has been applied in the design of MPA networks (e.g., DFO 2019). For example, meta-analyses on observed or predicted scales of adult movement and larval dispersal have been conducted for priority species within networks in the UK (Roberts et al. 2010), California (Shanks et al. 2003; California Department of Fish and Game (CDFG) 2008) and Canadian Pacific (Burt et al. 2014). These analyses provide specific connectivity design advice for the size and spacing of MPAs that is generalized within the planning region and among species. Though taxonomic, biophysical, and oceanographic attributes would vary considerably among these study regions, advice on size and spacing was remarkably consistent, with a target MPA size range of 10 to 100 km^2 in nearshore areas and increasing with depth, and inter-MPA distances not exceeding approximately 100 km. This consistency suggests that generalized connectivity benchmarks can be developed to evaluate network connectivity overtime. For example, 'ProtConn' (Saura et al. 2017) is a metric that quantifies the percentage of a planning region covered by connected protected areas. This metric can be calculated for specific habitat types or generalized for all protected areas, and it can accommodate inputs derived from the spatial arrangement of protected areas combined with either rules of thumb (e.g., dispersal distances of 1, 10, 30, and 100 km) or spatially explicit connectivity data (e.g., population genetics or animal telemetry – Section 4.2.1).

Considering the general biodiversity focus of the Canadian MPA Network, 'rules of thumb' approaches offer the advantage of integrating empirical observations or predictions (e.g., through biophysical models) into generalized design parameters, which can be updated, benchmarked, and monitored through time. For example, periodic updates of the inventory of estimated dispersal ranges (e.g., through new empirical tagging/genetic data or by improved biophysical model predictions) could be used to reassess benchmark size and spacing guidelines and the efficacy of existing/proposed network designs. Reassessments will be particularly important as conservation priorities for the MPA networks evolve over time and biological processes respond to climate change (see Section 5).

The successful application of 'rules of thumb' for the design and monitoring of MPA networks will require some direct or indirect measures of movement and dispersal within the planning region. Generalizing movement scales from different ocean systems or across latitudes may lead to inappropriate spatial considerations, particularly as the range of movement and, in particular, dispersal scale is expected to increase with latitude (Laurel and Bradbury 2006). Even within planning regions, spatial variation in connectivity (e.g., barriers to dispersal or gradients in temperature - Stanley et al. 2018) can influence the utility of generalized targets. These limitations serve as considerations for the development and application of 'rules of thumb' for MPA network monitoring and the need for ground-truthed assessments of connectivity within the planning region. When interlaced with targeted design attributes required for specific species, populations, or regions (see example prioritization framework - Smith and Metaxas 2018), 'rules of thumb' offer an informed approach by which to base assessment and monitoring at the scale of an MPA network. These generalized design principles are particularly relevant for the broad biodiversity focus of the Canadian MPA Network because they are not necessarily hindered by data limited to a subset of species, populations, or regions.

4.3 CONNECTIVITY SUMMARY

A variety of approaches can be used to incorporate or evaluate connectivity within the design of MPA networks. The approach by which ecological connections are incorporated into network design will depend on the available information and resources, ranging from generally relatively low cost 'rules of thumb' to direct observations of connectivity (e.g., population genetics, tags) that require considerably more resources and effort to collect. Evaluation of connectivity in network design can be used to iteratively compare different design configurations and identify gaps in connectivity. As new information becomes available, connectivity evaluations can be revised (Figure 3). The decision about whether the appropriate level of connectivity is achieved within a bioregional network will ultimately depend on the conservation priorities and whether their persistence depends on spatial linkages within the planning region (e.g., Smith and Metaxas 2018). The development of connectivity baselines for bioregional MPA network designs should be commensurate with the tools, data, and resources available, until additional information is gained about feasibility and limitations of each measurement approach.

5. MPA NETWORK MONITORING, CLIMATE CHANGE, AND ADAPTIVE MANAGEMENT

Climate change and the loss of biodiversity present two significant global sustainability challenges (IPCC 2018). These two threats are also inextricably linked in that climate change is both a driver of, and a dynamic threat to, biodiversity (Pressey et al. 2007; García Molinos et al. 2015), which can itself mediate the impact or magnitude of climate change (McLeod et al. 2009; Côté and Darling 2010). The influence of oceanic changes in response to climate change will influence ecosystems in myriad ways (Harley et al. 2006; Pörtner et al. 2014). For example, the spatial distribution of some species may shift in response to rising temperatures or sea levels, resulting in some species ranges shifting beyond the MPAs designed to protect them (Maxwell et al. 2013). Further, changes to trophic levels (Cheung et al. 2013) or increasing vulnerability of species to acidity or hypoxic events (Strong et al. 2014) may affect species interactions and community structure within MPAs.

Well-designed and connected MPA networks can increase the resilience of biological systems under the influence of climate change (McLeod et al. 2009), and MPAs are one of the few tools available to address such broad-scale impacts (Gaines et al. 2010). However, MPA networks offer little direct resistance to climate change, except by strategic placement in areas of low projected change (i.e., in thermal refugia; Magris et al. 2014). Further, static protected areas may fall short of mitigating climate change impacts in a rapidly changing environment, and the need for integrating spatially dynamic threats into conservation planning is increasingly important (Araujo et al. 2011). There is a growing interest in dynamic area-based management[11] as an adaptation tool in the marine environment to mitigate climate change impacts on biodiversity (e.g., Game et al. 2008; Lewison et al. 2015). D'Aloia et al. (2019) have proposed coupled networks of permanent and dynamic conservation areas to improve the adaptive capacity of reserve networks. In Canada, where MPA networks may use a variety of federal, provincial, and Indigenous spatial management tools, coupling permanent MPAs (e.g., Ocean Act MPAs) with more nimble and less permanent spatial tools (e.g., *Fisheries Act* closures) may provide an avenue for establishing integrated dynamic-permanent networks that can more readily adapt to a changing ocean. Although species' responses to climate change

---

[11] Areas are temporarily protected from anthropogenic stressors, and then released from formal protection when no longer needed.

remain difficult to predict, monitoring data can be used to better understand species movements, particularly when paired with historical data on species distributions (e.g., Perry et al. 2005). Ongoing evaluation of the MPA network for the key design elements (i.e., representation, replication and connectivity) will provide the valuable feedback needed to understand the spatio-temporal changes of the conservation priorities within the network footprint. In the decision framework provided by D'Aloia et al. (2019), monitoring data would feed into adaptive management and increase the robustness of the network design.

5.1 CLIMATE CHANGE AND REPRESENTATION AND REPLICATION

Replication and representation are recognized in MPA networks as measures of resilience and adaptive capacity in the face of uncertain conditions, or human, natural and/or climactic impacts (DFO 2013b; Canada – British Columbia Marine Protected Area Network Strategy 2014). Changes in ocean conditions resulting from climate change can have significant impacts on species distribution, range habitat suitability, and community dynamics (Kroeker et al. 2013; Maxwell et al. 2013). Biodiversity redistribution in response to climate change can thus lead to a reduction in representation and replication of conservation priorities within the static boundaries of MPA networks.

Several tools to measure and monitor representation and replication within MPA networks are available (reviewed in this paper), and can incorporate climate change projections, and associated implications, to better account for its influence on conservation objectives. Approaches and techniques for detecting changes in representation and replication of conservation priorities within an MPA network through time should consider both the vulnerability of a species or community to climate change (e.g., Stortini et al. 2015) and predicted ocean conditions to effectively monitor and assess MPA networks (Rilov et al. 2019). Understanding the varying degrees of the vulnerability of conservation priorities to climate change can help identify monitoring indicators and determine decision criteria to inform adaptive management and action (Whitney and Conger 2019).

The contraction or loss of suitable habitat and species range shifts beyond the boundaries of the existing network will impact the representation and replication of conservation features and limit the efficacy of the network under future conditions. Monitoring activities should contribute to improving and updating spatial datasets to integrate habitat quality indices so that repeat assessments of representation and replication can occur (Young and Carr 2015). In particular, information is needed on: habitat use, patch size, patch quality, and inside-outside comparisons (as discussed in Sections 2 & 3). GIS overlay analyses and assessments of biophysical classifications can document habitat loss, reductions in habitat quality, boundary changes and ecosystem shifts under climate change. Modelling approaches can also be used to predict how projected ocean conditions and climate projections will influence habitat quality and species ranges and how they are predicted to overlap with existing MPA boundaries through time (Gormley et al. 2013). Predictive models should be validated with ongoing monitoring and sampling activities to confirm that representative and suitable habitats and species distributions are maintained and replicated within the network (Fulton et al. 2015).

5.2 CLIMATE CHANGE AND CONNECTIVITY

Climate change will also have a profound influence on connectivity by restructuring the physical environment through which dispersal and movement occur. These changes can manifest in myriad interconnected ways, including reduced larval transport (shorter PLDs; Lett et al. 2010), altered survival (shorter duration and exposure to predication, physiological response to temperature change; O'Connor et al. 2007), changing phenology (earlier spawning of adults; Petitgas et al. 2013), changing prey composition (e.g., shifting copepod communities leading to emerging presence of North Atlantic Right Whale in the Gulf of St. Lawrence; Record et al. 2019), altered species distributions (presenting new or disrupting existing connections; Stanley et al. 2018), and disrupted transport (shifting hydrodynamic conditions changing physical linkages between areas; Cetina-Heredia et al. 2015). Circularly, the responses of impacted ecosystems will also depend themselves on connectivity, which influences the ability of organisms, populations, and ecosystems to respond and adapt to disturbance and change (e.g., via demographic or evolutionary 'rescue'; Xuereb et al. 2019).

These connections pose a significant challenge for the design and monitoring of MPA networks, particularly for the traditional static protected area paradigm (D'Aloia et al. 2019; Tittensor et al. 2019). Although connectivity and climate change are widely considered in marine conservation planning, their incorporation has been largely conceptual (Balbar and Metaxas 2019) and rarely integrated (Magris et al. 2014). As climate change begins to fundamentally and directionally alter marine ecosystems, connectivity monitoring may be an important tool to elucidate functional ecological changes and ultimately help to inform how conservation objectives and network performance are themselves changing. Monitoring connectivity across the MPA network can help to disentangle local and regional influences of climate change on conservation priorities and, thus, provide managers the information required to assess spatial elements of the MPA network (i.e., zoning and spatial network configuration).

Unsurprisingly, studies that evaluate or predict quantitative changes in connectivity in response to climate change report significant deviation in connectivity and self-seeding among MPAs (Andrello et al. 2015; Coleman et al. 2017), suggesting spatial network arrangements would/could be inadequate to maintain connectivity into the future. Adaptively managing MPA networks to maintain connectivity and conservation objectives will depend on continued evaluation of connectivity and species response to a changing ecosystem. In particular, any decisions about changes to the network to account for shifting biological systems (D'Aloia et al. 2017a; Tittensor et al. 2019) should consider how climate change will influence functional and structural linkages across the seascape.

Several reviews provide frameworks and approaches for anticipating the influence of climate change on connectivity (for example see review by Magris et al. 2014) and metrics for measuring MPA network connectivity have been reviewed in this working paper. Predictive approaches that evaluate how habitat and oceanographic change could be used as a basis to predict the temporal and spatial scales by which connectivity may change (e.g., Coleman et al. 2017). These approaches can be informed by global (e.g., the National Oceanic and Atmospheric Administration's Coupled Model Intercomparison Project - NOAA CMIP[12]) or regionally downscaled oceanographic models (e.g., Wang et al. 2018) and be used as a scaffold to ensure efficient monitoring investment (Field et al. 2007). Connectivity should not be assumed to be a static feature of a planning landscape, and existing linkages within the network will change in response to climate change, and thus the network itself, will be reorganized (Mumby et al. 2011). Monitoring how this reorganization is occurring should be applied as both a spatial and temporal question, whereby changes in seasonal elements (i.e., timing of spawning or productivity) should be considered in addition to spatial dependency (i.e., source-sink dynamics and landscape based resistance) between protected and unprotected areas.

Seascape-based approaches that integrate structural and functional connectivity in the marine realm (e.g., Wilcox et al. in prep.[9] - Figure 3) have taken advantage of physical projections of climate change to predict how dispersal and connectivity might change in response to a

---

[12] NOAA

changing marine environment (e.g., Lett et al. 2010). To add to this, biophysical modelling-based approaches have also included the element of changing ocean circulation patterns and their effects on dispersal and connectivity (e.g., Runge et al. 2010). Genetic approaches that evaluate how species and populations will respond to climatic vitiation (Lowen et al. 2019; Razgour et al. 2019) can improve predictive models and help to identify priority areas where changes in connectivity might be most pronounced (i.e., at the interface between population sub-units – inflection points of genetic clines; Stanley et al. 2018).

Often changing ocean climate conditions necessitate redistribution in concert with spatial shifts in physiological and ecological niches, given the canalized niches of many marine species (i.e., niche conditions are not evolutionarily labile; Wiens and Graham 2005). However, species or populations may also respond through adaptation to novel conditions (Aitken and Whitlock 2013; Sunday et al. 2014). Connectivity can have a strong influence on acclimation and adaptation by contributing to both standing genetic variation and gene flow across a planning landscape. The exchange of beneficial mutations and genetic variation, referred to as ‘evolutionary rescue’ (sensu Carlson et al. 2014), can increase the fitness of connected populations. In the context of monitoring, evaluating genetic diversity and structure across a planning landscape could provide important information regarding changes in connectivity (i.e., relatedness among MPAs or populations) and diversity associated with environment and environmental change. Applications of seascape genetics (evaluation of genomic-environmental associations) have provided novel information regarding structure and connectivity in the marine environment (e.g., Selkoe et al. 2016; Van Wyngaarden et al. 2017a; Jeffery et al. 2018; Lehnert et al. 2018) and can be readily applied with existing genomic processing pipelines (e.g., regional and industrial genomics labs). Despite relatively high upfront costs (tens of thousands of dollars for sample collection and sequencing), small (dozens to hundreds) of diagnostic genetic markers can be subsampled from the initial data and can be used to monitor adaptive gene regions, genetic diversity, and connectivity for orders of magnitude less cost.

Though tools to measure and monitor connectivity within and among network components are available (reviewed here and in this working paper), setting quantitative benchmarks or thresholds for change in connectivity that would inform conservation planning and management is challenging. Still, the role that climate and connectivity change might play in biological systems has been recognized (e.g., Pressey et al. 2007; Lett et al. 2010) and can be incorporated into the design of MPA networks (Magris et al. 2014; D'Aloia et al. 2019; Tittensor et al. 2019). The challenge remains on how to operationalize connectivity monitoring as a foundation to re-evaluate the efficacy of the current network configuration. Currently, there remains little practical guidance on how changes in connectivity within MPA network should trigger management action.

At a minimum, monitoring plans should periodically re-evaluate connectivity within the implemented and proposed network designs. Erosion of functional and structural linkages within the network should prompt action, particularity where these linkages are related to the long-term persistence and maintenance of the conservation objectives. The frequency and extent of these re-evaluations should be informed by models capable of predicting change. Wherever possible, genetic information should be incorporated into these assessments, as the maintenance of gene flow and standing genetic variation is directly linked to the maintenance of connectivity within an MPA network and planning area.

5. CASE STUDY: EVALUATION AND ASSESSMENT OF MPA NETWORK SCENARIOS IN THE NORTHERN SHELF BIOREGION USING PERFORMANCE MEASURES

These approaches were co-developed by members of the MPA Network Technical Team (MPATT) in the NSB: Chris McDougall (MPATT), Rebecca Martone (B C Ministry of Forest, Lands, Natural Resource Operations and Rural Development), Carrie Robb (DFO Science), Katie Gale (DFO Science), Karin Bodtker (MPATT), Greig Oldford (DFO Oceans), Lais Chaves (Haida Oceans Technical Team), Amos Chow (DFO Oceans), John Cristiani (University of British Columbia), and Emily Rubidge (DFO Science)[13].

5.1 STRUCTURED DECISION MAKING IN THE CONTEXT OF MPA NETWORK MONITORING

Structured decision making (SDM) is a transparent, inclusive, and informed approach to decision making that can help identify potential management options and make explicit any associated uncertainties and trade-offs (Tulloch et al. 2015). SDM is an iterative, objectives-oriented process that focuses on: 1) setting objectives and performance measures; 2) identifying possible management actions; 3) estimating the consequences of each action; 4) assessing possible trade-offs; and 5) identifying the preferred alternative to meet the specified objectives (Figure 4). Performance measures, incorporating thresholds based on ecological and stakeholder values, help to evaluate whether the objectives are met by the chosen management actions (Martin et al. 2009). Monitoring informs both performance measures and thresholds, helping to minimize uncertainties and allowing managers to iteratively assess the effectiveness of management actions against the objectives (Lyons et al. 2008).

Within resource management, SDM has been used to develop a framework known as management strategy evaluation (MSE), which is a systematic modeling approach that incorporates a suite of performance measures based on established objectives to help assess potential management procedures, provide advice on robust management actions, and identify the associated trade-offs that should be considered (Bunnefeld et al. 2011; Kronlund et al. 2014). MSE can facilitate the assessment of management actions as new information becomes available, help identify monitoring and data collection priorities, and enhance transparency by highlighting uncertainties inherent in the ecological systems, models and decision-making process (Bunnefeld et al. 2011). In a Canadian context, MSE has been identified as a method applicable to fulfilling the Precautionary Approach requirements of the Sustainable Fisheries Framework (Kronlund et al. 2014) and has been used in management assessments of the Redfish and Pollock fisheries (DFO 2011, 2018b).

SDM can also be used to support MPA network planning and be adapted for MPA network monitoring, as shown in Figure 4. Indicators and performance measures can be identified to help evaluate the effectiveness of a suite of alternative MPA network designs, with associated consequences estimated and clearly stated. Trade-off analyses can help to improve network efficiency so that a network design can be prioritized for implementation. The scenario evaluation SDM framework, with the addition of indicators and a monitoring plan, can be adapted to support network monitoring to ensure the network continues to meet its goals and objectives. In the monitoring context, the performance measure can be recalculated using data collected via a monitoring program to examine any potential changes in the network since

---

[13] MPATT is co-chaired by: Sheila Creighton (DFO), Steve Diggon (Coastal First Nations), and Kristin Worsley (British Columbia Ministry of Forests, Lands, Natural Resources Operations and Rural Development).

implementation. Instead of evaluating these metrics in the context of differing configurations of the network design, we would be evaluating these metrics on the network through time. The timeframe for evaluation would be determined based on network objectives, chosen indicators, and the rate at which new information is collected. Monitoring the network using an SDM framework will also reduce uncertainties associated with estimating the consequences of management actions in a dynamic, multi-species, multi-objective context.

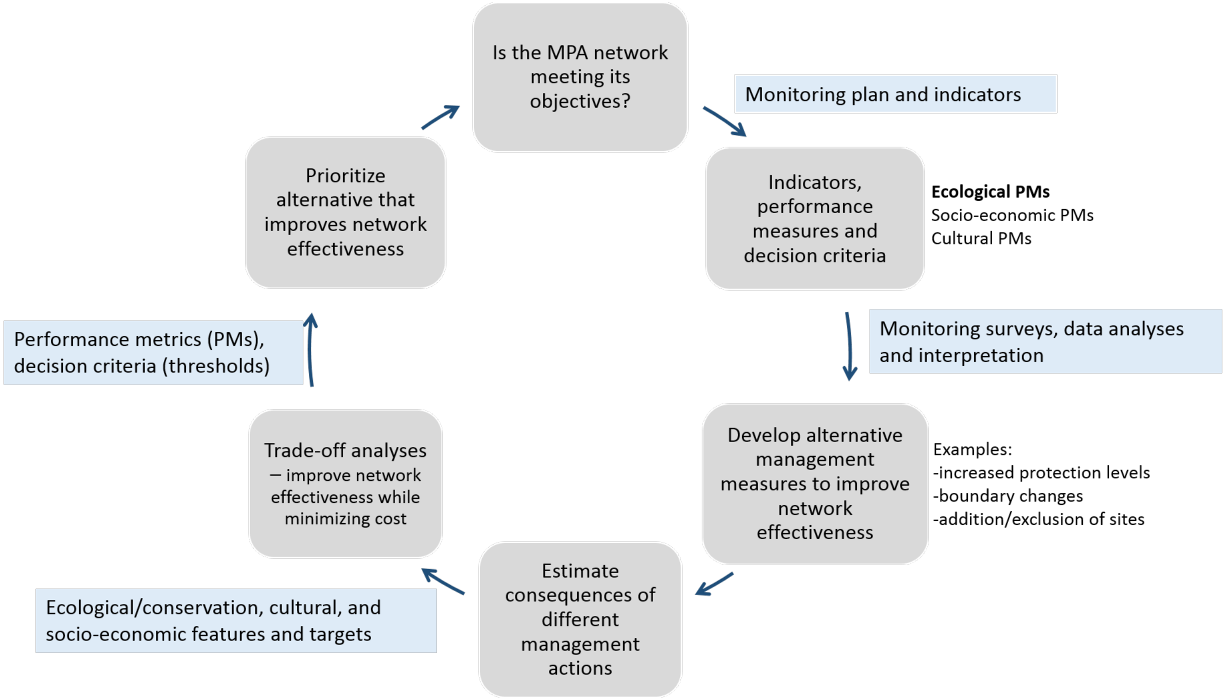

Figure 5. SDM framework for MPA network planning, adapted from the SDM approach described in Gregory et al. (2012). Grey boxes indicate steps in the planning process. Blue boxes indicate required inputs.

5.2 EXAMPLE PERFORMANCE MEASURES AND APPROACHES TO ASSESSING REPRESENTATION, REPLICATION, AND CONNECTIVITY IN THE NSB

To support MPA network planning in the NSB (Figure 5), the interdisciplinary MPA network technical team have developed an SDM framework, with a suite of draft performance measures (PMs) guided by network objectives, available spatial data, and feedback from stakeholders and an external science advisory committee. The PMs incorporate ecological, socioeconomic, cultural, and governance metrics; they are being used to compare draft network design scenarios and report on how well each iteration achieves network objectives. Although PMs are important for improved transparency and trade-off evaluations in support of MPA network design, they can also be used to evaluate the efficiency and efficacy of the resulting MPA network once implemented, particularly when combined with monitoring efforts that generate regularly updated data and information. Of particular relevance to the objectives of this paper are network-wide assessments related to the representation, replication, and connectivity of ecological conservation priorities.

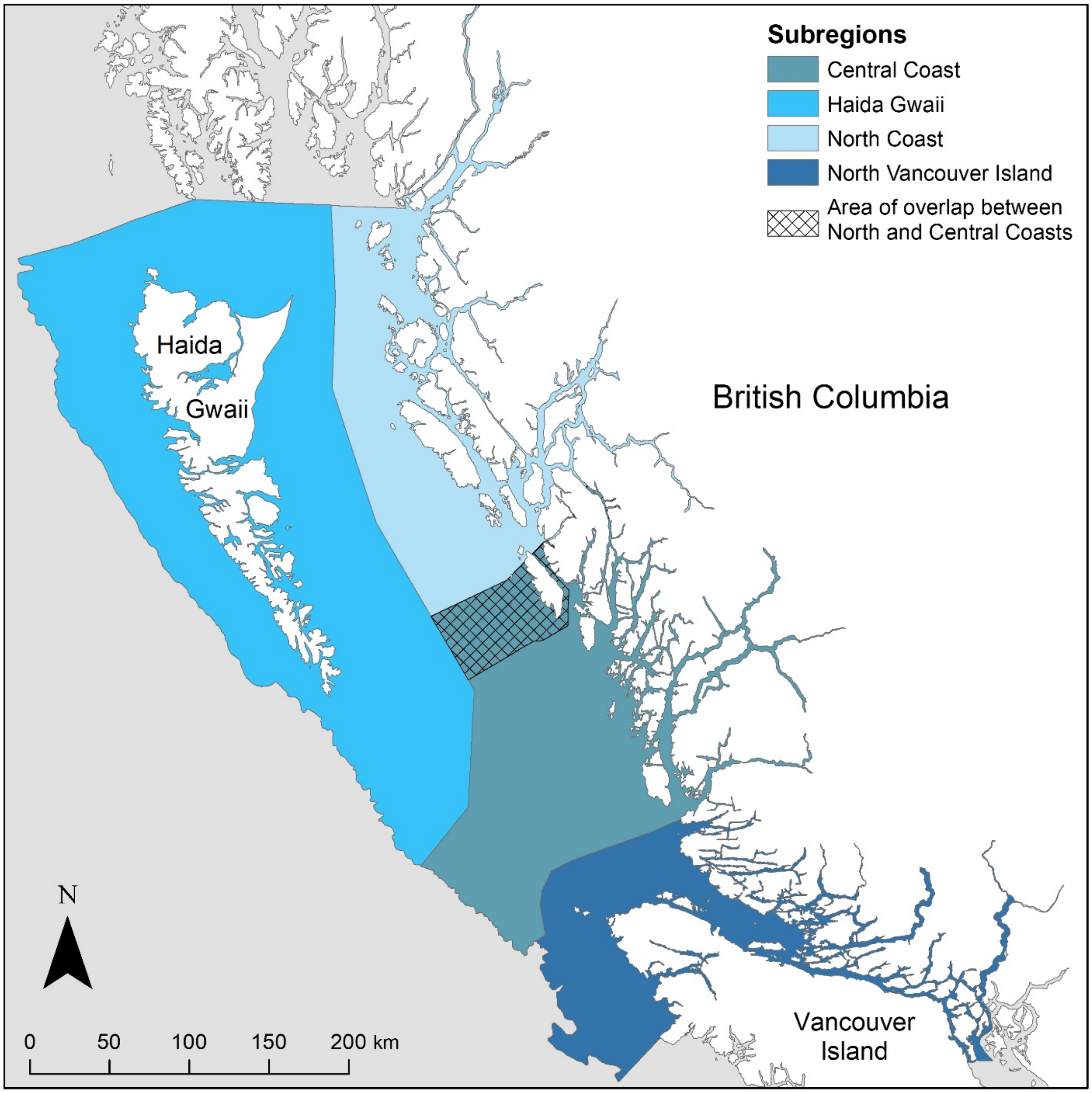

Figure 6. Map of the NSB including subregions delineated for MPA network planning.

5.2.1 Representation and EBSAs

The Canada – British Columbia Marine Protected Area Network Strategy (2014) specifies that the MPA network in the NSB should include the full range of biodiversity present in the study area. As in all Canadian bioregions, network planners in the NSB have used guidance from DFO's Canadian Science Advisory Secretariat (CSAS) processes to develop ecological conservation priorities (DFO 2017a; Gale et al. 2019) and ecological conservation target ranges (DFO 2019; Martone et al. in prep.[5]). Spatial datasets, termed ecological features, were compiled for site selection analyses using Marxan as one input into initial draft network designs. Using the PMs, representation can be iteratively assessed through metrics focused on feature-specific representation, species richness, and biodiversity to evaluate how well competing scenarios are meeting network objectives.

Species representation and richness is determined for the PMs by the presence of ecological features within a given network design scenario and the proportion of those spatial features that meet their recommended target ranges (Table 3). Although these are common indicators in the design and assessment of MPAs, species richness is also evaluated for the PMs in the context of the human activities proposed to be allowed in the draft sites. Incorporating the known stressors of the relevant conservation priorities during design and monitoring can increase the efficacy of MPA networks (Mach et al. 2017). Following CSAS guidance (DFO 2019), the potential cumulative impacts of allowed activities on each species or habitat within each site are assessed and the contribution of each MPA towards meeting each ecological conservation target is scaled accordingly, in an analysis termed the conservation gaps analysis (CGA) (Martone et al. 2018; Martone et al. in prep.[5]).

Table 3. Select draft performance measures related to the design features of representation, replication, and connectivity developed to support MPA network planning in the NSB. Spatial scale for the bioregion and subregions outlined in Figure 4.

Design Feature	Draft Performance Measure	Description	Scale
Representation	Ecological conservation priority target range	Conservation Target Assessment - Number and proportion of features below and meeting target ranges	Bioregion, subregion
	Ecological Marxan - average selection frequency	Average Marxan selection frequency score of planning units captured in the network	Bioregion, subregion, MPA
	Ecological Marxan - proportion high selection frequency	Proportion of high Marxan selection frequency planning units captured in the network	Bioregion, subregion, MPA
Replication	Ecological conservation priorities meeting minimum number of desired replicates	Number and proportion of features meeting desired replicates	Bioregion, subregion

Design Feature	Draft Performance Measure	Description	Scale
Connectivity	Spacing	Number and proportion of sites meeting spacing guidelines (40-200 km apart)	Bioregion, subregion
	Connectivity hotspots (Centrality)	Number and proportion of connectivity hotspots (e.g., Eigenvector centrality) captured in the network across different habitat types	Bioregion, subregion
	Connectivity hotspots (Betweenness)	Number and proportion of connectivity hotspots (betweenness) captured in the network across different habitat types	Bioregion, subregion

Through the CGA, species richness can be assessed at a site or network scale and can be parsed out using attributes of the proposed MPAs, such as protection level or designation type, or characteristics of the ecological features, such as functional group or conservation status (Martone et al. 2018). For example, the representation and richness of habitat classes from the Pacific Marine Ecological Classification System (PMECS; Rubidge et al. 2016) or identified EBSAs can be assessed independently. Alternately, features important for different life-history stages and the contribution of individual MPAs can be assessed to determine how well complementarity is achieved within a network design. A monitoring program can inform the effectiveness of the protection levels and identify the change in status of ecological features within specific functional groups or at a given conservation status.

The PMs also assess representation by considering areas identified through Marxan analyses as having high conservation value due to their elevated species richness (a proxy for biodiversity, based on available spatial data). In the NSB, Marxan analyses were run iteratively to identify a range of solutions based on the ecological features alone and ecological and cultural features together, both with and without consideration of socioeconomic information. Outputs of these analyses include a selection frequency map that shows how often each planning unit is selected to be part of a solution, with higher selection frequency planning units considered more critical across solutions (Ardron et al. 2010). To evaluate ecological representation, the PMs use the overlap of each network design scenario with the ecological-only Marxan analysis to determine the average selection frequency and the proportion of high selection frequency planning units captured by each scenario.

5.2.2 Replication

The assessment of replication for MPA network planning in the NSB is also guided by advice from CSAS (DFO 2019). The appropriate number of replicates for each ecological feature is based on its patch size and rarity within the NSB and is assessed at a subregional scale, with more replicates recommended for rarer, more spatially restricted features. The minimum number of replicates is 2-3 per subregion for the more common, broadly distributed features. For the PMs, replication achievement for a given network design scenario is based on the proportion of ecological features that achieve the minimum number of recommended replicates. This would be the same in a monitoring context as new information is acquired. For example, upon implementation an assessment of the network using available data may indicate that 70% of CPs and associated spatial features are meeting the replication objectives. After five years of monitoring, and integrating updates to available spatial datasets, this PM can be recalculated and we may find an increase in this PM. As ecosystems in the network recover, perhaps this PM is now at 80% five years post-implementation. Similar to the PMs related to representation, the metrics can be parsed out using the characteristics of the MPAs or ecological features, such as EBSAs. Monitoring replication at a finer scale would enable researchers to determine whether MPAs implemented using a specific tool or at a higher protection level are better able to meet replication targets or whether certain species or habitats are benefiting more from the protection afforded by an MPA network.

The calculations associated with the PMs for replication use the site-level outputs of the CGA and are therefore informed by the potential interactions between the ecological features and human activities within each site. To determine the recommended number of replicates for each ecological feature, the median amount of each ecological feature is calculated for all proposed sites and quartiles are used to assign features to a replicate class, with those features having the largest patches requiring the fewest replicates. Because the requisite information is not yet available for generating species-area curves like those developed in California (Saarman et al. 2013), a pragmatic approach was used so that MPAs within a network design contribute as a replicate for a given ecological feature if they contain more than 1% of the total amount of an ecological feature in the NSB. However, because 1% can vary depending on the size of the ecological feature, that amount was capped at 13 km^2 for coastal features and 50 km^2 for offshore features based on the recommendations for MPA sizes (DFO 2019). Lacking from this metric is an understanding of habitat patch quality and information about the diversity it supports. This information can be collected through ongoing monitoring efforts and improve the assessment of replicates as we learn more about the areas in the network.

5.2.3 Connectivity

To determine how well draft MPA network scenarios achieve ecological connectivity, the PMs assess the number and percent of connectivity hotspots for a suite of benthic habitat types that overlap with the proposed MPAs. Connectivity hotspots are based on Eigenvector Centrality, which indicates MPAs that are highly connected to others within the draft scenario, as well as Betweenness, which indicates MPAs that are key connectors to other MPAs (Friesen et al. 2019). Both of these metrics use distance thresholds to infer connectivity associated with adult movement for species with moderate adult home ranges (Friesen et al. 2019). This approach could be used to iteratively evaluate network performance in capturing connectivity hotspots as connectivity changes in a dynamic marine environment (Section 5.2), as well as suggest emerging areas of (connectivity) importance for consideration of any future network alterations.

The spacing between the proposed MPAs in a draft network scenario is also assessed as a proxy for connectivity. The spacing PM assesses the number and proportion of proposed MPAs within a draft scenario that meet the guidelines of at least 40 to 200 km between MPAs that were developed through CSAS (DFO 2019). These guidelines are based on the dispersal distance of intermediate dispersers, which may increase the extent of the coastline that is replenished by larvae produced within MPAs (Carr et al. 2017). The lower range of these spacing guidelines is similar to that for California’s nearshore (Kinlan and Gaines 2003) and would accommodate shorter-distance dispersers (DFO 2019). Spacing is unlikely to change once the network is implemented, so this would not make a useful monitoring PM. However, other metrics of connectivity that are being monitoring (e.g., summed resistance compiled using genetic, adult habitat, and larval connectivity - Section 4.2.2.2), could be used to better understand if the spacing or configuration of MPAs in the network needs to be adapted to ensure individual MPAs are well-connected.

5.3 FROM COMPARATIVE SCENARIO EVALUATION FRAMEWORK TO MPA NETWORK MONITORING

Repeat assessments of representation, replication, and connectivity are important as the MPA network design process in the NSB moves into implementation and monitoring. Targeted and ongoing survey efforts both within and outside of the MPA network will fill important gaps in available spatial data. For example, survey information detailing the spatial distribution of many key habitats, such as kelp beds, is often outdated and largely incomplete ((British Columbia Marine Conservation Analysis (BCMCA) Project Team 2011). However, work is underway to address this limitation and develop a comprehensive kelp dataset based on remote sensing imagery using the Google Earth Engine archive (Nijland et al. 2019). This dataset can be used in the future to evaluate representation and replication of kelp within the MPA network, when compared to the distribution of kelp for the entire NSB[14].

Species richness provides one measure of representation within an MPA network but is a metric that can be confounded by the complex interactions of the species and habitats within any ecosystem, which can be further investigated through monitoring efforts. Soykan and Lewison (2015) found that biomass and abundance information more consistently differentiated between MPAs and control sites than estimates of species richness and may be useful metrics as additional information is collected. Jantke et al. (2018) compiled representation into a single metric focused on mean target achievement using the Aichi target of 10% for all ecological features. Efforts are underway to update this metric to incorporate variable feature targets, such as those used in Canada’s priority bioregions. Regular reassessments of this metric can provide a simple yet intuitive performance time series of an MPA network. In the meantime, the metric could be calculated to assess the target achievement of sets of conservation priorities. For example, in the NSB, conservation priorities were assigned a low, medium, or high target class based on their ecological role, vulnerability, and conservation status. The Jantke et al. (2018) method could be used to ascertain how well the targets have been achieved over time for conservation priorities assigned higher targets (i.e., those species and habitats considered more vulnerable or threatened or with higher functional importance).

As new and more comprehensive ecological information is compiled through monitoring efforts, or as management measures are adjusted, feature representation and replication assessments can be updated and compared to determine whether the network continues to meet the ecological conservation targets and to identify sites and features that may have changed and may no longer contribute as much to the network. For example, studies have used updated species and habitat data to identify representative sites for monitoring work (Young and Carr 2015) and to evaluate the representation of ecological features within MPA networks originally designed using predictive models or proxy species (Young and Carr 2015; Virtanen et al. 2018). Further, Virtanen et al. (2018) have used updated ecological information in new site selection analyses to assess whether the final network design continues to capture areas of high

---

[14] Similar projects are being conducted on the East coast for coastal Eelgrass (*Zostera marina*).

conservation value based on their species richness or diversity, while House et al. (2017) have used Marxan analyses to identify ways to adaptively manage inefficient networks.

7. SUMMARY

Effective MPA networks must be **representative** of their conservation objectives (and the planning region as a whole), have sufficient **replication** (where appropriate) to ensure resilience to stochastic disturbance, and be **well-connected** so that individual network components interact with each other to maintain ecological function and provide conservation outcomes that exceed the summed results of network components. Network monitoring programs can provide the requisite information to determine the efficacy of the network design through time, as the network develops and as the environment changes. As marine ecosystems respond to climate change, monitoring programs will be essential for adaptive management and insurance that MPA networks continue to produce the conservation outcomes they were designed to produce in the most (spatially) efficient way possible.

Many tools exist for measuring representation, replication, and connectivity among design features. MPA Network monitoring, in some ways, is challenged by the very diversity networks are developed to protect. No one tool or approach should be used to monitor these design features. Monitoring efficiency is more than a cost-limited decision, and the selection of the most *appropriate* tools should explicitly consider the spatial-temporal scales of the ecological features of interest in addition to cost of deployment. Research that improves the efficiency of these tools, for both cost and (spatial, temporal, and taxonomic) comprehensiveness, should be prioritized for regional and national MPA programs. Given design features are shared within the Canadian MPA Network, bioregional monitoring programs should implement, wherever possible, standardized approaches for monitoring. These standardized approaches would provide for more efficient and targeted investments (i.e., shared technical equipment or expertise) and reporting for the Canadian MPA Network. Additionally, investment and integration with existing broad-scale monitoring programs within DFO (e.g., multi-species RV surveys, the Atlantic Zone Monitoring Program and other scientific regional monitoring programs (e.g., Parks Canada National Marine Conservation Area monitoring and Marine Plan Partnership Protected Management Zone monitoring in the Pacific Region) should be prioritized to ensure comprehensive data long-term baselines are available to evaluate network performance.

Network scenarios have been developed in each of the five priority bioregions; however, at the time of writing, no network has been completed, and the timeframe for implementation has not yet been set. Advice on monitoring program development and strategies for assessing the network design principles should be specific to the design of each bioregion and linked to their respective objectives. Guidance from this report could provide a useful framework outlining the approaches, requirements, and rationale for design-based monitoring moving forward; however, specific advice for the development of monitoring programs cannot occur until network configurations and management plans have been finalized.

NEXT STEPS

Marine Spatial Planning (MSP) is an initiative to manage ocean spaces in a collaborative and transparent manner that has been recently funded by the department. At its core, the MSP program seeks to map anthropogenic activities and marine resources to best understand usage patterns and areas of overlap. Conservation area planning falls within this broad program, also seeking to examine the footprint of activities like commercial fishing, aquaculture operations, and shipping routes, and areas of ecological and geomorphological importance. To deliver on broad objectives of sustainability, MSP would be well served by integrating ecological principles such as connectivity (Foley et al. 2010), representation, and replication. Integration of mapping products produced by the MSP program could be used as additional inputs when implementing monitoring at the network scale. For example, efforts to map the distribution of species, biodiversity (hotspots), and fishing within each planning region through the MSP program could be used by monitoring programs to assess representativity, connectivity (e.g., landscape connectivity metrics), and MPA network performance. The MSP program could be used to augment MPA networks to maintain or enhance structural or landscape connectivity within a network and help to enhance network performance by structuring adjacent activities (e.g., marine industries) to facilitate conservation objectives. This is particularly true as patterns of connectivity and anthropogenic activity (i.e., industrial activity, shipping, etc.) change as the underlying physical and biological seascape reorganize under climate change. Long-term planning achieved through MSP and MPA networks should thus be integrated when considering the impacts of changing ocean use and climate change on the conservation objectives.

8. ACKNOWLEDGEMENTS

We want to thank Katie Gale, Rebecca Martone, Isabelle Côté, David Beauchesne, and the participants of the national peer review for their suggestions and thoughtful edits, as well as Mark Wilcox for providing the resistance seascape map (Figure 4).

9. REFERENCES CITED

2008. Papahānaumokuākea Marine National Monument Management Plan. National Oceanic and Atmospheric Administration, United States Fish and Wildlife Service, Hawaiʻi Department of Land and Natural Resources. p. 411.

Aitken, S.N., and Whitlock, M.C. 2013. Assisted gene flow to facilitate local adaptation to climate change. Annual review of ecology, evolution, and systematics 44: 367-388.

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., and Williamson, D.H. 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28(2): 339-351. doi:10.1007/s00338-009-0484-x.

Andrello, M., Mouillot, D., Somot, S., Thuiller, W., and Manel, S. 2015. Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. Diversity and Distributions 21(2): 139-150. doi:10.1111/ddi.12250.

Araujo, M.B., Alagador, D., Cabeza, M., Nogues-Bravo, D., and Thuiller, W. 2011. Climate change threatens European conservation areas. Ecology Letters 14(5): 484-492. doi:10.1111/j.1461-0248.2011.01610.x.

Ardron, J.A., Possingham, H.P., and Klein, C.J., eds. 2010. Marxan Good Practices Handbook. Pacific Marine Analysis and Research Association, Vancouver: 155 p.

Baetscher, D.S., Anderson, E.C., Gilbert-Horvath, E.A., Malone, D.P., Saarman, E.T., Carr, M.H., and Garza, J.C. 2019. Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. Molecular Ecology 28(7): 1611-1623.

Balbar, A.C., and Metaxas, A. 2019. The current application of ecological connectivity in the design of marine protected areas. Global Ecology and Conservation 17: e00569. doi:10.1016/j.gecco.2019.e00569.

Ball, I.R., Possingham, H.P., and Watts, M. 2009. Marxan and relatives: Software for spatial conservation prioritisation. *In* Spatial conservation prioritisation: Quantitative methods and computational tools. *Edited by* A. Moilanen and K.A. Wilson and H.P. Possingham. Oxford University Press, Oxford, United Kingdom. pp. p. 185-195.

Ban, N.C., McDougall, C., Beck, M., Salomon, A.K., and Cripps, K. 2014. Applying empirical estimates of marine protected area effectiveness to assess conservation plans in British Columbia, Canada. Biological Conservation 180: 134-148. doi:10.1016/j.biocon.2014.09.037.

Barnett-Johnson, R., Teel, D.J., and Casillas, E. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. Environmental Biology of Fishes 89(3): 533-546. doi:10.1007/s10641-010-9662-5.

Bath, G.E., Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., and Lam, J.W.H. 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. Geochimica Et Cosmochimica Acta 64(10): 1705-1714. doi:10.1016/s0016-7037(99)00419-6.

Beacham, T.D., Gregory, R.S., and Brattey, J. 2000. Origins of two recruitment pulses of 0-group Atlantic cod (*Gadus morhua*) in Bonavista Bay, Newfoundland during 1999, determined from genetic variation. Department of Fisheries and Oceans Canada, Ottawa.

Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., and Possingham, H.P. 2010. Incorporating asymmetric connectivity into spatial decision making for conservation: Asymmetric connectivity in conservation planning. Conservation Letters 3(5): 359-368. doi:10.1111/j.1755-263X.2010.00123.x.

Benestan, L., Quinn, B.K., Maaroufi, H., Laporte, M., Clark, F.K., Greenwood, S.J., Rochette, R., and Bernatchez, L. 2016. Seascape genomics provides evidence for thermal adaptation and current-mediated population structure in American lobster (*Homarus americanus*). Molecular Ecology 25(20): 5073-5092.

Bird, C.S., Verissimo, A., Magozzi, S., Abrantes, K.G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea, D.M., Biais, G., Borrell, A., Bouchoucha, M., Boyle, M., Brooks, E.J.B., J., and al., e. 2018. A global perspective on the trophic geography of sharks. Nature Ecology & Evolution 2: 299-305.

Botsford, L.W., Micheli, F., and Hastings, A. 2003. Principles for the design of marine reserves. Ecological Applications 13(sp1): 25-31. doi:10.1890/1051-0761(2003)013[0025:PFTDOM]2.0.CO;2.

Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B., Largier, J.L., O'Farrell, M.R., Ralston, S., Soulanille, E., and Wespestad, V. 2009. Connectivity, sustainability, and yield: Bridging the gap between conventional fisheries management and marine protected areas. Rev Fish Biol Fisher 19(1): 69-95.

Bradbury, I.R., Snelgrove, P.V.R., and Fraser, S. 2000. Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua*, in relation to spawning time and location in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 57(9): 1761-1772.

Bradbury, I.R., Campana, S.E., and Bentzen, P. 2008. Estimating contemporary early life-history dispersal in an estuarine fish: integrating molecular and otolith elemental approaches. Molecular Ecology 17(6): 1438-1450. doi:10.1111/j.1365-294X.2008.03694.x.

Bradbury, I.R., DiBacco, C., Thorrold, S.R., Snelgrove, P.V.R., and Campana, S.E. 2011. Resolving natal tags using otolith geochemistry in an estuarine fish, rainbow smelt *Osmerus mordax*. Marine Ecology Progress Series 433: 195-U576. doi:10.3354/meps09178.

Bradbury, I.R., Wringe, B.F., Watson, B., Paterson, I., Horne, J., Beiko, R., Lehnert, S.J., Clément, M., Anderson, E.C., and Jeffery, N.W. 2018. Genotyping-by-sequencing of genome-wide microsatellite loci reveals fine-scale harvest composition in a coastal Atlantic salmon fishery. Evolutionary Applications 11(6): 918-930.

Bradbury, I.R., Bowman, S., Borza, T., Snelgrove, P.V.R., Hutchings, J.A., Berg, P.R., Rodríguez-Ezpeleta, N., Lighten, J., Ruzzante, D.E., Taggart, C., and Bentzen, P. 2014. Long Distance Linkage Disequilibrium and Limited Hybridization Suggest Cryptic Speciation in Atlantic Cod. PLoS One 9(9): e106380. doi:10.1371/journal.pone.0106380.

British Columbia Marine Conservation Analysis (BCMCA) Project Team. 2011. Marine Atlas of Pacific Canada: a product of the British Columbia Marine Conservation Analysis.

Bunnefeld, N., Hoshino, E., and Milner-Gulland, E.J. 2011. Management strategy evaluation: A powerful tool for conservation? Trends Ecol Evol 26(9): 441-447.

Burt, J.M., Akins, P., Lathem, E., Beck, M., Salomon, A.K., and Ban, N.C. 2014. Marine protected area network design features that support resilient human-ocean systems - applications for British Columbia, Canada. Simon Fraser University, BC, Canada. pp. 159 pp.

Cabral, R.B., Gaines, S.D., Lim, M.T., Atrigenio, M.P., Mamauag, S.S., Pedemonte, G.C., and Aliño, P.M. 2016. Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations. Ecosphere 7(11): e01533-n/a. doi:10.1002/ecs2.1533.

Calabrese, J.M., and Fagan, W.F. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2(10): 529-536.

California Department of Fish and Game (CDFG). 2008. Master Plan for Marine Protected Areas, Revised Draft.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263-297. doi:10.3354/meps188263.

Canada – British Columbia Marine Protected Area Network Strategy. 2014.

Carlson, S.M., Cunningham, C.J., and Westley, P.A.H. 2014. Evolutionary rescue in a changing world. Trends in Ecology & Evolution 29(9): 521-530.

Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J., and Williams, M. 2017. The central importance of ecological spatial connectivity to effective marine protected areas and to meeting the challenges of climate change in the marine environment. Aquatic Conservation: Marine and Freshwater Ecosystems 27(S1): 6-29.

Cetina-Heredia, P., Roughan, M., van Sebille, E., Feng, M., and Coleman, M.A. 2015. Strengthened currents override the effect of warming on lobster larval dispersal and survival. Global Change Biology 21(12): 4377-4386.

Cheney, B., Corkrey, R., Durban, J.W., Grellier, K., Hammond, P.S., Islas-Villanueva, V., Janik, V.M., Lusseau, S.M., Parsons, K.M., Quick, N.J., Wilson, B., and Thompson, P.M. 2014. Long-term trends in the use of a protected ara by small cetaceans in relation to changes in population status. Global Ecology and Conservation 2: 118-128.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frolicher, T.L., Lam, V.W.Y., Palomares, M.L.D., Watson, R., and Pauly, D. 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change 3: 254-258.

Choi, J.S., Vanderlaan, A.S.M., Lazin, G., McMahon, M., Zisserson, B., Cameron, B., and Munden, J. 2018. St. Anns Bank Framework Assessment. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/066. vi + 65 p.

Chow, M., Gaskin, E., Walton, A., and Andrews, A. 2015. Hawaiian Islands Humpback Whale National Marine Sanctuary Draft Management Plan (Plan/Draft). *In* Environmental Impact statement. Technical Report.

Clarke Murray, C., Agbayani, S., Alidina, H.M., and Ban, N.C. 2015. Advancing marine cumulative effects mapping: An update in Canada's Pacific waters. Marine Policy 58: 71-77. doi:10.1016/j.marpol.2015.04.003.

Coleman, M.A., Cetina-Heredia, P., Roughan, M., Feng, M., van Sebille, E., and Kelaher, B.P. 2017. Anticipating changes to future connectivity within a network of marine protected areas. Global Change Biology 23(9): 3533-3542. doi:doi:10.1111/gcb.13634.

Convention on Biological Diversity (CBD). 2010. Decisions adopted by the conference of the parties to the convention on biological diversity at its tenth meeting.

Convention on Biological Diversity (CBD). 2011. Strategic plan for biodiversity 2011-2020. IUNEP/CBD/COP/10/INF/12/Rev.1.

Convention on Biological Diversity (CBD). 2018. Protected areas and other effective area-based conservation measures. CBD/SBSTTA/22/L.2.

Costello, M.J., and Connor, D.W. 2019. Connectivity Is Generally Not Important for Marine Reserve Planning. Trends in Ecology & Evolution 34(8): P686-688. doi:10.1016/j.tree.2019.04.015.

Cote, D., Nicolas, J.-M., Whoriskey, F., Cook, A.M., Broome, J., Regular, P.M., and Baker, D. 2018. Characterizing snow crab (*Chionoecetes opilio*) movements in the Sydney Bight (Nova Scotia, Canada): a collaborative approach using multiscale acoustic telemetry. Canadian Journal of Fisheries and Aquatic Sciences 76(2): 334-346. doi:10.1139/cjfas-2017-0472.

Côté, I.M., and Darling, E.S. 2010. Rethinking Ecosystem Resilience in the Face of Climate Change. PLOS Biology 8(7): e1000438. doi:10.1371/journal.pbio.1000438.

Cowen, R.K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. Ann. Rev. Mar. Sci. 1: 443-466. doi:10.1146/annurev.marine.010908.163757.

Cronin, T.W., and Forward, R.B., Jr. 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science 205(4410): 1020-1022. doi:10.1126/science.205.4410.1020.

Crooks, K.R., and Sanjayan, M. 2006. Connectivity conservation. Cambridge University Press.

D'Aloia, C., Bogdanowicz, S., Majoris, J., Harrison, R., and Buston, P. 2013. Self-recruitment in a C aribbean reef fish: a method for approximating dispersal kernels accounting for seascape. Molecular Ecology 22(9): 2563-2572.

D'Aloia, C.C., and Neubert, M.G. 2018. The formation of marine kin structure: effects of dispersal, larval cohesion, and variable reproductive success. Ecology 99(10): 2374-2384.

D'Aloia, C.C., Xuereb, A., Fortin, M.-J., Bogdanowicz, S., and Buston, P. 2018. Limited dispersal explains the spatial distribution of siblings in a reef fish population. Marine Ecology Progress Series 607: 143-154.

D'Aloia, C.C., Daigle, R.M., Côté, I.M., Curtis, J.M.R., Guichard, F., and Fortin, M.-J. 2017a. A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biol. Conserv. 216: 93-100. doi:10.1016/j.biocon.2017.10.012.

D'Aloia, C.C., Daigle, R.M., Côté, I.M., Curtis, J.M., Guichard, F., and Fortin, M.-J. 2017b. A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biological Conservation 216: 93-100.

D'Aloia, C.C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J.M.R., Darling, E., Guichard, F., Leroux, S.J., Martensen, A.C., Rayfield, B., Sunday, J.M., Xuereb, A., and Fortin, M.-J. 2019. Coupled Networks of Permanent Protected Areas and Dynamic Conservation Areas for Biodiversity Conservation Under Climate Change. Frontiers in Ecology and Evolution 7(27). doi:10.3389/fevo.2019.00027.

D’Aloia, C.C., Bogdanowicz, S.M., Francis, R.K., Majoris, J.E., Harrison, R.G., and Buston, P.M. 2015. Patterns, causes, and consequences of marine larval dispersal. Proceedings of the National Academy of Sciences 112(45): 13940-13945.

D’Avignon, G., and Rose, G.A. 2013. Otolith elemental fingerprints distinguish Atlantic cod spawning areas in Newfoundland and Labrador. Fisheries Research 147(0): 1-9.

Daigle, R.M., and Metaxas, A. 2011. Vertical distribution of marine invertebrate larvae in response to thermal stratification in the laboratory. J. Exp. Mar. Bio. Ecol. 409(1): 89-98. doi:10.1016/j.jembe.2011.08.008.

Daigle, R.M., Chasse, J., and Metaxas, A. 2015. The relative effect of behaviour in larval dispersal in a low energy embayment. Progress in Oceanography 144: 93-117.

Daigle, R.M., Chassé, J., and Metaxas, A. 2016. The relative effect of behaviour in larval dispersal in a low energy embayment. Prog. Oceanogr. 144: 93-117. doi:10.1016/j.pocean.2016.04.001.

Daigle, R.M., Monaco, C.J., and Elgin, A.K. 2017. An adaptable toolkit to assess commercial fishery costs and benefits related to marine protected area network design. F1000Res. 4. doi:10.12688/f1000research.7312.2.

Daigle, R.M., Metaxas, A., Balbar, A., McGowan, J., Treml, E.A., Kuempel, C.D., Possingham, H.P., and Beger, M. 2018. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. bioRxiv. doi:10.1101/315424.

Dambach, J., Raupach, M.J., Leese, F., Schwarzer, J., and Engler, J.O. 2016. Ocean currents determine functional connectivity in an Antarctic deep-sea shrimp. Marine Ecology 37(6): 1336-1344.

Department of Fish and Wildlife, M.R. 2017. North Coast Marine Protected Area Monitoring Plan.

Devillers, R., Pressey, R.L., Grech, A., Kittinger, J.N., Edgar, G.J., Ward, T., and Watson, R. 2015. Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? Aquatic Conservation: Marine and Freshwater Ecosystems 25: 480-504.

DFO. 2010. Science Guidance on the Development of Networks of Marine Protected Areas (MPAs). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2009/061.

DFO. 2011. Western Component (4Xopqrs5) Pollock Management Strategy Evaluation. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2011/054.

DFO. 2013a. Guidance on the Formulation of Conservation Objectives and Identification of Indicators, Monitoring Protocols and Strategies for Bioregional Marine Protected Area Networks. Canadian Science Advisory Secretariat Science Advisory Report 2012/081.

DFO. 2013b. Science guidance on how to achieve representativity in the design of marine protected area networks. FO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2012/083.

DFO. 2013c. Monitoring protocols and strategies for selected indicators in the Tarium Niryutait Marine Protected Area (MPA). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2012/061.

DFO. 2015a. Eco-units and potential Priority Conservation Areas in the Western Arctic Bioregion. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2015/021.

DFO. 2015b. Monitoring Indicators, Protocols and Strategies for the Proposed Laurentian Channel Marine Protected Area (MPA). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2014/049.

DFO. 2016. Guidance on Identifying “Other Effective Area-Based Conservation Measures” in Canadian Coastal and Marine Waters. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/002.

DFO. 2017a. Framework for Identification of Ecological Conservation Priorities for Marine Protected Area Network Design and its Application in the Northern Shelf Bioregion. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2017/019. (Errata : October 2018)

DFO. 2017b. Science Guidance on Design Strategies for a Network of Marine Protected Areas in the Newfoundland and Labrador Shelves Bioregion. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2017/046.

DFO. 2017c. Adapting Monitoring Protocols and Strategies for the Gilbert Bay Marine Protected Area. DFO. Can. Sci. Advis. Sec. Sci. Advis. Rep. 2017/021.

DFO. 2018a. Design Strategies for a Network of Marine Protected Areas in the Scotian Shelf Bioregion. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/006.

DFO. 2018b. Units 1+2 Redfish Management Strategy Evaluation. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/033.

DFO. 2019. Design Strategies for the Northern Shelf Bioregional Marine Protected Area Network. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2019/026.

DiBacco, C., and Levin, L.A. 2000. Development and application of elemental fingerprinting to track the dispersal of marine invertebrate larvae. Limnology and Oceanography 45(4): 871-880.

Dickson, B.G., Albano, C.M., Anantharaman, R., Beier, P., Fargione, J., Graves, T.A., Gray, M.E., Hall, K.R., Lawler, J.J., and Leonard, P.B. 2019. Circuit-theory applications to connectivity science and conservation. Conservation Biology 33(2): 239-249.

Doerr, V.A.J., Barrett, T., and Doerr, E.D. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. Journal of Applied Ecology 48(1): 143-147. doi:10.1111/j.1365-2664.2010.01899.x.

Dorenbosch, M., Verberk, W., Nagelkerken, I., and Van der Velde, G. 2007. Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Marine Ecology Progress Series 334: 103-116.

Dunham, A., Mossman, J., Archer, S., Davies, S., Pegg, J., and Archer, E. 2018. Glass Sponge Reefs in the Strait of Georgia and Howe Sound: Status Assessments and Ecological Monitoring Advice. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/010: x + 221 p.

Evans, J.L., Pecket, F., and Howell, K.L. 2015. Combined application of biophysical habitat mapping and systematic conservation planning to assess efficiency and representativeness of the existing High Seas MPA network in the Northeast Atlantic. ICES Journal of Marine Science 72(5): 1483-1497.

Fernandes, L., Green, A., Tanzer, J., White, A., Alino, P., Jompa, J., Lokani, P., Soemodinoto, A., Knight, M., Pomeroy, B., and Possingham, H.P. 2012. Biophysical principles for designing resilient networks of marine protected areas to integrate fisheries, biodiversity and climate change objectives in the Coral Triangle. The Nature Conservancy, Jakarta, Indonesia.

Field, S.A., O'Connor, P.J., Tyre, A.J., and Possingham, H. 2007. Making monitoring meaningful. Austral Ecology 32: 485-491.

Fischer, A., Bhakta, D., Macmillan-Lawler, M., and Harris, P. 2019. Existing global marine protected area network is not representative or comprehensive measured against seafloor geomorphic features and benthic habitats. Ocean & Coastal Management 167: 176-187.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.M., Prahler, E., Rohr, N., Sivas, D., and Beck, M.W. 2010. Guiding ecological principles for marine spatial planning. Marine Policy 34(5): 955-966.

Foster, N.L., Rees, S., Langmead, O., Griffiths, C., Oates, J., and Attrill, M.J. 2017. Assessing the ecological conherence of a marine protected area network in the Celtic Seas. Ecosphere 8(2): e01688.

Frid, A., McGreer, M., Gale, K.S.P., Rubidge, E., Blaine, T., Reid, M., Olson, A., Hankewich, S., Mason, E., Rolston, D., and Tallio, E. 2018. The area-heterogeneity tradeoff applied to spatial protection of rockfish (*Sebastes* spp.) species richness. Conservation Letters 11: e12589.

Friesen, S.K., Martone, R.G., Rubidge, E., Baggio, J.A., and Ban, N.C. 2019. An approach to incorporating inferred connectivity of adult movement into marine protected area design with limited data. Ecological Applications 29(4): e01890.

Fuentes-Pardo, A.P., and Ruzzante, D.E. 2017. Whole-genome sequencing approaches for conservation biology: Advantages, limitations and practical recommendations. Molecular ecology 26(20): 5369-5406.

Fulton, E.A., Bax, N.J., Bustamante, R.H., Dambacher, J., Dichmont, C., Dunstan, P.K., Hayes, K.R., Hobday, A.J., Pitcher, R., Plagányi, É., Punt, A.E., Savina-Rolland, M., Smith, A.D.M., and Smith, D.C. 2015. Modelling marine protected areas: Insights and hurdles. Phil. Trans. R. Soc. B 370: 20140278.

Gagnaire, P.A., Broquet, T., Aurelle, D., Viard, F., Souissi, A., Bonhomme, F., Arnaud-Haond, S., and Bierne, N. 2015. Using neutral, selected, and hitchhiker loci to assess connectivity of marine populations in the genomic era. Evolutionary Applications 8(8): 769-786.

Gaines, S.D., White, C., Carr, M.H., and Palumbi, S.R. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107(43): 18286-18293. doi:10.1073/pnas.0906473107.

Gale, K.S.P., Frid, A., Lee, L., McCarthy, J.-B., Robb, C.K., Rubidge, E., Steele, J., and Curtis, J.M.R. 2019. A framework for identification of ecological conservation priorities for Marine Protected Area network design and its application in the Northern Shelf Bioregion. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/055: viii + 186 p.

Game, E.T., Watts, M.E., Wooldridge, S., and Possingham, H.P. 2008. Planning for persistence in marine reserves: A question of catastrophic importance. Ecological Applications 18(3): 670-680. doi:10.1890/07-1027.1.

Gao, Y., and Beamish, R.J. 2003. Stable isotopic composition of otoliths from tagged Pacific halibut, *Hippoglossus stenolepis*. Environmental Biology of Fishes 67(3): 253-261.

Gao, Y.W., and Beamish, R.J. 1999. Isotopic composition of otoliths as a chemical tracer in population identification of sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 56(11): 2062-2068. doi:10.1139/f99-145.

García Molinos, J., Halpern, Benjamin S., Schoeman, David S., Brown, Christopher J., Kiessling, W., Moore, Pippa J., Pandolfi, John M., Poloczanska, Elvira S., Richardson, Anthony J., and Burrows, Michael T. 2015. Climate velocity and the future global redistribution of marine biodiversity. Nature Climate Change 6: 83. doi:10.1038/nclimate2769.

Gatto, C.R., Rotger, A., Robinson, N.J., and Tomillo, P.S. 2018. A novel method for photo-identification of sea turtles using scale patterns on the front flippers. Journal of Experimental Marine Biology and Ecology 506: 18-24.

George, J.C.C., Zeth, J., Suydam, R., and Clark, C. 2004. Abundance and population trend (1978-2001) of Western Arctic bowhead whales survyed near Barrow, Alaska. Marine Mammal Science 20(4): 755-773.

Gillanders, B.M. 2005. Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuarine Coastal and Shelf Science 64(1): 47-57. doi:10.1016/j.ecss.2005.02.005.

Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S., and Bräger, S. 2012. First evidence that marine protected areas can work for marine mammals. Journal of Applied Ecology 49: 474-480.

Gormley, K.S.G., Porter, J.S., Bell, M.C., Hull, A.D., and Sanderson, W.G. 2013. Predictive habitat modelling as a tool to assess teh change in distribution and extent of an OSPAR priority habitat in an increased ocean temperature scenario: Consequences for marine protected area networks and management. PloS One 8(7): e68263.

Government of Canada. 2011. National Framework for Canada’s Network of Marine Protected Areas. Fisheries and Oceans Canada, Ottawa. 31 p.

Green, B.C., Smith, D.J., Grey, J., and Underwood, G.J.C. 2012. High site fidelity and low site connectivity in temperate salt marsh fish populations: A stable isotope approach. Oecologia 168(1): 245-255.

Gregory, R., Failing, L., Harstone, M., Long, G., McDaniels, T., and Ohlson, D. 2012. Structured decision making: A practical guide to environmental management choices. Wiley-Blackwell, Oxford, UK.

Grorud-Colvert, K., Claudet, J., Carr, M.H., Caselle, J.E., Day, J., Friedlander, A.M., Lester, S.E., Lison de Loma, T., Tissot, B.N., and Malone, D. 2011. Networks - The assessment of marine reserve networks: Guidelines for ecological evaluation. *In* Marine Protected Areas - a multidiscplinary approach. *Edited by* J. Claudet. Cambridge University Press, Cambridge, UK. p. 376 pp.

Grorud-Colvert, K., Claudet, J., Tissot, B.N., Caselle, J.E., Carr, M.H., Day, J.C., Friedlander, A.M., Lester, S.E., de Loma, T.L., Malone, D., and Walsh, W.J. 2014. Marine protected area networks: assessing whether the whole is greater than the sum of its parts. PLoS One 9(8): e102298. doi:10.1371/journal.pone.0102298.

Haggarty, D. 2015. An evaluation of the effectiveness of rockfish conservation areas in British Columbia, Canada. Department of Zoology, University of British Columbia, Vancouver, BC.

Haggarty, D., and Yamanaka, L. 2018. Evaluating Rockfish Conservation Areas in southern British Columbia, Canada using a Random Forest model of rocky reef habitat. Estuarine, Coastal and Shelf Science 208: 191-204.

Hamilton, S.L., Caselle, J.E., Malone, D.P., and Carr, M.H. 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. PNAS 107(43): 18272-18277.

Hammond, P.S., Mizroch, S.A., and Donovan, G.P. 1990. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Cambridge.

Hanski, I. 1982. Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis. Oikos 38(2): 210-221. doi:10.2307/3544021.

Harley, C.D., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S., Rodriguez, L.F., Tomanek, L., and Williams, S.L. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9(2): 228-241. doi:10.1111/j.1461-0248.2005.00871.x.

Hastie, G.D., Barton, T.R., Grellier, K., Hammond, P.S., Swift, R.J., Thompson, P.M., and Wilson, B. 2003. Distribution of small cetaceans within a candidate Special Area of Conservation; implications for management. Journal of Cetacean Research and Management 5(3): 261-266.

Hesslein, R.J., Capel, M.J., Fox, D.E., and Hallard, K.A. 1991. Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River Basin, Canada. Canadian Journal of Fisheries and Aquatic Sciences 48(11): 2258-2265.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., and Moilanen, A. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46(5): 964-969.

Hoie, H., Otterlei, E., and Folkvord, A. 2004. Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). ICES Journal of Marine Science 61(2): 243-251. doi:10.1016/j.icesjms.2003.11.006.

House, C., Redmond, D., and Phillips, M.R. 2017. An assessment of the efficiency and ecological representativity of existing marine resere networks in Wales, UK. Ocean & Coastal Management 149: 217-230.

IPCC (ed). 2007. Climate Change 2007: Impacts, adaptation, and vulnerability. Cambridge University Press.

IPCC. 2018. Summary for Policymakers. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty.

IUCN-WCPA. 2008. Establishing marine protected area networks - making it happen. IUCN World Commission on Protected Areas, National Oceanic and Atmospheric Administration and The Nature Conservancy. Washington, DC. 118 p.

Iverson, S.J., Fisk, A.T., Hinch, S.G., Mills Flemming, J., Cooke, S.J., and Whoriskey, F.G. 2019. The Ocean Tracking Network: Advancing frontiers in aquatic science and management. Canadian Journal of Fisheries and Aquatic Sciences 76(7): 1041-1051. doi:10.1139/cjfas-2018-0481.

Jantke, K., Kuempel, C.D., McGowan, J., Chauvenet, A.L.M., and Possingham, H.P. 2018. Metrics for evaluating representation target achievement in protected area networks. Diversity and Distributions 25: 170-175.

Jeffery, N., DiBacco, C., Wringe, B., Stanley, R., Hamilton, L., Ravindran, P., and Bradbury, I. 2017. Genomic evidence of hybridization between two independent invasions of European green crab (*Carcinus maenas*) in the Northwest Atlantic. Heredity 119(3): 154.

Jeffery, N.W., Bradbury, I.R., Stanley, R.R.E., Wringe, B.F., Van Wyngaarden, M., Lowen, J.B., McKenzie, C.H., Matheson, K., Sargent, P.S., and DiBacco, C. 2018. Genomewide evidence of environmentally mediated secondary contact of European green crab (*Carcinus maenas*) lineages in eastern North America. Evolutionary Applications 11(6): 869-882. doi:doi:10.1111/eva.12601.

Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S., van Oppen, M.J.H., and Willis, B.L. 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28(2): 307-325. doi:10.1007/s00338-009-0469-9.

Kenchington, E., Callery, O., Davidson, F., Grehan, A., Morato, T., Appiott, J., Davis, A., Dunstan, P., Du Preez, C., Finney, J., Gonzalez-Irusta, J.M., Howell, K.L., Knudby, A., Lacharité, M., Lee, J., Murillo, F.J., Beazley, K., Roberts, J.M., Roberts, M., Rooper, C., Rowden, A., Rubidge, E.M., Stanley, R.R.E., Stirling, D., Tanaka, K.R., Vanhatalo, J., Weigel, B., Wooley, S., and Yesson, C. 2019. Use of Species Distribution Modeling in the Deep Sea. Canadian Technical Report of Fisheries and Aquatic Sciences 3296: 86 pp.

Kenchington, T.J. 2013. A monitoring framework for the St. Anns Bank Area of Interest. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/117: vi + 77 p.

Kerr, Q., Fuentes-Pardo, A.P., Kho, J., McDermid, J.L., and Ruzzante, D.E. 2019. Temporal stability and assignment power of adaptively divergent genomic regions between herring (*Clupea harengus*) seasonal spawning aggregations. Ecology and evolution 9(1): 500-510.

Kess, T., Bentzen, P., Lehnert, S.J., Sylvester, E.V., Lien, S., Kent, M.P., Sinclair-Waters, M., Morris, C.J., Regular, P., and Fairweather, R. 2019. A migration-associated supergene reveals loss of biocomplexity in Atlantic cod. Science Advances 5(6): eaav2461.

Kininmonth, S., Weeks, R., Abesamis, R.A., Bernardo, L.P.C., Beger, M., Treml, E.A., Williamson, D., and Pressey, R.L. 2019. Strategies in scheduling marine protected area establishment in a network system. Ecological Applications 29(1): e01820. doi:10.1002/eap.1820.

Kinlan, B.P., and Gaines, S.D. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology 84(8): 2007-2020. doi:10.1890/01-0622.

Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M., and Gattuso, J.-P. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Global Change Biology 19(6): 1884-1896. doi:10.1111/gcb.12179.

Kronlund, A.R., Holt, K.R., Cleary, J.S., and Shelton, P.A. 2014. Current approaches for the provision of scientific advice on the Precautionary Approach for Canadian fish stocks: Section 8 - Management Strategy Evaluation. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/081: v + 26 p.

Krueck, N.C., Ahmadia, G.N., Green, A., Jones, G.P., Possingham, H.P., Riginos, C., Treml, E.A., and Mumby, P.J. 2017. Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecological Applications 27(3): 925-941. doi:10.1002/eap.1495.

Laurel, B.J., and Bradbury, I.R. 2006. "Big" concerns with high latitude marine protected areas (MPAs): Trends in connectivity and MPA size. Canadian Journal of Fisheries and Aquatic Sciences 63(12): 2603-2607.

Le Port, A., Montgomery, J., Smith, A., Croucher, A., McLeod, I., and Lavery, S. 2017. Temperate marine protected area provides recruitment subsidies to local fisheries. Proceedings of the Royal Society B: Biological Sciences 284(1865): 20171300.

Lehnert, S., Kess, T., Bentzen, P., Kent, M., Lien, S., Gilbey, J., Clément, M., Jeffery, N., Waples, R., and Bradbury, I. 2019. Genomic signatures and correlates of widespread population declines in salmon. Nature communications 10: 2996.

Lehnert, S.J., DiBacco, C., Van Wyngaarden, M., Jeffery, N.W., Lowen, J., Sylvester, E.V., Wringe, B.F., Stanley, R.R., Hamilton, L.C., and Bradbury, I.R. 2018. Fine-scale temperature-associated genetic structure between inshore and offshore populations of sea scallop (*Placopecten magellanicus*). Heredity 122(1): 69-80.

Lett, C., Ayata, S.-D., Huret, M., and Irisson, J.-O. 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Progress in Oceanography 87(1-4): 106-113.

Lewison, R.L., Hobday, A.J., Maxwell, S., Hazen, E., Hartog, J.R., Dunn, D.C., Briscoe, D., Fossette, S., O'Keefe, C.E., Barnes, M., Abecassis, M., Bograd, S., Bethoney, N.D., Bailey, H., Wiley, D., Andrews, S., Hazen, L., and Crowder, L.B. 2015. Dynamic Ocean Management: Identifying the Critical Ingredients of Dynamic Approaches to Ocean Resource Management. Bioscience 65(5): 486-498. doi:10.1093/biosci/biv018.

Lilley, R.J., and Unsworth, R.K.F. 2014. Atlantic cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. Global Ecology and Conservation 2(C): 367-377.

Lloyd, M.J., Metaxas, A., and deYoung, B. 2012. Physical and biological factors affect the vertical distribution of larvae of benthic gastropods in a shallow embayment. Marine Ecology Progress Series 464: 135-151. doi:10.3354/meps09872.

Lowen, B., Hart, D.R., Stanley, R.R.E., Lehnert, S.J., Bradbury, I.R., and DiBacco, C. 2019. Assessing effects of genetic, environmental, and biotic gradients in species distribution modelling. ICES Journal of Marine Science *76*(6): 1762-1775.

Lyons, J.E., Runge, M.C., Laskowski, H.P., and Kendall, W.L. 2008. Monitoring in the context of structured decision-making and adapative management. The Journal of Wildlife Management 72(8): 1683-1692.

MacArthur, R.H., and Wilson, E.O. 2001. The theory of island biogeography. Princeton University Press.

Mach, M.E., Wedding, L.M., Reiter, S.M., Micheli, F., Fujita, R.M., and Martone, R.G. 2017. Assessment and management of cumulative impacts in California's network of marine protected areas. Ocean & Coastal Management 137: 1-11.

Magris, R.A., Pressey, R.L., Weeks, R., and Ban, N.C. 2014. Integrating connectivity and climate change into marine conservation planning. Biological Conservation 170: 207-221.

Magris, R.A., Treml, E.A., Pressey, R.L., and Weeks, R. 2016. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography 39(7): 649-664. doi:10.1111/ecog.01507.

Margules, C.R., and Pressey, R.L. 2000. Systematic conservation planning. Nature 405(6783): 243-253.

Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C., and Kendall, W.L. 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. Ecological Applications 19(5): 1079-1090.

Martone, R.G., Oldford, G., McDougall, C., Cristiani, J., Chow, A., Robb, C.K., Rubidge, E., Gale, K.S.P., Chaves, L., Damkjar, E., Mahaux, P., and Ban, S. 2018. Assessing the contribution of established protected areas towards meeting MPA network objectives in the Northern Shelf Bioregion. *In* State of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems in 2017. *Edited by* P.C. Chandler and S.A. King and J. Boldt. pp. 230-235. .

Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B., Teutschel, N.M., Crowder, L.B., Benson, S., Dutton, P.H., Bailey, H., Kappes, M.A., Kuhn, C.E., Weise, M.J., Mate, B., Shaffer, S.A., Hassrick, J.L., Henry, R.W., Irvine, L., McDonald, B.I., Robinson, P.W., Block, B.A., and Costa, D.P. 2013. Cumulative human impacts on marine predators. Nature Communications 4: 2688. doi:10.1038/ncomms3688.

McCoy, E., Burce, R., David, D., Aca, E.Q., Jardy, J., Labaja, J., Snow, S.J., Ponzo, A., and Araujo, G. 2018. Long-term photo-identification reveals the popultaion dynamics and strong site fidelity of adult whale sharks to the coastal waters of Donsol, Philippines. Frontiers in Marine Science 5: 271.

McLeod, E., Salm, R., Green, A., and Almany, J. 2009. Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment 7(7): 362-370. doi:10.1890/070211.

Metaxas, A., and Saunders, M. 2009. Quantifying the "Bio-" Components in Biophysical Models of Larval Transport in Marine Benthic Invertebrates: Advances and Pitfalls. The Biological Bulletin 216(3): 257-272. doi:10.1086/BBLv216n3p257.

Morris, C.J., and Green, J.M. 2014. MPA regulations should incorporate adaptive management: The case of Gilbert Bay Labrador Atlantic cod (*Gadus morhua*). Marine Policy 49(20-28).

Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enriquez, S., Iglesias-Prieto, R., Cherubin, L.M., and Stevens, J.R. 2011. Reserve design for uncertain responses of coral reefs to climate change. Ecology Letters 14(2): 132-140. doi:10.1111/j.1461-0248.2010.01562.x.

Munguía-Vega, A., Sáenz-Arroyo, A., Greenley, A.P., Espinoza-Montes, J.A., Palumbi, S.R., Rossetto, M., and Micheli, F. 2015. Marine reserves help preserve genetic diversity after impacts derived from climate variability: Lessons from the pink abalone in Baja California. Global Ecology and Conservation 4: 264-276.

Nagelkerken, I., Bothwell, J., Nemeth, R., Pitt, J., and Van der Velde, G. 2008. Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (Haemulidae) depends on habitat accessibility. Marine Ecology Progress Series 368: 155-164.

Nijland, W., Reshitnyk, L., and Rubidge, E. 2019. Satellite remote sensing of canopy-forming kelp on a complex coastline: A novel procedure using the Landsat image archive. Remote Sensing of the Environment 220: 41-50.

O'Brien, K., and Whitehead, H. 2013. Population analysis of Endangered northern bottlenose whales on the Scotian Shelf seven years after the establishment of a Marine Protected Area. Endangered Species Research 21(3): 273-284.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P., and Weiss, J.M. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Natl. Acad. Sci. U. S. A. 104(4): 1266-1271. doi:10.1073/pnas.0603422104.

Olds, A.D., Connolly, R.M., Pitt, K.A., and Maxwell, P.S. 2012. Habitat connectivity improves reserve performance. Conservation Letters 5(1): 56-63. doi:10.1111/j.1755-263X.2011.00204.x.

Pelc, R.A., Warner, R.R., Gaines, S.D., and Paris, C.B. 2010. Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences 107(43): 18266-18271. doi:10.1073/pnas.0907368107.

Perry, A.L., Low, P.J., Ellis, J.R., and Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. Science 308(5730): 1912-1915. doi:10.1126/science.1111322.

Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K., Drinkwater, K., Huret, M., and Nash, R.D.M. 2013. Impacts of climate change on the complex life cycles of fish. Fisheries Oceanography 22(2): 121-139. doi:10.1111/fog.12010.

Pineda, J., Hare, J.A., and Sponaugle, S.U. 2007. Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. Oceanography 20(3): 22-39.

Pittman, S.J., Caldow, C., Hile, S.D., and Monaco, M.E. 2007. Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. Marine Ecology Progress Series 348: 273-284.

Pörtner, H.-O., Karl, D.M., Boyd, P.W., Cheung, W.W.L., Lluch-Cota, S.E., Nojiri, Y., Schmidt, D.N., and Zavialov, P.O. 2014. Ocean systems. *In* Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* C.B. Field and V.R. Barros and D.J. Dokken and K.J. Mach and M.D. Mastrandrea and T.E. Bilir and M. Chatterjee and K.L. Ebi and Y.O. Estrada and R.C. Genova and B. Girma and E.S. Kissel and A.N. Levy and S. MacCracken and P.R. Mastrandrea and L.L. White. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. pp. 411-484.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., and Wilson, K.A. 2007. Conservation planning in a changing world. Trends in Ecology & Evolution 22(11): 583-592.

Quinn, B.K., Rochette, R., Ouellet, P., and Sainte-Marie, B. 2013. Effect of temperature on development rate of larvae from cold-water American lobster (*Homarus americanus*). Journal of Crustacean Biology 33(4): 527-536.

Rassweiler, A., Costello, C., Hilborn, R., and Siegel, D.A. 2014. Integrating scientific guidance into marine spatial planning. Proceedings of the Royal Society B 281: 20132252.

Razgour, O., Forester, B., Taggart, J.B., Bekaert, M., Juste, J., Ibáñez, C., Puechmaille, S.J., Novella-Fernandez, R., Alberdi, A., and Manel, S. 2019. Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proceedings of the National Academy of Sciences 116(21): 10418-10423. doi:10.1073/pnas.1820663116.

Record, N., Runge, J.A., Pendleton, D., Balch, W., Davies, K.F., Pershing, A., Johnson, C.J., Stamieszkin, K., Ji, R., and Feng, Z. 2019. Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography 32(2): 162-169.

Riggio, J., and Caro, T. 2017. Structural connectivity at a national scale: Wildlife corridors in Tanzania. PLoS One 12(11): e0187407. doi:10.1371/journal.pone.0187407.

Rilov, G., Mazaris, A.D., Stelzemüller, V., Helmuth, B., Wahl, M., Guy-Haim, T., Mieszkowska, N., Ledoux, J.-B., and Katsanevakis, S. 2019. Adaptive marine conservation planning in the face of climate change: What can we learn from physiological, ecological and genetic studies? Global Ecology and Conservation 17: e00566.

Roberts, C.M., Hawkins, J.P., Fletcher, J., Hands, S., Raab, K., and Ward, S. 2010. Guidance on the size and spacing of marine protected areas in England. Environment Department, University of York, York.

Roff, J.C. 2014. Networks of marine protected areas - the demonstrability dilemma. Aquatic Conservation: Marine and Freshwater Ecosystems 24(1): 1-4.

Rubidge, E., Gale, K.S.P., Curtis, J.M.R., McClelland, E., Feyrer, L., Bodtker, K., and Robb, C. 2016. Methodology of the Pacific Marine Ecological Classification System and its application to the Northern and Southern Shelf Bioregions. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/035: xi + 124 p.

Runge, J.A., Kovach, A.I., Churchill, J.H., Kerr, L.A., Morrison, J.R., Beardsley, R.C., Berlinsky, D.L., Chen, C., Cadrin, S.X., Davis, C.S., Ford, K.H., Grabowski, J.H., Howell, W.H., Ji, R., Jones, R.J., Pershing, A.J., Record, N.R., Thomas, A.C., Sherwood, G.D., Tallack, S.M.L., and Townsend, D.W. 2010. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. 87(1): 251-263. doi:10.1016/j.pocean.2010.09.016.

Ryan, M.R., Killen, S.S., Gregory, R.S., and Snelgrove, P.V.R. 2012. Predators and distance between habitat patches modify gap crossing behaviour of juvenile Atlantic cod (*Gadus morhua*, L. 1758). Journal of Experimental Marine Biology and Ecology 422: 81-87. doi:10.1016/j.jembe.2012.04.017.

Saarman, E., Gleason, M., Ugoretz, J., Airamé, S., Carr, M., Fox, E., Frimodig, A., Mason, T., and Vasques, J. 2013. The role of science in supporting marine protected area network planning and design in California. Ocean & Coastal Management 74: 45-56.

Saenz-Agudelo, P., Dibattista, J.D., Platek, M.J., Gaither, M.R., Harrison, H.B., Nanninga, G.B., and Berumen, M.L. 2015. Seascape genetics along environmental gradients in the Arabian Peninsula: Insights from ddRAD sequencing of anemonefishes. Molecular Ecology 24(24): 6241-6255.

Saura, S., Bastin, L., Battistella, L., Mandrici, A., and Dubois, G. 2017. Protected areas in the world's ecoregions: How well connected are they? Ecological Indicators 76: 144-158. doi:10.1016/j.ecolind.2016.12.047.

Sawaya, N.A., Djurhuus, A., Closek, C.J., Hepner, M., Olesin, E., Visser, L., Kelble, C., Hubbard, K., and Breitbart, M. 2019. Assessing eukaryotic biodiversity in the Florida Keys National Marine Sanctuary through environmental DNA metabarcoding. Ecology and Evolution 9(3): 1029-1040.

Schroeder, S.B., Dupont, C., Boyer, L., Juanes, F., and Costa, M. 2019. Passive remote sensing technology for mapping bull kelp (*Nereocystis luetkeana*): A review of techniques and regional case study. Global Ecology and Conservation 19: e00683.

Selkoe, K., and Toonen, R.J. 2011. Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. Marine Ecology Progress Series 436: 291-305.

Selkoe, K.A., Aloia, C.C., Crandall, E.D., Iacchei, M., Liggins, L., Puritz, J.B., von der Heyden, S., and Toonen, R.J. 2016. A decade of seascape genetics: contributions to basic and applied marine connectivity. Marine Ecology Progress Series 554: 1-19.

Shah, V.B., and McRae, B. 2008. Circuitscape, a tool for landscape ecology. SciPy Conference California: 62-66.

Shanks, A.L. 2009. Pelagic larval duration and dispersal distance revisited. The Biological Bulletin 216(3): 373-385. doi:10.1086/bblv216n3p373.

Shanks, A.L., Grantham, B.A., and Carr, M.H. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13(sp1): 159-169. doi:10.1890/1051-0761(2003)013[0159:pddats]2.0.co;2.

Silva, M.A., Borrell, A., Prieto, R., Gauffier, P., Bérubé, M., Palsbøl, P.J., and Colaço, A. 2019. Stable isotopes reveal winter feeding in different habitats in blue, fin and sei whales migrating through the Azores. Royal Society Open Science 6(8): 181800.

Simard, Y., Roy, N., Giard, S., and Aulanier, F. 2019. North Atlantic right whale shift to the Gulf of St. Lawrence in 2015, revealed by long-term passive acoustics. Endangered Species Research 40: 271-284.

Sinclair-Waters, M., Bentzen, P., Morris, C.J., Ruzzante, D.E., Kent, M.P., Lien, S., and Bradbury, I.R. 2018. Genomic tools for management and conservation of Atlantic cod in a coastal marine protected area. Canadian Journal of Fisheries and Aquatic Sciences 75(11): 1915-1925.

Smith, J., and Metaxas, A. 2018. A decision tree that can address connectivity in the design of Marine Protected Area Networks (MPAn). Marine Policy 88: 269-278.

Smith, S.J., and Campana, S.E. 2010. Integrated stock mixture analysis for continous and categorical data, with application to genetic-otolith combinations. Canadian Journal of Fisheries and Aquatic Sciences 67(10): 1533-1548. doi:10.1139/f10-078.

Sorochan, K.A., Plourde, S., Morse, R., Pepin, P., Runge, J., Thompson, C., and Johnson, C.L. 2019. North Atlantic right whale (*Eubalaena glacialis*) and its food: (II) interannual variations in biomass of Calanus spp. on western North Atlantic shelves. Journal of Plankton Research 41(5): 687-708.

Soykan, C.U., and Lewison, R.L. 2015. Using community-led metrics to monitor the effects of marine protected areas on biodiversity. Conservation Biology 29(3): 775-783.

Stanley, R.R.E., de Young, B., Snelgrove, P.V.R., and Gregory, R.S. 2013. Factors regulating early life history dispersal of Atlantic cod (*Gadus morhua*) from coastal Newfoundland. PloS One 8(9): e75889.

Stanley, R.R.E., Bradbury, I.R., DiBacco, C., Snelgrove, P.V.R., Thorrold, S.R., and Killen, S.S. 2015a. Environmentally mediated trends in otolith composition of juvenile Atlantic cod (*Gadus morhua*). ICES Journal of Marine Science 72(8): 2350-2363. doi:10.1093/icesjms/fsv070.

Stanley, R.R.E., Belley, R., Snelgrove, P.V.R., Morris, C.J., Pepin, P., and Metaxas, A. 2015b. A critical review of monitoring needs and strategies for marine protected areas and areas of interest in Newfoundland and Labrador. Ecosystems Management Publication Series, Newfoundland and Labrador Region 001: 192 p.

Stanley, R.R.E., Bradbury, I.R., DiBacco, C., Thorrold, S.R., Snelgrove, P.V.R., Morris, C.J., Gregory, R.S., and Campana, S. 2016. Spatial variation in otolith geochemistry of juvenile Atlantic cod, *Gadus morhua*, in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences.

Stanley, R.R.E., DiBacco, C., Lowen, B., Beiko, R.G., Jeffery, N.W., Van Wyngaarden, M., Bentzen, P., Brickman, D., Benestan, L., Bernatchez, L., Johnson, C., Snelgrove, P.V.R., Wang, Z., Wringe, B.F., and Bradbury, I.R. 2018. A climate-associated multispecies cryptic cline in the northwest Atlantic. Science Advances 4(3). doi:10.1126/sciadv.aaq0929.

Staveley, T.A.B., Perry, D., Lindborg, R., and Gullström, M. 2017. Seascape structure and complexity influence temperate seagrass fish assemblage composition. Ecography 40(8): 936-946. doi:10.1111/ecog.02745.

Stortini, C.H., Shackell, N.L., Tyedmers, P., and Beazley, K. 2015. Assessing marine species vulnerability to projected warming on the Scotian Shelf, Canada. ICES Journal of Marine Science 72(6): 1731-1743.

Strong, A.L., Kroeker, K.J., Teneva, L.T., Mease, L.A., and Kelly, R.P. 2014. Ocean Acidification 2.0: Managing our Changing Coastal Ocean Chemistry. BioScience 64(7): 581-592. doi:10.1093/biosci/biu072.

Sunday, J.M., Calosi, P., Dupont, S., Munday, P.L., Stillman, J.H., and Reusch, T.B.H. 2014. Evolution in an acidifying ocean. Trends in Ecology & Evolution 29(2): 117-125.

Sylvester, E.V., Beiko, R.G., Bentzen, P., Paterson, I., Horne, J.B., Watson, B., Lehnert, S., Duffy, S., Clément, M., and Robertson, M.J. 2018. Environmental extremes drive population structure at the northern range limit of Atlantic salmon in North America. Molecular Ecology 27(20): 4026-4040.

Thorrold, S.R., Latkoczy, C., Swart, P.K., and Jones, C.M. 2001. Natal homing in a marine fish metapopulation. Science 291(5502): 297-299. doi:10.1126/science.291.5502.297.

Tittensor, D.P., Berger, M., Boerder, K., Boyce, D.G., Cavanagh, R., Cosandey-Godin, A., Ortuño Crespo, G., Dunn, D., Ghiffary, W., Grant, S.M., Hannah, L., Halpin, P.N., Harfoot, M., Heaslip, S.G., Jeffery, N.W., Kingston, N., Lotze, H.K., McLoed, E., McGowan, J., McOwen, C., O'Leary, B.C., Schiller, L., Stanley, R.R.E., Westhead, M.C., Wilson, K., and Worm, B. 2019. Integrating climate adaptation and conservation of biodiversity in the global ocean. Science Advances 5(11): eaay9969.

Truelove, N.K., Kough, A.S., Behringer, D.C., Paris, C.B., Box, S.J., Preziosi, R.F., and Butler, M.J. 2017. Biophysical connectivity explains population genetic structure in a highly dispersive marine species. Coral Reefs 36(1): 233-244.

Tulloch, V.J.D., Tulloch, A.I.T., Visconti, P., Halpern, B.S., Watson, J.E.M., Evans, M.C., Auerbach, N.A., Barnes, M., Beger, M., Chadès, I., Giakoumi, S., McDonald-Madden, E., Murray, N.J., Ringma, J., and Possingham, H.P. 2015. Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Frontiers in Ecology and the Environment 13(2): 91-99.

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R.S., Berggren, P., Durban, J., Eguchi, T., Rayment, W., and Hammond, P.S. 2015. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. Marine Mammal Science 31: 298-321. doi:10.1111/mms.12141.

Van Wyngaarden, M., Snelgrove, P.V., DiBacco, C., Hamilton, L.C., Rodríguez-Ezpeleta, N., Jeffery, N.W., Stanley, R.R., and Bradbury, I.R. 2017a. Identifying patterns of dispersal, connectivity and selection in the sea scallop, *Placopecten magellanicus*, using RAD seq-derived SNP s. Evolutionary Applications 10(1): 102-117.

Van Wyngaarden, M., Snelgrove, P.V.R., DiBacco, C., Hamilton, L.C., Rodríguez-Ezpeleta, N., Jeffery, N.W., Stanley, R.R.E., and Bradbury, I.R. 2017b. Identifying patterns of dispersal, connectivity and selection in the sea scallop, Placopecten magellanicus, using RADseq-derived SNPs. Evolutionary Applications 10(1): 102-117. doi:10.1111/eva.12432.

Virtanen, E.A., Viitasalo, M., Lappalainen, J., and Moilanen, A. 2018. Evaluation, gap analysis, and the potential expansion of the Finnish marine protected area network. Frontiers in Marine Science 5: 402.

Wang, Z., Lu, Y.Y., Greenan, B., Brickman, D., and DeTracey, D. 2018. BNAM: An eddy-resolving North Atlantic Ocean model to support ocean monitoring. Canadian Technical Report of Hydrography and Ocean Sciences 327: 25.

White, J.W., Schroeger, J., Drake, P.T., and Edwards, C.A. 2014. The Value of Larval Connectivity Information in the Static Optimization of Marine Reserve Design: Connectivity in marine reserve optimization. Conservation Letters 7(6): 533-544. doi:10.1111/conl.12097.

Whitehead, H., Gowans, S., Faucher, A., and Mccarrey, S.W. 1997. Population analysis of northern bottlenose whales in the Gully, Nova Scotia. Marine Mammal Science 13(2): 173-185.

Whitney, C., and Conger, T. 2019. Northern Shelf Bioregion climate change assessment: Projected climate changes, sectoral impacts, and recommendations for adaptation strategies across the Canadian North Pacific coast. MarXiv.

Wiens, J.J., and Graham, C.H. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology, Evolution, and Systematics 36(1): 519-539. doi:10.1146/annurev.ecolsys.36.102803.095431.

Wimmer, T., and Whitehead, H. 2004. Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters. Canadian Journal of Zoology 82(11): 1782-1794.

Woodroffe, R., and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. Science 280(5372): 2126-2128. doi:10.1126/science.280.5372.2126.

Worboys, G.L. 2010. The connectivity conservation imperative. *In* Connectivity Conservation Management. Routledge. pp. 33-51.

Wringe, B., Anderson, E.C., Jeffery, N.W., Stanley, R.R.E., and Bradbury, I.R. 2018. Development and evaluation of SNP panels for the detection of hybridization between wild and escaped Atlantic salmon (*Salmon salar*) in the western Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 76(5): 695-704.

Xuereb, A., Benestan, L., Normandeau, É., Daigle, R.M., Curtis, J.M.R., Bernatchez, L., and Fortin, M.-J. 2018. Asymmetric oceanographic processes mediate connectivity and population genetic structure, as revealed by RADseq, in a highly dispersive marine invertebrate (*Parastichopus californicus*). Molecular Ecology 27(10): 2347-2364. doi:10.1111/mec.14589.

Xuereb, A., D’Aloia, C.C., Daigle, R.M., Andrello, M., Dalongeville, A., Manel, S., Mouillot, D., Guichard, F., Côté, I.M., and Curtis, J.M. 2019. Marine Conservation and Marine Protected Areas. *In* Population Genomics: Marine Organisms. *Edited by* M. Oleksiak and O. Rajora. Springer, Cham. pp. 423-446.

Young, M., and Carr, M.H. 2015. Assessment of habitat representation across a network of marine protected areas with implications for the spatial design of monitoring. PloS One 10(3): e0116200.