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A decision tree that can address connectivity in the design of Marine Protected Area Networks (MPAn)

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ABSTRACT

A marine protected area (MPA) is an area of the ocean designated for the conservation and protection of natural or cultural resources. MPAs are spatial tools used to preserve the ecological integrity and biodiversity of an area, protecting ecosystem functions, species and habitats for future generations. In 2015, the Canadian government committed to increasing protection of its coastal and marine areas up to 10% by 2020. To reach this goal, the Federal Department of Fisheries and Oceans (DFO) is currently in the process of designing and implementing a network of MPAs in the Maritimes Region, on the Atlantic coast of Canada. The design process needs to consider population connectivity, which in turn requires an understanding of life-histories for target species (i.e. the movement of adults and the dispersal of larval life-stages). The population parameters that repeatedly emerge as necessary for deriving estimates of MPA dimensions include the spatial distribution of the conservation priority (species or habitat), movement patterns and oceanographic processes. A decision tree was developed that uses information on species larval dispersal, and juvenile, and adult movement to provide guidelines that can inform definition of size and spacing of individual MPAs in a network. Case studies of species targeted for protection on the Scotian Shelf are presented, to illustrate its use. The decision tree can be used as a tool to help design networks that ensure population connectivity where there is a paucity of biological information, or as a quality control method for assessing other spatial design tools.

1. Introduction

Ocean ecosystems are facing increasing pressures and multiple human induced stressors through warming, acidification, habitat loss, invasive species and unsustainable extraction of natural resources [21]. Recognition of the potential impacts of these threats has called increased attention to the urgency of effective conservation of coastal and marine areas. Many tools and approaches can be used to conserve marine ecosystems, including spatial tools of protection. Marine protected areas (MPAs) are the most commonly used spatial approach to protect marine ecosystems and ensure their resilience to the multiple stressors they currently face. MPAs are clearly defined geographic locations that are identified, dedicated and managed, through legal or other means, with the goal of achieving the conservation of ecosystems and their associated services, as well as the cultural values associated with a particular area [36]. MPAs generally address two overarching objectives, to preserve the biodiversity of an area, and manage fisheries [57]. Benefits derived from MPAs include increased population density, biomass, size and diversity for the target species, as well as recovery of marine life from disturbance and restoration of depleted fisheries [31,36,58,59].

MPAs can be effective tools for ecosystem protection if they consider basic ecological principles and set clear conservation goals [66]. For ecological protection, MPAs aim for the conservation of marine populations, communities or ecosystems [12]. The criteria for the selection of suitable MPA sites include (i) the protection of critical habitats or ecologically sensitive or unique ecosystems; (ii) adequate size; (iii) adequate shape; (iv) representation of the full range of biodiversity of the environment; and (v) replication to safeguard against disturbance [10,51].

The benefits afforded by MPAs generally increase with size [26]. However, large MPAs may not be socially or politically feasible to establish [36] and single MPAs, irrespective of size, may not be effective at maintaining viable, self-sustaining populations of some species [25]. Thus, efforts for designing effective MPAs have shifted focus from establishing individual MPAs to networks of MPAs (MPAn). These MPAn are a collection of single MPAs that offer a variety of protection benefits, but synergistically meet conservation objectives that are greater than what a single MPA could achieve independently [36]. The design of MPAn has the additional criterion that the individual MPAs must be

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spatially connected (i.e. allow for connections between spatially distinct areas). Spatial connectivity might occur at different scales where individual MPAs must allow for either population, genetic, community or ecosystem connectivity [12].

A species' range may span a large geographic area, with the entire population being divided into subpopulations, representing a metapopulation. Population connectivity is the rate of exchange of individuals among geographically separated subpopulations and plays a fundamental role in ensuring population resilience to disturbance and in maintaining genetic diversity, particularly in the face of climate change [19,48,51,53,55,58,59,67]. Exchange of individuals can occur either through movement of mobile adults and juveniles, or dispersal of larvae [61]. Most marine benthic species have complex life cycles which entail a sessile or near-sessile adult and a dispersive larval stage [19,20,28]. Larval dispersal, the transport of larvae from the site where they were produced to the site where they settle and metamorphose, is often used as a measure of population connectivity in marine benthic systems [15,18–20,28]. Measuring the extent of larval dispersal can be challenging [41]; it can be estimated from measures of genetic structure [60] and parentage analysis [15,6] or inferred from the length of time larvae spend in the water column (larval duration) and the physical processes that transport them (i.e. advection by currents) [18,69].

Because the data required to measure connectivity are difficult to acquire and the information needed to derive these estimates is lacking, connectivity has been rarely considered explicitly in MPA design to date [43]. Instead, to address connectivity in the design process, consideration of the size and spacing of individual MPAs is used as an alternative approach [48,54]. Several guiding documents for establishing MPAs and MPAn have been published, suggesting minimum and maximum sizes to allow for adequate protection within a single MPA and minimum spacing distances to allow for ecological connectivity. These documents outline general rules of thumb, based on distances of larval dispersal derived in 1–2 studies, and almost all recommend values that are not species- or region-specific (for e.g. see [56,74,13,37,66,10,48,45]). However, an effective network design must consider the species and oceanographic processes particular to an area under consideration for protection to derive appropriately sized and adequately spaced MPAs [15,18]. This requires knowledge of distributions of species or features in the target area, species' life-histories and population parameters. In all cases, a trade-off must be reached between the size of individual MPAs that ensures self-recruitment and population viability and the number of MPAs in a network that ensures population connectivity and metapopulation resilience to perturbations.

Conservation objectives vary across MPAs and their designs must reflect these objectives. In particular, the overall objective of the MPA will influence how MPA size and spacing should be considered. For example, designs will vary depending on the mobility of the target species, and between conserving single or multiple species in an area. If data are available for all species, connectivity matrices may be constructed and optimization software can identify the best spatial design for protecting multi-species connectivity [22]. When there is a lack of scientifically-derived information, applying general rules of thumb to MPAn design could be a starting point for making management decisions [13]. However, efforts to encompass multiple species may overlook important ecological processes that occur at different scales for different species. To ensure that the network will adequately perform its overall objective, the design process needs to carefully consider each species or ecological processes specific to that region and be scientifically-informed. An approach is needed in order to streamline the design process.

Given the urgency to protect global marine resources, the UN Convention on Biological Diversity (CBD) has set a goal for its ratifying countries to increase protection of their marine and coastal areas to 10% by 2020. This is known as Aichi Target 11. The Canadian government has set an interim national target to protect 5% of its internal, coastal and marine waters and territorial seas in its Exclusive Economic Zone (EEZ) by the end of 2017, and 10% by 2020 to meet Aichi Target 11 [24]. Globally, approximately 3% of the total ocean is currently protected, with 7% protection occurring in EEZs [49]. To reach their goals, the Canadian government is in the process of implementing a network of MPAs in the coastal and marine areas in Atlantic Canada [40]. This implementation provides this study with an opportunity to develop a simplified approach that can be used by marine managers to inform decisions on adequate size and spacing of MPAs included in a network.

In this study, an approach for MPAn design was developed that incorporates connectivity, through sizing and spacing of individual MPAs, into a network design. It focuses on a subset of species and habitats targeted for protection by the Canadian Department of Fisheries and Oceans (DFO) in the Maritimes region, on the Atlantic coast of Canada, as case studies. A review of available information identified the pertinent population parameters that repeatedly emerge as necessary for deriving estimates of MPA dimensions and spacing. Based on the necessary considerations for designing adequately sized and spaced MPAs, a set of general guidelines were developed that could be used to incorporate connectivity in a regional network design. The aim was to make these guidelines broad enough so that they can be used in any geographic location, and for a range of conservation priorities and targets.

2. Methods

DFO-Maritimes (Oceans Branch) is currently in the process of establishing a network of MPAs in the Maritimes Region on the Canadian east coast, encompassing the coastal and offshore waters of the Scotian Shelf, referred to as the Scotian Shelf Bioregion (Fig. 1). To achieve this, they have identified priorities for conservation, determined the amount of protection for each conservation priority (CP), and have set targets for achieving these levels of protection [40]. DFO-Maritimes defines CPs as individual populations or species, a group of species, habitats, communities, or ecological processes (e.g. productivity) or other ecological features to be conserved by an MPA network (MPAn). CPs are classified as coarse-filter features (e.g. broad-scale seascapes, ecosystems or habitats) or fine-filter features (e.g. individual species or small scale ecological features). The conservation objectives and targets for an MPA will vary with the CP, and depending on those, the size and spacing in the MPAn will be based on movement and demographics of the species of concern.

In this study, a subset of CPs was chosen to represent species that fall within a wide range of life-history characteristics and different data availabilities. Species that exhibit a range of motility and life-histories were examined to derive size and spacing recommendations that could be used to, in turn, derive recommendations for other species with similar characteristics, but for which little information is available. Specifically, we selected the highly mobile and widely distributed Atlantic cod (*Gadus morhua*) from the list of 'depleted species'. 'Depleted species' are CPs that identify species with depleted populations in Canada, and for which the primary conservation goal is to increase population size. The list of 'depleted species' includes cetaceans, turtles, sharks and demersal fishes [40]. Atlantic cod (*Gadus morhua*) were chosen to represent a widely-distributed species with mobile adult, larval and juvenile life-history stages, which may occupy spatially separated habitats and for which data on distribution and life-history are available. The term 'biogenic habitats' encompasses species that are important habitat formers on the Scotian Shelf, generally have sessile adults and dispersing larvae, and may have either spatially limited or wide distributions. From the list of 'biogenic habitats', those for which distribution and life-histories are relatively well known (or predicted) from our region and elsewhere were selected, such as large gorgonian corals (*Octacorallia*), soft coral gardens (*Alcyonacea*), reef-building corals (*Lophelia pertusa),* sea pen fields (*Pennatulacea*), and

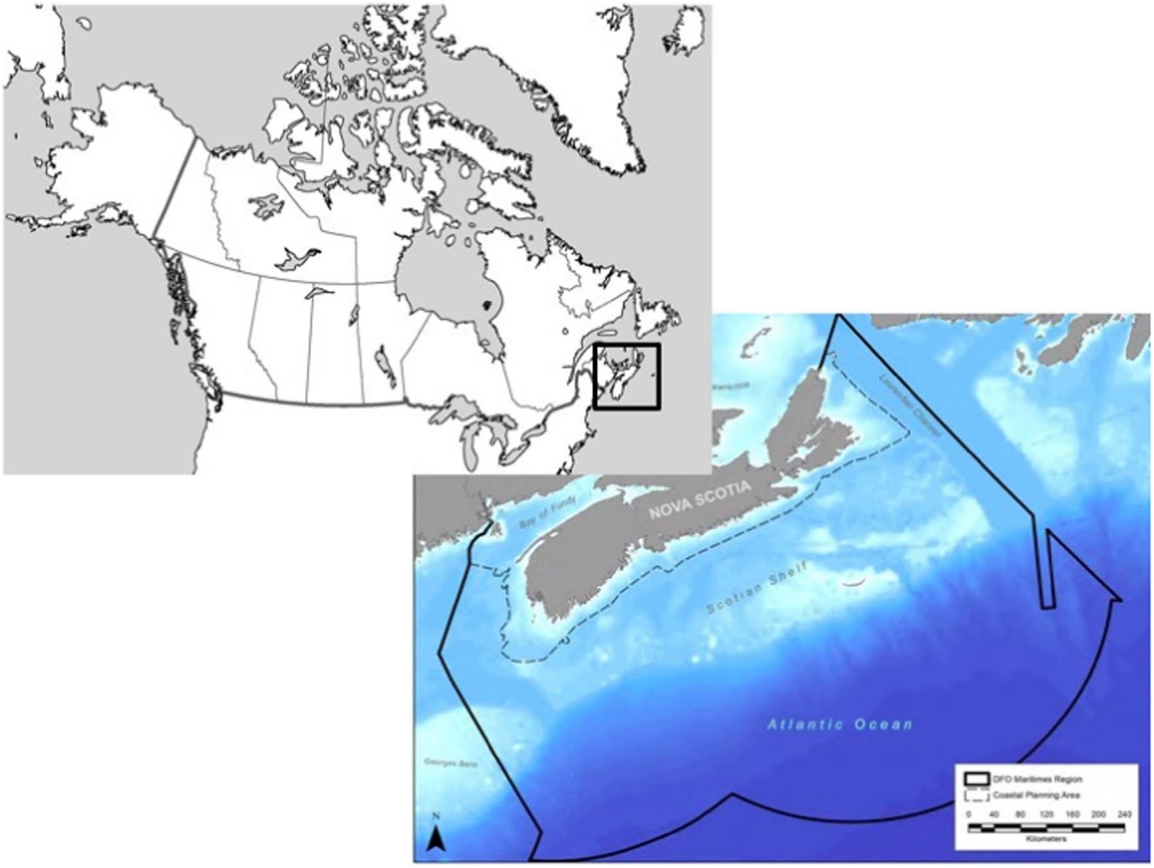


Fig. 1. Map of the Scotian Shelf Bioregion and its location on the east coast of Canada. The outlined area is the boundary of the spatial planning region of the DFO-Maritimes (Ocean Branch). Scotian Shelf map from DFO.

Russian hat sponges (*Vazella pourtalesi*).

For each CP, we synthesized the literature for available data on species distribution and areas occupied by different life-stages, size of adult home range, and range of larval dispersal or of movement by another life-history stage (Table S1). Sources included peer-reviewed scientific publications, governmental reports, and previously-produced species distribution maps (Table S1). To determine the range of larval dispersal, we extracted data on larval duration (Table S1), mean current velocities, and retention times within minor ocean gyres for some of the offshore banks of the Scotian Shelf (Table S2; Table S3). We used information from the Scotian Shelf whenever available; if not available for this region or target species, we used another area for the same or a similar species.

Based on the collated information for the CPs (Table S4; Table S5), illustrations of the distribution of populations of some CPs, as well as potential connections between populations, were generated. These data allowed us to identify the necessary parameters to derive appropriate size and spacing rules for individual MPAs in a network for different combinations of spatial distributions and life-histories. A decision tree was designed based on these different combinations to guide the selection of size and spacing of individual MPAs. For a particular CP, the tree proceeds systematically through: (1) identification of a location that should be considered for conservation; (2) consideration of size of the MPA, based on life-history information; (3) identification of life-history attributes that inform connectivity; (4) consideration of spacing of MPAs in a network, informed by distance measures; and (5) determination of the trade-offs between size and spacing.

3. Results

Overall, the population parameters to consider when appropriately sizing and spacing individual MPAs vary depending on the species chosen as the conservation priority (CP) and the conservation objective of the MPA. The number of life-history attributes to consider ranged from few as for the Russian Hat sponges, to many as for the Atlantic cod. For each of the conservation priorities, the guidelines for size and spacing of individual MPAs depend on the location of important areas, life-history and oceanographic processes. The details of selected cases are provided below.

3.1. *Case studies*

3.1.1. *Atlantic cod – Gadus morhua*

Areas identified for Atlantic cod on the Scotian Shelf include the Bay of Fundy, Georges

Bank, Browns Bank, Emerald/Western/Sable Island Bank Complex, the Gully, Banquereau, Misaine Banks and Sydney Bight in the Laurentian Channel (Fig. 2). Adult Atlantic cod are broadcast spawners, releasing eggs and sperm into the water column. Fertilized eggs develop into passive larvae that drift in the plankton for an average of ~90 days ([34,7]; Table S4).

3.1.1.1. Adult cod. Based on their genetic structure, cod on the Western Scotian Shelf are divided into distinct populations from Georges Bank, Browns Bank and the Bay of Fundy (Fig. 2). These populations are also distinct from those on the eastern banks of the Scotian Shelf, such as Western and Banquereau Bank, which show lower levels of differentiation [65]. The genetic structure suggests that, for most populations, the movement of adults is limited to the banks where they are located, with occasional exchange between areas. For example, some adults appear to move from Georges Bank into the Bay of Fundy in summer and return in autumn [78], generating possible connections.

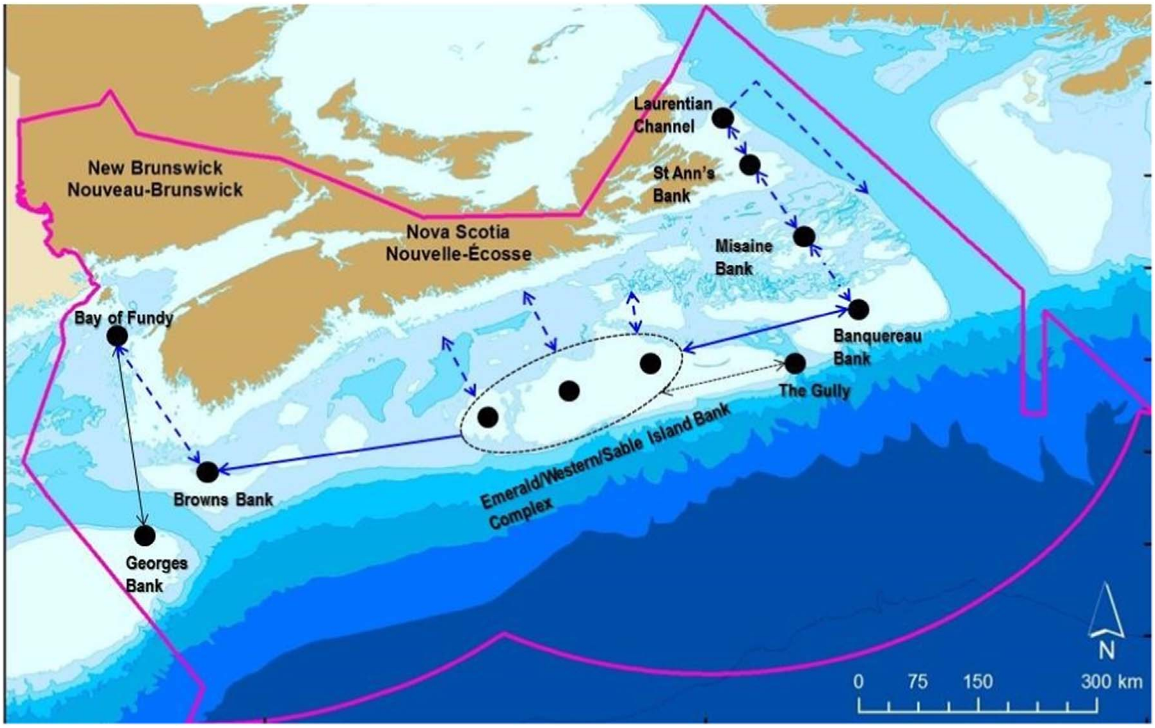


Fig. 2. Distribution of identified important areas for the Scotian Shelf Atlantic cod populations (black dots). Emerald, Western and Sable Island Banks are generally considered as a complex and an important offshore spawning area (dashed circle). Solid black arrows indicate connections between areas, based on adult cod movement, confirmed by the literature. Lighter arrows indicate connections between areas that are maintained by larval dispersal based on confirmed observations of larval exchange (solid) or presumed from studies on particle tracking (dashed). Base map of Scotian Shelf Bioregion (outline) taken from DFO.

However, cod on Georges Bank, despite their proximity to Browns Bank, show no mixing of spawning products or adult migration and thus no connections with that population [65].

3.1.1.2. Spawning areas. On the Scotian Shelf, the offshore banks show persistent egg and larval concentrations [65], indicating spawning areas. Although linear dispersal distances could be large (on the scale of hundreds to thousands of km) (Table S4), larval dispersal may be limited by the retentive dynamics on offshore banks due to gyres [17]. Residence times within the gyre on a bank can range between 5 and 50 days (Table S3) and for larval cod, the spatial scale of larval retention of some banks can range between 50 and 80 km (Table S4). These scales are much smaller than the estimated linear dispersal distances.

3.1.1.3. Juvenile nursery areas. Larval cod metamorphose to demersal juveniles, known to settle in benthic environments with structural complexity, such as gravel, pebbles or boulders [1]. Juvenile nursery habitats provide protection from predators and can influence juvenile survival [77]. Nurseries may be critical in maintaining some of the offshore adult stocks [50]. Although juvenile home ranges are not well resolved for the Scotian Shelf, in Newfoundland they range between 545.3 and 2581.6 m^2 [16] and 3.47 km^2 [70].

3.1.1.4. Connections between areas. Cod from the Scotian Shelf have both offshore and inshore adult spawning aggregations [35], and juveniles can settle in both nearshore and offshore nurseries [1]. If spawned on banks where there are strong retentive dynamics, the adult, larval and juvenile distributions may coincide [47]. In this case, connections between areas occupied by different life-stages are likely not strong. However, areas occupied by different life-stages may be spatially separated, and connections between areas occupied by different life-stages likely exist. For example, on the Eastern Scotian Shelf, the Emerald/Western/Sable Island Bank complex, is one main offshore spawning area [62] (Fig. 2), which has a retentive gyre. However, neighbouring areas are also identified as important juvenile areas, such as Middle Bank, Sable Island, Emerald Bank, Misaine Bank as well as Banquereau and the Gully [62,72]. This spawning complex may be the source for the juvenile populations, and these offshore areas may be connected by larval dispersal. Also, it seems that cod juveniles are usually found in nearshore nurseries (Clark D, pers. comm.), but they may have been spawned offshore. For example, in the Gulf of St-Lawrence, there is a distinct adult spawning aggregation identified in Sydney Bight [23] and coastal juvenile areas, such as the Bird Islands, are identified as important nurseries [9]. For juveniles to occupy their inshore areas, larval dispersal likely connects offshore spawning areas with inshore nurseries.

3.1.2. Habitat forming invertebrates

Sponges *(Porifera)* are broadly distributed along the Scotian Shelf, but the only identified significant concentration of Russian Hat sponges (*Vazella pourtalesi*) occurs in the Emerald Basin [38,39,5]. Sessile adults release larvae into the water, and larval duration is ~1 day ([57]; Table S5), with larvae likely settling within or near the adult populations [27].

Large gorgonian corals (Octacorallia) show a fragmented distribution on the Scotian Shelf, with significant concentrations, mostly identified in canyons along the shelf edge (Fig. 3). The life-history of large gorgonian corals includes a sessile adult stage, which releases planktonic larvae into the water column. With larval durations of ~60 days ([63]; Table S5) the larvae can be advected by the shelf-edge current (Fig. 3). As this is a linear current, larval duration and the mean current velocity (4.3 km day^{-1}) can be used to determine potential larval dispersal distance which can be estimated as up to 260 km.

Soft coral gardens of Alcyonacea are similar to those of large gorgonian corals in terms of life-history and distribution. Stationary adults release larvae that remain in the plankton for up to 30 days ([76]; Table S5). Significant concentrations are mainly found along the shelf edge, where the current can potentially advect larvae away from the sessile

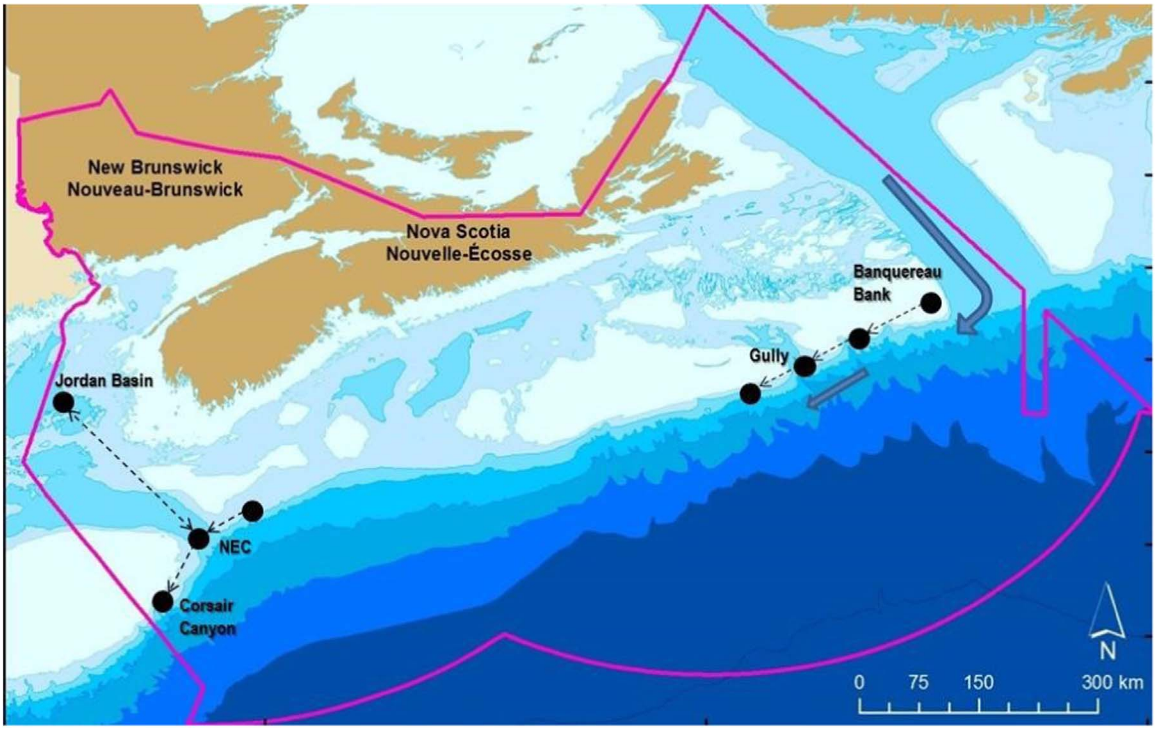


Fig. 3. Distribution of significant concentrations of large gorgonian coral (Octacorallia) populations (black dots). Dashed arrows represent presumed connections between populations based on current velocity. Bold arrows indicate direction of mean currents. NEC stands for Northeast Channel. Map of Scotian Shelf Bioregion (outline) from DFO.

adult populations.

The reef-building coral *Lophelia pertusa* also has a fragmented population and is found on St Ann's Bank, in the *Lophelia* Coral Conservation Area (LCCA), the Gully, as well as other canyons on the edge of the Eastern Scotian Shelf. *Lopehlia pertusa* share life-history characteristics with the other coral groups, in that they are sessile as adults and their larval duration is 15–30 days ([42]; Table S5).

In contrast to the other corals, sea pens (Pennatulacea) are widely distributed, with occurrences of significant concentrations in canyons along the shelf edge, as well as on offshore banks. However, sea pens have short larval durations of ~7 days ([14]; Table S5).

3.2. Decision tree

Based on the information from the subset of the conservation priorities reviewed (Table 1), a decision tree was developed to help inform decisions about appropriate size and spacing of individual MPAs (Fig. 4).

3.2.1. General description of decision tree

The information needed to proceed with the decision tree includes spatial data on the distribution of a conservation priority (CP) (species or feature) which may be derived empirically or from models. If the CP only occurs at a single location, the location should be included within the network in its entirety. The size of the area to be afforded protection will depend on either (1) physical characteristics, such as the presence of a distinct boundary, e.g. an outcrop, a reef or the walls of a canyon; or (2) in the absence of a distinct feature, the range of adult movement or larval dispersal can be used instead, to ensure a self-sustaining population.

The decision tree can be used to help inform size and spacing of MPAs, if the CP occurs at more than one location. The MPAn should aim to protect areas that support the viability of a population or health of the species or feature to be conserved (Fig. 4). For biogenic habitats, areas to be protected should encompass significant concentrations of the habitat engineering species, whereas for other species, the function of an area either as an important habitat or a core area must be identified (Fig. 4, “Type of feature”). The information required to inform the size of the protected area will differ depending on the CP and will be based on knowledge of the life-history characteristics of the target species (Fig. 4, “Size”). For example, if areas are being protected as important habitat for an associated life-stage, such as feeding or mating adults, MPA size should be large enough to accommodate adult movements within those areas [13]. In contrast, if the area is designed to protect a sessile, habitat-forming species, it is suggested that a sufficient size is one that ensures self-recruitment based on larval dispersal. Once size is determined for each single area, spacing of multiple areas can be considered based on life-history attributes that inform connectivity, such as distance and direction of larval dispersal (most simplistically determined by ocean circulation and planktonic larval duration), and range and directionality of juvenile and adult movement (typically measured or inferred empirically) (Fig. 4, “Life-history attributes”). The outcome will depend on whether the population shows a fragmented distribution, but also on the ability of species to move between suitable areas. A minimum spacing should be maintained that reflects the ranges of larval dispersal or adult movement [15,58,59] (Fig. 4, “Spacing”). Based on these data, connections may not necessarily exist among all (or even some) targeted areas. If a given species is not maintained by a metapopulation structure that necessitates connectivity between sub-populations (either linked adult populations or ontogenetic connections), then explicit consideration of connectivity and spacing between MPAs is not relevant. In those instances, consideration should be given to the size of the MPA to ensure the viability of populations. Overall, depending on spatial distribution and life-history characteristics of the CP, considerations of either size of individual MPAs or spacing among MPAs or of both may be required for the design of the network (Fig. 4, “Design considerations”). Ultimately, a trade-off between the two will produce the most efficient solution [30].

Table 1
Summary of the pertinent population parameters and information required for deriving sizing and spacing estimates of individual MPAs and recommendations to accommodate the individual conservation priorities from the case studies of the Scotian Shelf.

Conservation Priority	Information used to inform size	Size recommendation	Information used to inform spacing	Spacing recommendation
Atlantic Cod	If different life-stage distributions overlap: minimum MPA size should be guided by the larger of: (1) the scale of retention or (2) adult movement so that the various life-stages are adequately protected. If the life-stage distributions do not overlap, size should reflect the movement of the life-stage within the area. Use larval dispersal (or scale of retention), juvenile home ranges, adult home ranges	In Western Scotian Shelf: Based on larval retention: radius of 50–80 km; however, based on adult movement the suggestion is 74–111 km. Size should be guided by larger of the two.	Adult movement / Home range Juvenile movement/ Home ranges Larval dispersal- using larval duration and current velocity or scale of retention in gyres	On the Western Scotian Shelf: Adult movement between the offshore banks and (1) the coast of Nova Scotia and (2) Bay of Fundy suggest movement range of: ~100–475 km.
Large Gorgonian Corals (Octacorallia)	Size defined by boundary of significant concentration.	On shelf edge: size likely encompasses entire canyon where aggregations are found	Larval dispersal- using larval duration and current velocity	Minimum spacing of ~260 km to allow for connectivity.
Soft Coral Gardens (Alcyonacea)		Size should encompass aggregation of > 70% of population to ensure viability.		Minimum spacing of ~130 km to allow for connectivity
Reef-Building Corals – (*Lophelia pertusa*)		Size should encompass aggregation of > 70% of population to ensure viability.		Minimum spacing of ~130 km to allow for connectivity
Sea Pea Fields (Pennatulacea)		Size should encompass aggregation of > 70% of population to ensure viability. Minimum radius of ~30 km.		Larval duration is shorter, connectivity may be less important.
Russian Hat Sponges	Minimum size to accommodate larval dispersal/settlement around the population of spawning sedentary adults. Size to boundary of adult population that sustains 70% of population to ensure persistence.	Radius of 5–90 km	Not relevant	

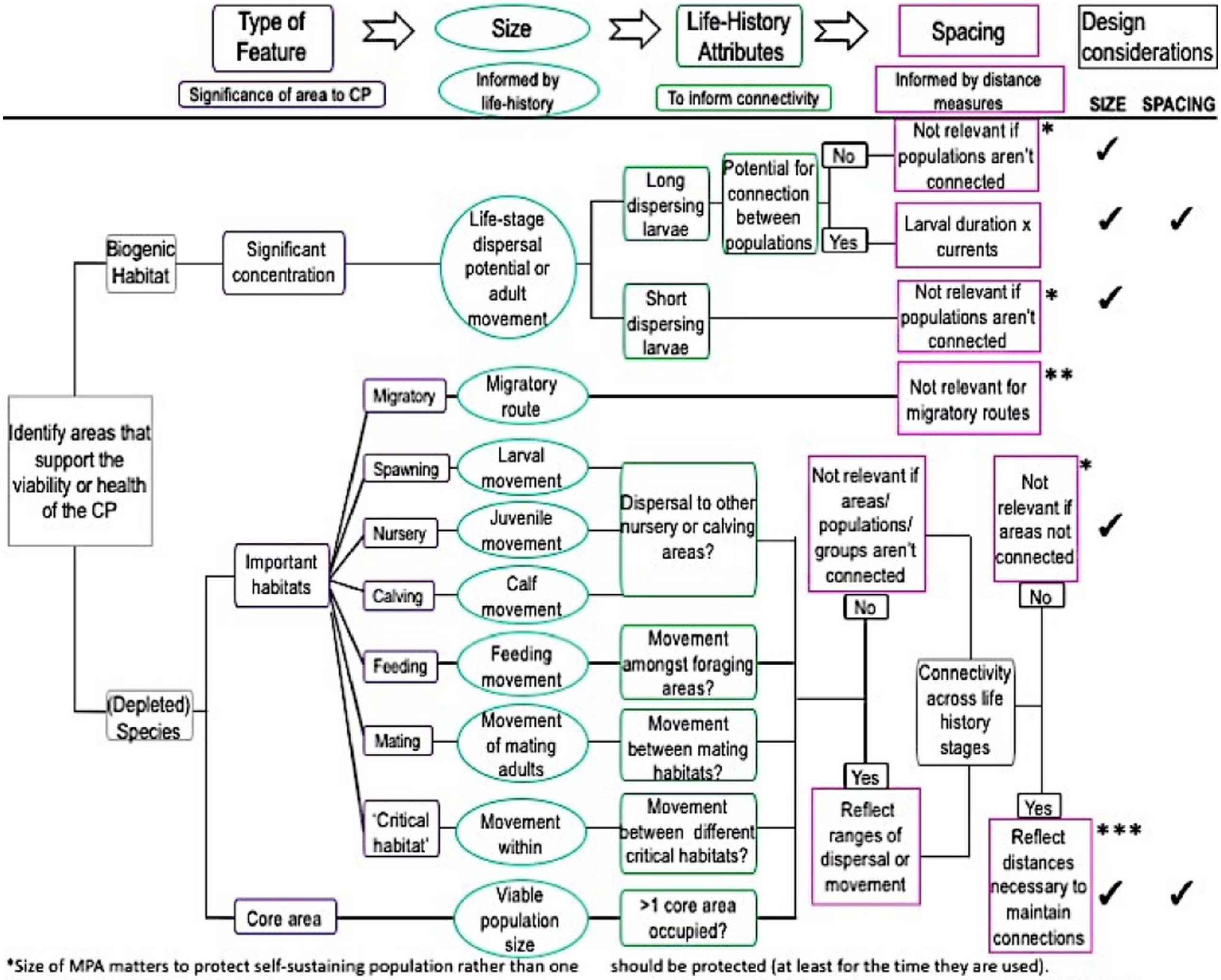
3.2.2. Examples using the decision tree to derive size and spacing recommendations

Species distribution models of Russian Hat sponges indicate that a significant concentration occurs only at a single area, the Emerald Basin [5]. A single MPA would protect the entire known sponge population, and its size should reflect the range of larval dispersal. Using larval duration [44] and the range of current velocities in this area [75], the estimated range of larval dispersal should be 5–90 km (Table S5). Based on the recommendation that size should equal twice the larval dispersal distance [30], the radius for this MPA should be at least 5–90 km (Table S5). The actual MPA size should also capture a large enough proportion of the population to ensure viability (e.g. 70%, []in prep). Because these sponges are known to only exist in one area and have short dispersing larvae, connectivity among MPAs in a network is not considered.

Like sponges, corals and sea pens have sessile adults, but their larvae have a higher dispersal potential than sponge larvae. On the Scotian Shelf, significant concentrations of gorgonians, Alcyonaceans, *L. pertusa* and sea pens occur in more than one area. Due to retentive dynamics in canyons where gorgonian corals are most abundant, the size of the area would be best informed by the boundary outline of the adult population and should likely encompass the entire canyon. Some self-recruitment is possible in some canyons, for example in the Gully, where there is a residence time of 5–30 days [68]. For Alcyonaceans, *L. pertusa* and sea pens, MPAs should be sited in areas where significant concentrations occur. Individual MPAs on the Scotian Shelf should be large enough to maintain viable populations. For sea pens, which have a 7 -day larval duration, larval dispersal distance can define a minimum radius of an MPA equal to ~ 30 km to ensure self-recruitment. However, because of the relatively long larval dispersal periods of the rest of these groups (30–60 days), connectivity between populations distributed along the continental slope, must be considered. To ensure connectivity, MPAs should not be spaced farther than the maximum linear dispersal distance of ~260 km for gorgonian corals, and ~130 km for soft corals and reef-building corals.

Distribution maps for Atlantic cod also show occupancy of more than one area (Fig. 2; [33]). Because cod is considered a depleted species, the areas to conserve are identified as important habitats. Based on genetic distinctness, two networks could be set up, protecting the Western and Eastern Scotian Shelf. On the Western Scotian Shelf, the Bay of Fundy, Browns Bank and Georges Bank (Fig. 2) could each be an individual MPA, with a size that allows for a self-sustaining population. Georges Bank and Browns Bank have been identified as important feeding habitats [35] and this function should be reflected in the size of the area. Adult cod have a range of adult movement estimated at 111 km on Georges Bank and ~ 74 km at Browns Bank ([64]; Table S4). These distances could determine the radius of the MPAs.

These offshore banks, are also important spawning grounds [11,35], and the range of larval dispersal could be used to inform the size, if the objective is to protect spawning activity. At Browns Bank, the presence of a gyre results in a residence time of ~20 days ([71]; Table S3). This is shorter than the 90-day larval duration of cod [34,7], leading to potential larval dispersal away from the bank, as far as 585 km (at an average current velocity of 6.5 km day^{-1}, [11]; Table S4). However, larval retention has been measured on scales of ~80 km [11], allowing self-recruitment at that scale. Similarly, on Georges Bank, the gyre has a residence time of 20–50 days [46], and larval dispersal (at a mean current of 4.32 km day^{-1} [47]) 389 km away from the bank is possible; however, again, the scale of larval retention for this bank has been determined as ~50 km [47]. These realized dispersal distances and retention rates can be used to inform size of an MPA that aims to protect spawning on Browns Bank and Georges Bank. Because both banks are important for both adult and larval life-history stages, the appropriate size would be a trade-off between the scales of movement of each stage. Since the scale of larval retention is smaller than the range of adult movement, the minimum size should reflect adult movement. Thus, a radius of 111 km and 74 km would be appropriate for Georges Bank and



*Size of MPA matters to protect self-sustaining population rather than one sustained via meta-population structure.

**Spacing between migratory areas is not as critical as these are inherently connected by movement through the whole area; extent of route should be protected (at least for the time they are used).

***If areas that support different life-history stages are shown to be connected (e.g. spawning and nursery areas) considering spacing distances between these areas is important.

Fig. 4. Decision tree to guide the sizing and spacing of individual MPAs within a Network of MPAs. The steps involved in and the information used to inform the decision are shown along the top. Some terms (e.g. biogenic habitat, depleted species) were taken from the guiding document for the design of MPAn in the Maritimes in Atlantic Canada [40], but are broadly applicable to other regions. 'Important Habitats' are defined in this case as areas where > 70% probability of occurrence is predicted from species distribution models (based on [40]) but other definitions can be inserted depending on conservation priorities and targets of individual practitioners. Important habitat, for example, may be associated with a particular life-stage. In our case, 'Important Habitats' include 'Critical Habitat', a formally defined area within the geographically occupied area of a species-at-risk in Canada, containing a physical or biological feature essential to their conservation. 'Core Area' applies to mobile species and is defined as the area of highest biomass based on a relative distribution map [in our case, created based on DFO research vessel survey data, as in [40].

Browns Bank, respectively.

Given the potential for dispersal away from the banks, connectivity must also be considered in the design of a MPAn for cod. Georges and Browns Bank are genetically distinct [65], but drift dynamics could allow for connectivity between the offshore banks and the Bay of Fundy [32]. Mixing and adult movement appears to occur between Georges Bank and the Bay of Fundy [78] and larvae displaced from Browns Bank could be entrained in the coastal current, advecting them to the mouth of the Bay of Fundy ([11]; Fig. 2). Additionally, larvae spawned on offshore banks show net shoreward movement [11] and since inshore nursery areas are also important for cod, ontogenetic movement must be considered for connectivity [77]. Georges Bank and Browns Bank are located ~150 and ~ 100 km, respectively, from the coast in Nova Scotia; and 475 and 250 km, respectively, from the Bay of Fundy. These distances fall within the range of larval dispersal from each of the banks, and would ensure connectivity among them for a MPAn. Movement between nursery areas appears limited [16], but would need to be resolved to determine the relevance of connectivity between key inshore nursery areas.

4. Discussion

Approaches to marine conservation planning can vary by region and may also depend on the desired conservation outcomes [43]. In marine spatial planning, computer-based spatial design software [4,73] or biophysical modelling [29,8] are some of the methods that can be employed to design a network of potential sites. These approaches can highlight suitable sites for meeting objectives of either individual or networks of protected areas. This study developed a decision tree that can be applied as an approach to incorporate population connectivity, developed using case studies from the Scotian Shelf in Atlantic Canada, but that can be used as a broad tool for sizing and spacing of individual MPAs in different proposed MPA networks.

The lack of connectivity data can pre-empt its explicit consideration during the design process, despite its importance as an ecological criterion for designing effective MPAn [12]. The decision tree is proposed as a method that can be used by marine managers to bring together the information that is of value in designing and assessing different proposed networks of MPAs and ensuring they explicitly consider connectivity. The decision tree is intended to replace the application of general “rules-of-thumb” for sizing and spacing which are derived by compiling and averaging the ranges in movement of several individual species [10,37,45,66,74]. For example, after reviewing information available for CP species on the Scotian Shelf and trying to apply rules-of-thumb to the case studies, it was found that they could not adequately inform size and spacing rules to be specific enough for each CP. A closer look at each CP was necessary by using available data on distribution and life-history to predict how species may move within particular locations of interest and potentially exchange.

It was found that the processes and mechanisms related to movement and dispersal of adults, juveniles or larvae, are key in considering size and spacing guidelines, in accordance with existing MPA design theory. The challenge with deriving general guidelines for sizing and spacing MPAs is that each location includes species with variation in life-history characteristics and movement patterns across life stages, and that experience different oceanographic conditions. The decision tree allows for species-specific size and spacing estimates to be derived based on information that should guide decisions such as the distributions, oceanographic conditions, and conservation priorities particular to a region. By proceeding through individual decisions for each species and its life stages, derived estimates can be combined for an integrated decision on adequate size and spacing necessary for protecting that conservation priority. Since MPA planning is aimed at protecting multiple species, the next step would be to overlay the collection of possible species-specific MPAs and determine a collection of MPAs that would best meet the criteria for as many species as possible.

4.1. *Applications of the decision tree*

One application of the decision tree described in this study could be in conjunction with a Marxan analysis. In many instances, decision support software, such as Marxan [3], is used in the design of MPAn to select sites for protection. This tool requires a specified size of an area as a target, and results in an output design that provides the minimum number of sites needed to represent all species given associated costs [2]. The layers included in the analysis can result in different spatial configurations of different solutions [4]. Using the decision tree, conservation priorities for which connectivity between individual MPAs is particularly relevant can be identified. For species where information is available to derive size and spacing estimates, such as cod or corals in this study, the outcome of the tree can be used to evaluate the size and spacing of MPAs in the Marxan generated network. In this case, the decision tree can be applied as a way of assessing different proposed networks.

One challenge to MPA design is the paucity of ecological knowledge, particularly of the life-history of marine benthic species [28]. Biophysical models are one tool increasingly being employed to assess population connectivity and they account for the effect of biological characteristics, such as larval duration, on larval dispersal [52]. Models that account for spawning season and pelagic larval duration, as biological considerations to assess the relevance of connectivity, show that even for species with short larval duration, connectivity is possible, at least to some degree [29], highlighting the need for its inclusion in MPA design. For species that lack information, it may not be possible to generate models and the general size and spacing guidelines may not accurately match with their distribution characteristics.

In those cases where little biological information is available, a decision tree is a tool that can ensure that connectivity can still be included on principle in the design. As long as the distribution of the target species is known and general life-history patterns can be assumed, decision makers can proceed with the decision tree. Depending on the conservation priority, the tree: (1) will, at minimum, identify the areas to focus on and the basic information necessary to size and space those areas; and (2) will identify those necessary data that are not available. For example, the presence of tube-dwelling anemone fields on the Scotian Shelf has been noted [40], but their life-history is not known. Estimates of the size and spacing needed for MPAs to protect them are imprecise and indicate that further research on larval duration and dispersal distance would provide increased accuracy.

4.2. *Challenges of incorporating connectivity in spatial design*

The effectiveness of spatial protection tools for conservation varies depending on the conservation priority. Spatial protection is best suited for sessile benthic marine species that at minimum have a limited range of movement, compared to a species with several mobile life-history stages. For example, the incidence of Russian Hat sponges in a significant concentration in a single area simplifies the decision on which areas to target. In addition, these sponges only have a single, short-dispersing larval stage which makes spacing irrelevant. This is a case which highlights the importance of size as the main factor in the design of an effective MPA. In contrast, mobile species, such as cod, require a more complex decision process to incorporate connectivity in the design of MPAn. Since their life-history includes more than one dispersing life-stage, sizing and spacing needs of each life-stage must be accommodated separately. The tree will generate multiple estimates depending on the focus life-stage, and decision makers must integrate all outcomes to generate a single estimate for the species.

There are some limitations to using the simplified approach of a decision tree to incorporate connectivity in spatial design. Since the outcome of the tree determines which information is necessary for size and spacing of a single priority at a time, it may not be as useful for a planning approach that needs to account for several species being the concurrent focus of the conservation objectives. One way to adjust the decision tree approach is to take it one step further and compare the outcomes from all conservation priorities that are being considered for a particular MPA and determine the ranges in size and spacing that encompass most or all priorities. An alternative method for evaluating multi-species networks has been derived by D’Aloia et al. [22], using a conceptual framework, which combines information on larval duration and adult home range for multiple species, assuming that information is available. This is also the approach applied by Saarman et al. [66] in the design of MPAn in California, USA. D’Aloia et al. [22] used the framework in conjunction with a Marxan analysis, but it can also be used in conjunction with the decision tree in this study.

One further limitation of marine spatial design is that it only considers size and spacing guidelines for incorporating connectivity, but these factors alone may not ensure population persistence. It has been suggested that spatially explicit population dynamic models should be used to provide a comprehensive evaluation of whether the MPA is effective in ensuring population viability [54]. However, these are computationally demanding, the data to parameterize them are rarely available and may not be easily accessible to managers.

5. Conclusion

Proper designation and implementation of MPAs is one of the current foci for marine management. Networks of MPAs that are adequately sized and spaced, and ensure connectivity are considered to be best practice in MPAn design and this study helps inform that process. A variety of tools can be used to design a comprehensive MPAn and a decision tree can be one of them. The proposed decision tree can be used to design MPAn where there is a paucity of biological information, or as a complementary method to other tools, such as Marxan, in areas where ecological information is available. The proposed decision tree deals with meeting the ecological goals of a network; however, developing the most comprehensive solution must incorporate a variety of tools that ensure the consideration of the biological goals, as well as the social and economic goals of an MPA network.

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Appendix A. Supporting information

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References

[1] J.T. Anderson, Gordon D.C. Jr. Report of the spatial utilization of benthic habitats by demersal fish on the Scotian Shelf synthesis meeting 2007. St. Johns (NL): Fisheries and Oceans Canada. vii + 82 p. Canadian technical report of fisheries and aquatic sciences 2770.

[2] J.A. Ardron, H.P. Possingham, C.J. Klein (Eds.), Marxan Good Practices Handbook, Version 2, Pacific Marine Analysis and Research Association, Victoria (BC), 2010, p. 165.

[3] I.R. Ball, H.P. Possingham, M. Watts, Marxan and relatives: software for spatial conservation prioritisation, in: A. Moilanen, K.A. Wilson, H.P. Possingham (Eds.), Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools, Oxford University Press, Oxford (UK), 2009, pp. 185–195.

[4] N.C. Ban, Minimum data requirements for designing a set of marine protected areas, using commonly available abiotic datasets, Biodivers. Conserv. 18 (7) (2009) 1829–1845.

[5] L. Beazley, E. Kenchington, F.J. Murillo, C. Lirette, J. Guijarro, A. McMillan, A. Knudby. Species distribution modelling of corals and sponges in the Maritimes region for use in the identification of significant benthic areas. Dartmouth (NS): Fisheries and Oceans Canada, Ocean and Ecosystems Division, Maritimes Region. vi + 189 p. Canadian technical report of fisheries and aquatic sciences 3172, 2016.

[6] M.L. Berumen, G.R. Almany, S. Planes, G.P. Jones, P. Saenz-Agudelo, S.R. Thorrold, Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network, Ecol. Evol. 2 (2012) 444–452.

[7] G.R. Bolz, R.G. Lough, Growth through the first six months of Atlantic cod, *Gadus morhua,* and haddock, *Melanogrammus aeglefinus,* based on daily otolith increments, Fish. Bull. 88 (2) (1988) 223–235.

[8] L.W. Botsford, J.W. White, M.H. Carr, J.E. Caselle, Marine protected area networks in California, USA. In: Johnson M.L., Sandell J. (eds): Marine Managed Areas and Fisheries. Adv Mar Biol. 69: 205-251, 2014.

[9] A. Bundy, J.S. Themelis, N. den Heyer. Inshore Scotian Shelf ecosystem overview report: status and trends. Dartmouth (NS): Fisheries and Oceans Canada, Population Ecology Division. xii + 213 p. DFO Canadian science advisory secretariat research document 2014/065.

[10] J.M. Burt, P. Akins, E. Lathem, M. Beck, A.K. Salomon, N.C. Ban, Marine Protected Area Network Design Features that Support Resilient Human-ocean Systems - Applications for British Columbia, Canada, Simon Fraser University, Burnaby (BC), 2014, p. 159.

[11] S.E. Campana, S.J. Smith, P.C.F. Hurley, An age-structured index of cod larval drift and retention in the waters off southwest Nova Scotia, Rapp. P-V. Reun. Cons. Int. Explor. Mer. 191 (1989) 50–62.

[12] M.H. Carr, S.P. Robinson, C. Wahle, G. Davis, S. Kroll, S. Murray, E.J. Schumacker, M. Williams, The central importance of ecological spatial connectivity to effective marine protected areas and to meeting the challenges of climate change in the marine environment, Aquat. Conserv. 27 (S1) (2017) 6–29.

[13] M.H. Carr, E. Saarman, M. Caldwell, "Rules of thumb" in science-based environmental policy: California's marine life protection act as a case study, Stanf. J. Law Sci. Pol. 2 (2010) 1–17.

[14] F.S. Chia, B.J. Crawford, Some observations on gametogenesis, larval development and substratum selection of the sea pen *Ptilosarcus guerneyi*, Mar. Biol. 23 (1) (1973) 73–82.

[15] M.R. Christie, B.N. Tissot, M.A. Albins, J.P. Beets, Y. Jia, D.M. Ortiz, S.E. Thompson, M.A. Hixon, Larval connectivity in an effective network of marine protected areas, PLoS One 5 (2010) e15715.

[16] D.S. Clark, J.M. Green, Activity and movement of juvenile Atlantic cod, *Gadus morhua,* in Conception Bay, Newfoundland, as determined by sonic telemetry, Can. J. Zool. 68 (7) (1990) 1434–1442.

[17] L. Cong, J. Sheng, K.R. Thompson, A retrospective study of particle retention on the outer banks of the Scotian Shelf, 1956-1993. Dartmouth (NS): Fisheries and Oceans Canada, Ocean Sciences Division, Maritimes Region. viii + 132 p. Canadian technical report of hydrography and ocean sciences 170, 1996.

[18] G.S. Cook, P.E. Parnell, L.A. Levin, Population connectivity shifts at high frequency within an open-coast marine protected area network, PLoS One 9 (2014) e103654.

[19] R.K. Cowen, G. Gawarkiewicz, J. Pineda, S.R. Thorrold, F.E. Werner, Population connectivity in marine systems: an overview, Oceanography 20 (3) (2007) 14–21.

[20] R.K. Cowen, S. Sponaugle, Larval dispersal and marine population connectivity, Annu. Rev. Mar. Sci. 1 (2009) 443–466.

[21] C.M. Crain, B.S. Halpern, M.W. Beck, C.V. Kappel, Understanding and managing human threats to the coastal marine environment, Ann. N. Y. Acad. Sci. 1162 (2009) 39–62.

[22] C.C. D'Aloia, R.M. Daigle, I.M. Coté, J.M.R. Curtis, F. Guichard, M.-J. Fortin, A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas, Biol. Conserv. 216 (2017) 93–100.

[23] DFO, Recovery potential assessment (RPA) for the southern designatable unit (NAFO divs. 4X5Yb and 5Zjm) of Atlantic cod (Gadus morhua). Dartmouth (NS): Fisheries and Oceans Canada, Centre for Science Advice, Maritimes Region. 25 p. DFO Canadian science advisory secretariat science advisory report 2011/034, 2011.

[24] DFO. Canada's plan to reach marine conservation targets [Internet]. Ottawa (ON): Fisheries and Oceans Canada; [modified 2016 June 8; cited 2017 Mar 15], 2016. Available from: 〈http://news.gc.ca/web/article-en.do?Mthd=tp&crtr.page=1&nid=1081789〉.

[25] M. Di Lorenzo, G. D'Anna, F. Badalamenti, V.M. Giacalone, R.M. Starr, P. Guidetti, Fitting the of no-take zones to species movement patterns: a case study on a Mediterranean seabream, Mar. Ecol. Prog. Ser. 502 (2014) 245–255.

[26] G.J. Edgar, R.D. Stuart-Smith, T.J. Willis, S. Kininmonth, S.C. Baker, S. Banks, N.S. Barrett, M.A. Becerro, A.T.F. Bernard, J. Berkhout, et al., Global conservation outcomes depend on marine protected areas with five key features, Nature 506 (7487) (2014) 216–220.

[27] S.D. Fuller, Diversity of Marine Sponges in the Northwest Atlantic (Ph.D. Dissertation), Dalhousie University, Halifax (NS), 2011, p. 229.

[28] S.D. Gaines, B. Gaylord, L.R. Gerber, A. Hastings, B.P. Kinlan, Connecting places: the ecological consequence of dispersal in the sea, Oceanography 20 (3) (2007) 90–99.

[29] A. Gallego, F.M. Gibb, D. Tullet, P.J. Wright, Bio-physical connectivity patterns of benthic marine species used in the designation of Scottish nature conservation marine protected areas, ICES J. Mar. Sci. (2016) (fsw174).

[30] A.L. Green, A.P. Maypa, G.R. Almany, K.L. Rhodes, R. Weeks, R.A. Abesamis, M.G. Gleason, P.J. Mumby, A.T. White, Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design, Biol. Rev. 90 (2015) 1215–1247.

[31] B.S. Halpern, The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl. 13 (1) (2003) 8117–8137 (2003 Suppl).

[32] C.G. Hannah, J.A. Shore, J.W. Loder, The drift-retention dichotomy on Browns Bank: a model of study of interannual variability, Can. J. Fish. Aquat. Sci. 57 (2000) 2506–2518.

[33] T. Horsman, N. Shackell, Atlas of important habitat for key fish species of the Scotian Shelf, Canada. Dartmouth (NS): Fisheries and Oceans Canada, Oceans, Habitat and Species at Risk Branch, Maritimes Region. viii + 82 p. Canadian technical report of fisheries and aquatic sciences 2835, 2009.

[34] E.D. Houde, Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. United States National Marine Fisheries Service, Fish. Bull. 87 (1989) 471–496.

[35] ICES, Spawning and Life History Information for North Atlantic Cod Stocks, International Council for the Exploration of the Sea, Copenhagen, Denmark, 2005, p. 152 (ICES cooperative research report no. 274).

[36] IUCN-WCPA, Establishing Marine Protected Area Networks—Making It Happen, IUCN World Commission on Protected Areas, National Oceanic and Atmospheric Administration and The Nature Conservancy, Washington, D.C., 2008, p. 118.

[37] S. Jessen, K. Chan, I. Côté, P. Dearden, E. De Santo, M.J. Fortin, F. Guichard, W. Haider, G. Jamieson, D.L. Kramer, et al., Science-based Guidelines for MPAs and MPA Networks in Canada, Canadian Parks and Wilderness Society, Vancouver (BC), 2011, p. 58.

[38] E. Kenchington, C. Lirette, A. Cogswell, D. Archambault, P. Archambault, H. Benoit, D. Bernier, B. Brodie, S. Fuller, K. Gilkinson et al., Delineating coral and sponge concentrations in the biogeographic regions of the East coast of Canada using spatial analyses. Dartmouth (NS): Fisheries and Oceans Canada. vi + 202 p. DFO Canadian science advisory secretariat research document 2010/041. (Erratum: December 2012), 2010.

[39] M. King, D. Fenton, J. Aker, A. Serdynska. Offshore ecologically and biologically significant areas in the Scotian Shelf bioregion. Dartmouth (NS): Fisheries and Oceans Canada, Ecosystems Management Branch, Maritimes Region, Oceans and Coastal Management Division. viii + 92 p. DFO Canadian science advisory secretariat research document 2016/007, 2016.

[40] M. King, A. Gerhartz Abraham, T. Koropatnick, G. Pardy, A. Serdynska, E. Will, H. Breeze, A. Bundy, E. Edmondson, K. Allard. Design strategies for the Scotian Shelf Bioregional Marine Protected Area Network. Dartmouth (NS): Fisheries and Oceans Canada, Ecosystem Management Branch, Maritimes Region, Oceans and Coastal Management Division. vi + 86 p. CSAM working paper 2016/14 (In preparation), 2017.

[41] B.P. Kinlan, S.D. Gaines, Propagule dispersal in marine and terrestrial environments: a community perspective, Ecology 84 (2003) 2007–2020.

[42] A.I. Larsson, J. Jarnegren, S.M. Stromberg, M.P. Dahl, T. Lundalv, S. Brooke, Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*, PLoS One 9 (7) (2014) e102222.

[43] H.M. Leslie, A synthesis of marine conservation planning approaches, Conserv. Biol. 19 (6) (2005) 17011713.

[44] S.P. Leys, G.O. Mackie, H.M. Reiswig, The biology of glass sponges, Adv. Mar. Biol. 52 (2007) 1–145.

[45] L.M. Lieberknecht, J.A. Ardron, N.C. Ban, N.J. Bennet, L. Eckert, T.E.J. Hooper, C.L. K. Robinson. Recommended guidelines for applying Canada-BC Marine Protected Area Network Principles in Canada's Northern Shelf Bioregion: Principles 1,2,3,5,6,

7,8,9,11,14 and 15. Victoria (BC): PacMARA. 152 p. Report produced by PacMARA for the British Columbia Marine Protected Areas Technical Team (MPATT), 2016.

[46] J.W. Loder, C.K. Ross, P.C. Smith, A space- and time-scale characterization of circulation and mixing over submarine banks with application to the northwestern Atlantic continental shelf, Can. J. Fish. Aquat. Sci. 45 (1988) 1860–1885.

[47] R.G. Lough, P.C. Valentine, D.C. Potter, P.J. Auditore, G.R. Bolz, J.D. Neilson, R.I. Perry, Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank, Mar. Ecol. Prog. Ser. 56 (1989) 1–12.

[48] R.A. Magris, R.L. Pressey, R. Weeks, N.C. Ban, Integrating connectivity and climate change into marine conservation planning, Biol. Conserv. 170 (2014) 207–222.

[49] MCI (Marine Conservation Institute). MPAtlas [Internet]. Seattle (WA): Marine Conservation Institute; [cited 2017 Mar13], 2017. Available from: 〈www.mpatlas.org〉.

[50] J.S. McCain, R.W. Rangeley, D.C. Schneider, H.K. Lotze, Historical abundance of juvenile commercial fish in coastal habitats: implications for fish habitat management in Canada, Mar. Pol. 73 (2016) 235–243.

[51] E. McLeod, R. Salm, A. Green, J. Almany, Designing marine protected area networks to address the impacts of climate change, Front. Ecol. Environ. 7 (7) (2009) (362-320).

[52] A. Metaxas, M. Saunders, Quantifying the “bio-” components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls, Biol. Bull. 216 (3) (2009) 257–272.

[53] F. Micheli, A. Saenz-Arroyo, A. Greenley, L. Vazquez, J.A.E. Montes, M. Rossetto, G.A. De Leo, Evidence that marine reserves enhance resilience to climatic impacts, PLoS One 7 (2012) e40832.

[54] E.A. Moffit, J.W. White, L.W. Botsford, The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks, Biol. Conserv. 144 (1) (2011) 306–318.

[55] MPAFAC (Marine Protected Areas Federal Advisory Committee), Harnessing Ecological Spatial Connectivity for Effective Marine Protected Areas and Resilient Marine Ecosystems: Scientific synthesis and action agenda. 68pp, 2017.

[56] P.J. Mumby, Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales, Biol. Conserv. 128 (2006) 215–222.

[57] R. O’Boyle, Benefits of marine protected areas and fisheries closures in the Northwest Atlantic. Can. Tech. Rep. Fish. Aquat. Sci. 2948: iii + 68 p, 2011.

[58] A.D. Olds, R.M. Connolly, K.A. Pitt, P.S. Maxwell, Habitat connectivity improves reserve performance, Conserv. Lett. 5 (2012) 56–63.

[59] A.D. Olds, K.A. Pitt, P.S. Maxwell, R.M. Connolly, Synergistic effects of reserves and connectivity on ecological resilience, J. Appl. Ecol. 49 (2012) 1195–1203.

[60] S.R. Palumbi, Population genetics, demographic connectivity, and the design of marine reserves, Ecol. Appl. 13 (1) (2003) S146–S158 (2003 Suppl).

[61] J. Pineda, J.A. Hare, S. Sponaugle, Larval transport and dispersal in the coastal ocean and consequences for population connectivity, Oceanography 20 (3) (2007) 22–39.

[62] C.S. Reiss, G. Panteleev, C.T. Taggart, J. Sheng, B. DeYoung, Observations on larval fish transport and retention on the Scotian Shelf in relation to geostrophic circulation, Fish. Oceanogr. 9 (3) (2000) 195–213.

[63] J.M. Roberts, A. Wheeler, A. Freiwald, S. Cairns, Cold-water Corals: The Biology and Geology of Deepsea Coral Habitats, Cambridge University Press, Cambridge, UK, 2009, p. 334.

[64] D. Robichaud, G.A. Rose, Migratory behaviour and range in Atlantic cod: inference from a century of tagging, Fish Fish. 5 (2004) 185–214.

[65] D.E. Ruzzante, C.T. Taggart, D. Cook, A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank, Mol. Ecol. 7 (1998) 1663–1680.

[66] E. Saarman, M. Gleason, J. Ugoretz, S. Airame, M.H. Carr, E.W. Fox, A. Frimodig, T. Mason, J. Vasques, The role of science in supporting marine protected area network planning and design in California, Ocean Coast. Manag. 74 (2013) 45–56.

[67] R.V. Salm, T. Done, E. McLeod, Marine protected area planning in a changing climate, in: J.T. Phinney, O. Hoegh-Guldberg, J. Kleypas, et al. (Eds.), Coral Reefs and Climate Change: Science and Management, American Geophysical Union, Washington, DC, 2006, p. 244.

[68] S. Shan, Eulerian and Lagrangian Studies of Circulation on the Scotian Shelf and Adjacent Deep Waters of the North Atlantic with Biological Implications (Ph.D. Dissertation), Dalhousie University, Halifax (NS), 2016, p. 203.

[69] A.L. Shanks, B.A. Grantham, M.H. Carr, Propagule dispersal distance and the size and spacing of marine reserves, Ecol. Appl. 13 (1) (2003) S159–S169.

[70] M. Shapiera, R.S. Gregory, C.J. Morris, C.J. Pennell, P.V.R. Snelgrove, Season and site fidelity determine home range of dispersing and resident juvenile Greenland cod, *Gadus ogac,* in a Newfoundland fjord, Mar. Ecol. Prog. Ser. 503 (2014) 235–246.

[71] J.A. Shore, C.G. Hannah, J.W. Loder, Drift pathways on the western Scotian Shelf and its environs, Can. J. Fish. Aquat. Sci. 57 (2000) 2488–2505.

[72] A. Sinclair, Fish distribution and partial recruitment; the case of eastern Scotian Shelf cod, J. Northw. Atl. Fish. Sci. 13 (1992) 15–24.

[73] R.J. Smith, P.D. Eastwood, Y. Ota, S.I. Rogers, Developing best practice for using Marxan to locate marine protected areas in European waters, ICES J. Mar. Sci. 66 (1) (2009) 188–194.

[74] J. Smith, M. Patterson, H.M. Alidina, J. Ardron, Criteria and Tools for Designing Ecologically Sound Marine Protected Area Networks in Canada's Marine Regions, WWF-Canada, Halifax (NS), 2009, p. 30.

[75] Stantec. Strategic environmental assessment for the Eastern Scotian Shelf- Middle and Sable Island banks (Phase 1a). Dartmouth (NS): Stantec Consulting Ltd. 206 p. Report prepared for CanadaNova Scotia Offshore Petroleum Board 121511015, 2012.

[76] Z. Sun, Reproductive Biology of Deep-sea Soft Corals in the Newfoundland and Labrador Region (Masters thesis), Memorial University of Newfoundland, St. John's (NL), 2009, p. 178.

[77] M. Tupper, R.G. Boutilier, Effects of habitat on settlement, growth, and post settlement survival of Atlantic cod (*Gadus morhua*), Can. J. Fish. Aquat. Sci. 52 (1995) 1834–1842.

[78] D.R. Zemeckis, D. Martins, L.A. Kerr, S.X. Cadrin, Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach, ICES J. Mar. Sci. 71 (6) (2014) 1490–1506.