



Comparing approaches for estimating ecological connectivity at a local scale in a marine system

Arieanna C. Balbar^{1,*}, Anna Metaxas¹, Yongsheng Wu²

¹Dalhousie University, Department of Oceanography, 1355 Oxford Street, Halifax, Nova Scotia B3H 4R2, Canada

²Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada

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

KEY WORDS: Marine protected area · Dispersal · Kelp beds · Ocean currents · Hydrodynamic model · Coastal marine ecosystems · NW Atlantic Ocean · Life history traits · Ocean management

1. INTRODUCTION

Marine protected areas (MPAs) are implemented globally to meet high-level objectives, such as maintaining persistence and promoting resilience of populations, species, and communities (Chambers et al. 2019, Begger et al. 2022). Population connectivity, defined as the linkage of distinct populations mediated by the dispersal of propagules, juveniles, and adults (Pineda et al. 2007, Kool et al. 2013), is one ecological criterion used to site MPAs and can support these objectives, even in the face of climate

change (Dakos et al. 2015, Carr et al. 2017, Chambers et al. 2019, Wilson et al. 2020). Identifying patterns of connectivity allows for the identification of source and sink populations across a wider region or metapopulation (Cowen & Sponaugle 2009, Kool et al. 2013). Despite the stated importance of connectivity, in only 11% of MPAs was connectivity considered as an ecological criterion in their design, and 9.7% of terrestrial protected areas are structurally connected (Balbar & Metaxas 2019, Ward et al. 2020), with geographic biases that mirror those identified in the scientific studies (Bryan-Brown et al. 2017). The

*Corresponding author: abalbar@dal.ca

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post-2020 Convention on Biological Diversity framework proposes 30% of national land and waters to be designated as 'well-connected systems' of MPAs by 2030 (CBD 2022). Managers will be challenged to include connectivity into the design of networks of MPAs because of a paucity of baseline data, models, and capacity.

In the marine environment, dispersal (the movement of organisms through their environment from a source to a destination site) of sessile, benthic invertebrates is realized by the earliest life history stages or propagules and is often employed as a proxy for connectivity (similarly to trees on land). The spatial and temporal scales over which propagules disperse depend on several physical (e.g. currents, proximity to coastline, bathymetry) and biological factors (e.g. timing of spawning, fecundity, pelagic duration, mortality, and behaviour) (Largier 2003, Levin 2006, Metaxas & Saunders 2009, Daigle et al. 2014, D'Aloia et al. 2017). In particular, planktonic duration (PD) is a biological factor which correlates directly with dispersal distance (Shanks 2009). Competent propagule duration (CPD) refers to the developmental period when a propagule has reached a developmental stage capable of recruiting to habitat and becoming sessile, and its timing largely influences metapopulation persistence (Cecino & Treml 2021). In the marine realm, it is not feasible to track propagules because they are small, often occur in low concentrations, and the timing of release cannot be predicted accurately.

Operationalizing measurements of dispersal and connectivity in the design of MPAs requires a suite of tools (Lagabriele et al. 2014). 'Rules of thumb' are less resource intensive, more easily interpreted, and therefore easier to apply to decision-making processes than more complex measures (Hilty et al. 2020). In the marine realm, the simplest rule of thumb estimates dispersal distance using a linear relationship between average ocean current speed and PD. This and other data-limited approaches have been proposed to inform size and spacing guidelines for networks of MPAs such as adult home range (Friesen et al. 2019), dispersal ability binned by species in different depth classes (intertidal, nearshore, offshore), and PD (Blackford et al. 2021), or dispersal based on important habitats for species (e.g. migration, nursery, mating) and average currents (Smith & Metaxas 2018). Biophysical modelling provides a more intense data-informed approach to estimate patterns of connectivity, coupling ocean circulation models with particle tracking, and is therefore considered the state-of-the-art approach for studying propagule dispersal (Treml et al. 2008, Schill et al. 2015, Briton et

al. 2018, Lequeux et al. 2018, Cristiani et al. 2021). A Lagrangian approach can integrate several factors that influence dispersal, such as fecundity, small-scale variations in currents from wind, tides, and topographic complexity, propagule mortality, and precise spawning time, but it is computationally expensive and requires specialized expertise. Consensus in outputs among multiple approaches for estimating connectivity increases the reliability and confidence in the predicted patterns of dispersal; however, outputs from multiple approaches are seldom compared (but see Christie et al. 2010, Jahnke et al. 2017).

The Eastern Shore Islands (ESI) proposed MPA site along the Atlantic coast of Nova Scotia, Canada, provides an excellent case study for using knowledge on connectivity to inform decision making. In the shallow subtidal zone, kelp beds, dominated by *Laminaria digitata* and *Saccharina latissima*, form a prominent biogenic, complex 3-dimensional habitat, providing protection and nursery grounds for fish and benthic invertebrates (Steneck et al. 2002, Graham 2004, Smale et al. 2013). Kelps reduce flow (Eckman et al. 1989) and increase food quality (Krumhansl & Scheibling 2011), supporting a large diversity of marine life, including economically important species (Smale et al. 2013). The green sea urchin *Strongylocentrotus droebachiensis* is a key species in the dynamics of kelp bed ecosystems. Historically, dense fronts of *S. droebachiensis* grazed kelps, promoting 2 alternative stable states: kelp beds and urchin barrens (Scheibling et al. 1999, Filbee-Dexter & Scheibling 2017). Disease outbreaks of the pathogenic amoeba *Paramoeba invadens* significantly reduced sea urchin populations from the 1980s to early 2000s, resulting in the return of the kelp bed stable state (Scheibling 1986, Feehan & Scheibling 2014, Buchwald et al. 2018). However, since the 1950s, the biomass of kelp beds has concurrently decreased by at least 85% at 3 long-term study sites along the Atlantic coast of Nova Scotia, as a result, in large part, of the introduction of the invasive bryozoan species *Membranipora membranacea* (Watanabe et al. 2010, Filbee-Dexter et al. 2016). On the southwestern shore of Nova Scotia, regime shifts from luxuriant kelp beds to a new, turf-dominated benthos are increasing the vulnerability of coastal kelp ecosystems to other stressors (Kelly et al. 2011, Filbee-Dexter et al. 2016). It is imperative to prioritize planning of MPAs to protect high-quality patches of kelp and the biological communities they support.

In this study, we estimated dispersal and inferred ecological connectivity using 3 approaches of increasing complexity, and thus of increasing require-

ments for computational and human resources, for 3 taxa of ecological significance (laminarian kelps, *S. droebachiensis*, and *M. membranacea*) at a proposed MPA site in Nova Scotia, the ESI. The 3 approaches differ in terms of the specificity of ecological inputs as well as the number of spatial dimensions used to estimate ocean currents: (1) current speed depth-averaged over time (in x ; 1D approach); (2) current velocity decomposed into along-shore and cross-shore components and depth-averaged over time (in x and y ; 2D); and (3) spatially modelled current velocity (in x , y , and z ; 3D). For each taxon, we compared dispersal metrics (area, maximum dispersal distance, Jaccard index) among approaches, and connectivity from the ESI to other potential future coastal MPAs in Nova Scotia. We predicted that the approaches would produce different estimates of dispersal area, but that the 2D and 3D approaches would be more similar to one another than to the 1D approach because they account for directionality of currents in the calculation of dispersal potential. We also predicted that taxa with a medium–long CPD (*S. droebachiensis* and *M. membranacea*) would have a substantially greater dispersal area, maximum dispersal distance, and number of connections to other potential future MPAs than taxa with short CPD (laminarian kelps). Lastly, we evaluated the benefits and costs of applying each approach and provide guidance and tools for managers to determine which approach is best applied depending on the input data and resources available.

2. MATERIALS AND METHODS

2.1. Estimating kelp distribution

We compiled data on the presence and absence of kelp habitat along the eastern shore of Nova Scotia, from the shoreline to a depth of 40 m, between 2017 and 2020 ($n = 492$; Fig. S1 in Section 1 of the Supplement at www.int-res.com/articles/suppl/m731p051_supp.pdf). The data were from surveys with a drop-

camera system done by Fisheries and Oceans Canada (DFO) in 2017 and 2019, as well as surveys done by snorkelling or with SCUBA in 2018 and 2020 (Supplement Section 2). Data on the abundance of kelp habitat were collected as either presence/absence or percent cover. For modelling purposes, all data points were converted to presence (1) or absence (0) of kelp habitat. We optimized a classification random forest model to predict the distribution of suitable habitat for kelps using 3 ecological predictors: depth, presence of hard substrate, and an index of relative wave exposure, with presence or absence of kelp habitat as the response variable (Supplement Sections 1 and 2).

2.2. Approaches for estimating dispersal

We considered CPD, fecundity, timing, and location of spawning as ecological inputs to generate taxon-specific estimates of dispersal (Table 1). We estimated the area over which propagules disperse, in km^2 , from kelp patch centroids or survey-based start locations (Table S2) using 3 approaches of increasing complexity and computational requirements. The approaches differed in ecological and oceanographic inputs.

The first, one-dimensional (1D), approach, applies the simplest and most frequently used metric by managers for estimating dispersal distance. In the 1D approach, dispersal distance is estimated by multiplying depth-averaged, time-mean current speed by propagule duration (Shanks 2009). In this article, we considered CPD, a period during which the developmental stage of a propagule is physiologically competent to readily settle onto the seafloor. In this 1D approach, 2 circular polygons are calculated: a larger one with a radius equal to the current speed multiplied by total propagule period; and a smaller one with a radius equal to the pre-competency period. To obtain the dispersal area during competency, we subtracted the pre-competency polygon from the one calculated for the total propagule period. For each taxon, we mapped these spatial polygons onto the

Table 1. Life history characteristics of the 3 taxa used in this study. CPD: competent planktonic propagule duration

Taxon	CPD (d)	Spawning period	Settlement period	Resources
Laminarian kelps	0–2	October–December	October–December	Chapman (1984)
<i>Membranipora membranacea</i>	14–28	July–September	Mid-July–September	Saunders & Metaxas (2007, 2010)
<i>Strongylocentrotus droebachiensis</i>	28–60	February–March	March–May	Strathmann (1978), Himmelman (1978), Pearce & Scheibling (1991), Meidel & Scheibling (1998)

coast of Nova Scotia centered at the release locations. We produced maps of in-water dispersal area only by subtracting the area of the polygon that intersected with land.

The second approach (2D) employs current velocity rather than speed. We obtained current velocity data from 2 acoustic Doppler current profilers deployed in the ESI from 2018 to 2019 from DFO over periods that covered the spawning windows of the taxa of interest (Table 1); data from Ship Harbour were used for laminarian kelps, and data from Liscomb for *Membranipora membranacea* and *Strongylocentrotus droebachiensis* (Table S3). We produced a polygon that represents dispersal area for the 3 target taxa using the same distance relationship as the 1D approach combined with ellipse geometry using the following steps (Fig. 1):

(1) Using a rotation matrix, the u and v components of velocity were rotated relative to the dominant topographic feature (Fig. 1a,b). In our case study, this corresponded to the angle of the mainland of Nova Scotia between 63° W and 62° W longitude. In the rotated time-series of velocity, the rotated u -axis rep-

resents the alongshore current direction, and the rotated v -axis represents the cross-shore current direction.

(2) Using the rotated components of velocity, dispersal was calculated. A current velocity time series allowed us to decompose the magnitude of velocity in 4 directions, 90° apart. For each component of velocity, we multiplied current speed averaged over depth and between the period from spawning to settlement, by the pre-competency period and the total propagule period, representing the beginning and end of the CPD, respectively. We subtracted the pre-competency polygon from the former, as in the 1D approach, to illustrate the dispersal area for the competent period (Table 1, Fig. 1c).

(3) For each of the 4 quadrants, an ellipse was produced with radii equal to the dispersal distances calculated in step 2. For example, the ellipse in the NE quadrant was calculated using the rotated north and east radii (Fig. 1d). This approach considers that the magnitude of the positive and negative (rotated east vs. west and north vs. south) components of velocity may not be equal. Each ellipse was then cropped to

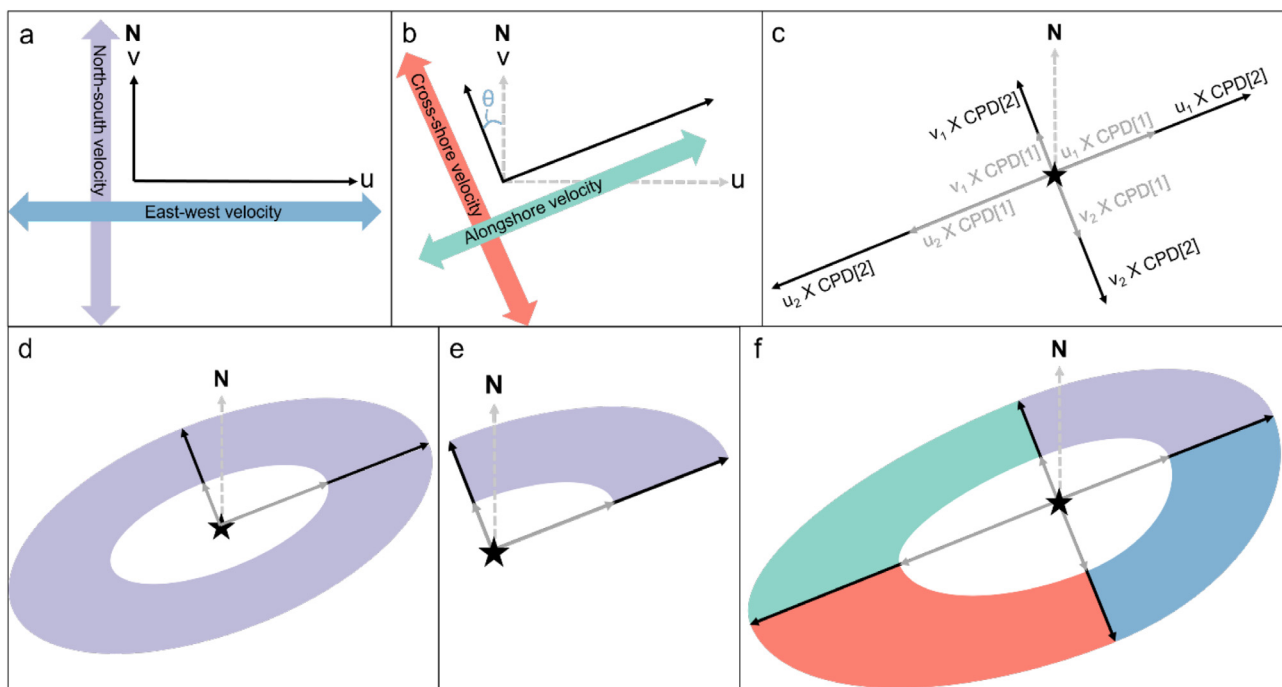


Fig. 1. Graphical explanation of the 2D approach. (a) Horizontal components of velocity (depth-averaged). (b) Components of velocity rotated about angle θ representing alongshore and cross-shore components of velocity. (c) Magnitude of dispersal distance in 4 directions, where u_1 = positive rotated u (east), u_2 = negative rotated u (west), v_1 = positive rotated v (north), v_2 = negative rotated v (south), and CPD = competent propagule duration. Arrows represent example length scales. Star denotes the example release location/ellipse centroid. (d) Ellipse with radii equal to dispersal distances in north ($v_1 \times \text{CPD}$) and east ($u_1 \times \text{CPD}$) directions. Dispersal area during the period when larvae are not competent to settle is shown as the white interior of the ellipse and was not included in the estimation of dispersal area. (e) Ellipse cropped to northeast quadrant. (f) Concatenation of ellipses for all 4 quadrants forming full dispersal area

retain the quadrant corresponding to the radii used to produce it. For example, only the upper right quadrant was retained for the ellipse produced with positive alongshore and cross-shore velocities (Fig. 1e).

(4) The 4 retained quadrants were concatenated to produce a continuous, oblong ellipse (Fig. 1f).

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

The 1D and 2D approaches assume spatial uniformity in ocean currents. In the 3D approach, representing components of velocity in x , y , and z , we tracked passive propagules through space and time using a Lagrangian particle tracking module. The module was driven by hourly 3D velocity fields derived from a hydrodynamic model based on the Finite-Volume Community Ocean Model (FVCOM). The model domain covers the Scotian Shelf and the Gulf of Maine with a horizontal resolution varying from approximately 100 m in the ESI area to several kilometres in the open ocean. A generalized sigma coordinate was used in the vertical direction. The model is driven by air forcing from the surface and by open boundary conditions along the lateral boundaries. The model outputs were evaluated against observed water elevations, currents, temperature, and salinity. More detailed description and information about the model setup and validation can be found in Feng et al. (2022). Release locations were the same as in the 1D and 2D approaches. For each taxon at each location and for each release, the number of particle trajectories was equal to the fecundity (calculated based on empirical data; Supplement Section 2) over 1 m² of seabed. Estimated total fecundities for laminarian kelps, *M. membranacea*, and *S. droebachiensis* were 100 000, 50 000, and 2500 spores or ova m⁻² seabed, respectively, which we assumed equalled the total number of propagules produced by each taxon over the season (Supplement Section 2). To produce unique trajectories for each particle, we employed vertical random walk in the particle tracking simulations. To represent the spawning pattern over the season, we released propagules every 5 d, for 5 releases in total during each of 2 periods, in turn separated by 1 mo, for a total of 10 simulations per taxon (Table S4). Propagule locations were extracted every 12, 84, and 96 h for kelps, *M. membranacea*, and *S. droebachiensis*, respectively. Output locations for the period of CPD were summed across the 10 runs and mapped onto a raster grid (210 m by 210 m), then log-transformed and plotted as a 2D density histogram of points per cell. Lastly, we only considered dispersal in the open coastal ocean, therefore excluding the Bras d'Or

lakes, which have limited physical exchange with the open ocean (Tremblay 2002).

There are a few limitations in our approach. Firstly, because we only included a single year of modelled currents, the model outputs could be underestimating potential dispersal in the direction opposite to the dominant current (as in Aiken et al. 2007). Secondly, since we are focussed on horizontal displacement, vertical diffusion was not accounted for in the 1D and 2D approaches as currents are depth-averaged. For the 3D approach, we applied vertical random walk, not vertical diffusion. Thirdly, because of computing limitations, we modelled the number of propagules proportional to the density of fecund individuals of each taxon over a full spawning season for 1 m² seabed; for kelps, we were constrained to 1 order of magnitude less than the calculated spore production rate. We expect the magnitudes of absolute propagule dispersal, and therefore connectivity, to be much greater than our modelling predictions. Fourthly, dispersal area for the 3D approach is dependent on the size of the grid cell selected to convert particle tracks to an area-based value. For instance, as Δx approaches 0, so does our dispersal area. However, the comparisons of relative outcomes among approaches are valid if the dispersal area predicted from the 3D approach is the greatest (as was the case; see Section 3). Lastly, we did not consider propagule behaviour or mortality to better align estimates from the 3D approach with those from the 1D and 2D approaches, which cannot include those parameters.

2.3. Metrics of dispersal/connectivity and comparison of approaches

For each taxon, we compared dispersal for the 3 approaches using 3 metrics: dispersal area (km²), maximum in-water dispersal distance (km), and connectedness to ecologically relevant spatial units. Dispersal area was calculated as the in-water area (km²) travelled through by propagules during the CPD. For the 3D approach, this corresponded to the area of the 2D density plot with a cell resolution of 210 m. Maximum dispersal distance was calculated as in-water least-cost path (km) either to the furthest point in the polygon, for the 1D and 2D approaches, or as maximum displacement by any released particle for the 3D approach. Connections between management units were calculated as a binary intersection of polygons for the 1D and 2D approaches (0 = no connection, 1 = connection), or mean proportion of total particle tracks (\pm SD), averaged over CPD and across all runs (10 runs

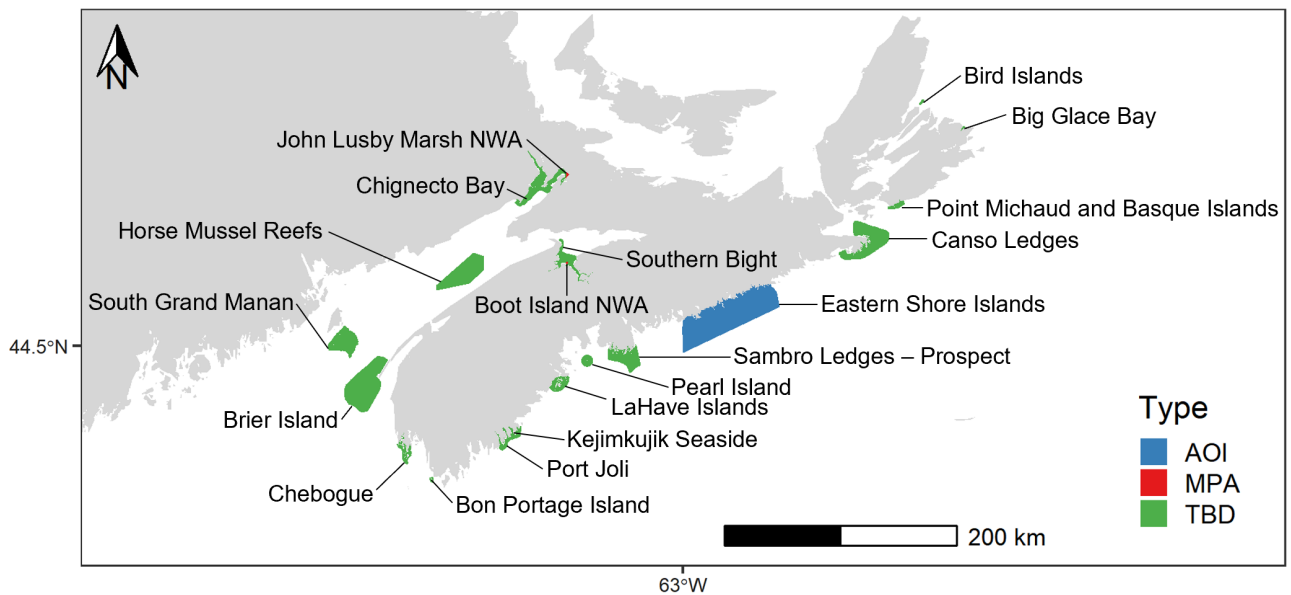


Fig. 2. Existing (marine protected area, MPA), proposed (area of interest, AOI), and other potential future (to be determined, TBD) coastal MPAs along the Atlantic Coast of Nova Scotia and Bay of Fundy, corresponding to entries listed in Table 4. NWA: National Wildlife Area, currently designated MPAs

per taxon), for the 3D approach. For our case study, spatial units were coastal areas in the draft Marine Conservation Network Design for the Scotian Shelf – Bay of Fundy Bioregion, provided by DFO (Fig. 2). The proposed areas within the draft network design represent potential future MPAs identified through a systematic conservation planning process. DFO is currently consulting on the draft network design, so the locations of these areas may be subject to change before they are ultimately proposed for designation as MPAs or other types of spatial conservation measures.

To quantify the overlap in dispersal area, we calculated the Jaccard index for each pair of approaches for each taxon. The Jaccard index is calculated as the geometric intersection divided by the geometric union, producing a number between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap (Real & Vargas 1996). All calculations were completed in R with the packages 'tidyverse' (1.3.2), 'sf' (1.0-9), 'gdistance' (1.3-6), and 'raster' (3.6-14) (van Etten 2017, Pebesma 2018, Wickham et al. 2019, R Core Team 2020, Hijmans 2023).

To facilitate the adoption of our 2D approach to on-the-ground conservation efforts, we developed an R package, called 'rcove', which can be downloaded from GitHub at <https://github.com/abalbar/rcove> (Balbar 2023). The 'rcove' function takes ocean current data and species life history information as input and outputs a shapefile describing the dispersal area that can be visualized in R or any other GIS software.

3. RESULTS

3.1. Patterns of dispersal

Dispersal patterns differed between taxon with medium–long CPD and the laminarian kelps with short CPD. For kelps, propagules released from within the boundaries of the ESI, and tracked in 3D, dispersed throughout the entire proposed ESI MPA and outside its boundaries (Fig. 3a). The dispersal area for the 3D approach was greater than that for the 1D and 2D approaches, which were limited to areas immediately surrounding each kelp patch (Fig. 3a). Propagules of the bryozoan *Membranipora membranacea*, when tracked in 3D, dispersed along the entire Atlantic coast of Nova Scotia, with most propagules dispersing southwest of their initial release locations (Fig. 3b). The 1D and 2D approaches predicted dispersal along a greater distance to the northeast and shorter distance to the southwest than the 3D approach, spanning 450 and 340 km of coastline, respectively. Similarly for the sea urchin *Strongylocentrotus droebachiensis*, propagules released from within the ESI boundaries dispersed along the entire Atlantic Coast of Nova Scotia and into the Bay of Fundy, although most propagules were retained within the southwestern shore (Fig. 3c). Using the 2D approach, sea urchins dispersed along ~700 km of coastline, with greater dispersal southwest than northeast of the initial release locations (Fig. 3c). The dispersal area using the 1D

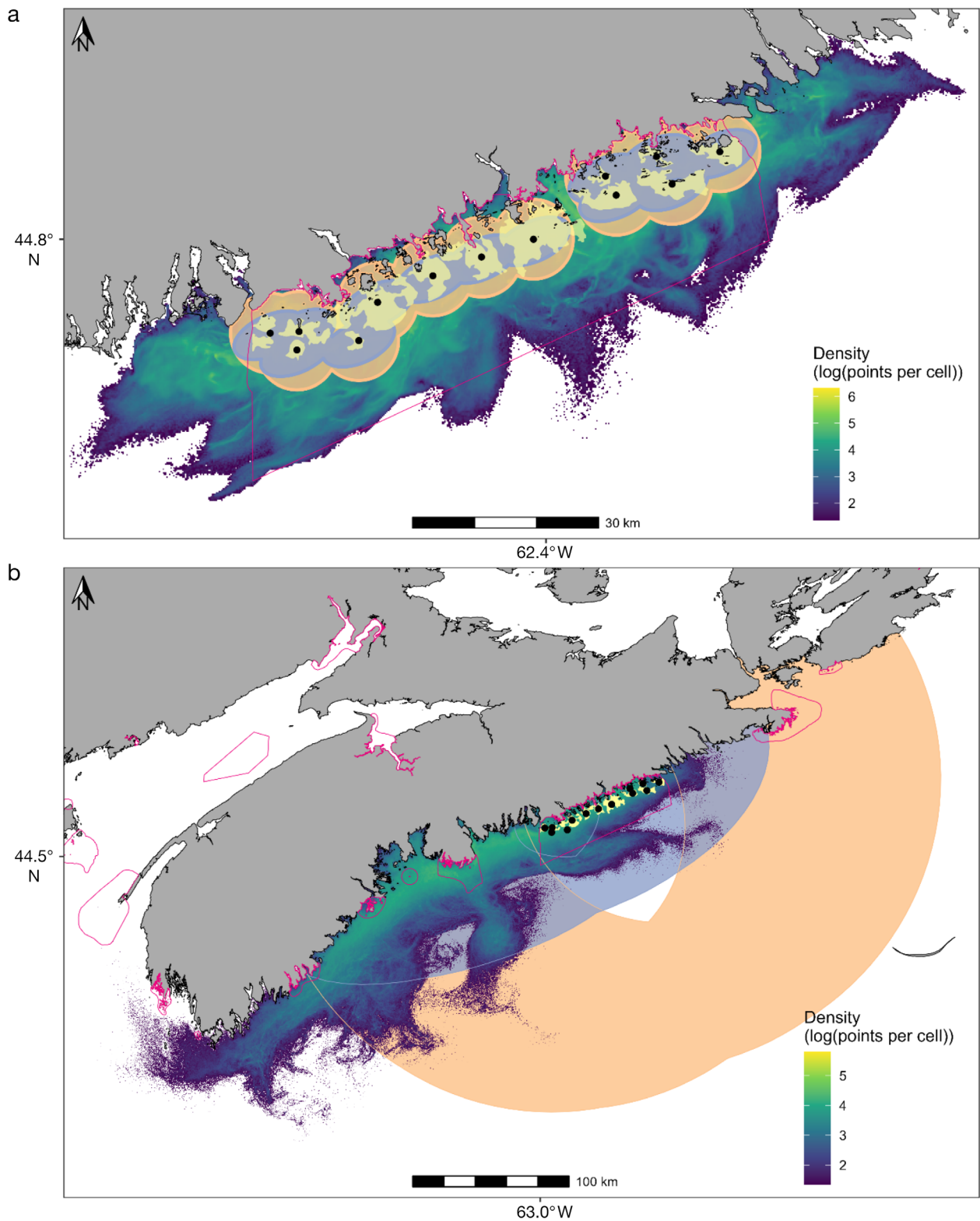


Fig. 3 continued on next page

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

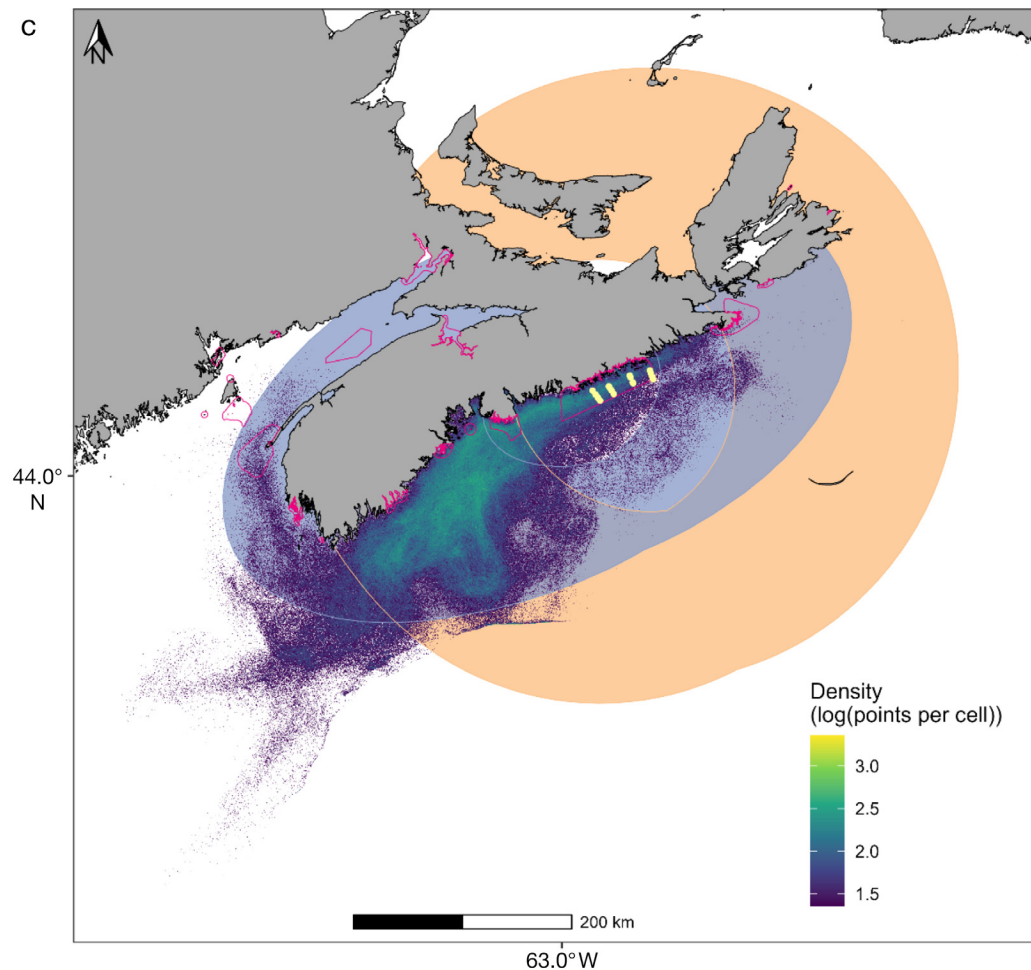


Fig. 3 (continued)

approach was much greater than that of both the 3D and 2D approaches and extended along the entire Atlantic coast of Nova Scotia to Prince Edward Island.

3.2. Comparison of approaches for estimating dispersal

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

based on the 1D and 2D approaches, respectively, and the Jaccard index was greatest between the 1D and 2D approaches (Tables 2 & 3). For the bryozoan and sea urchin, dispersal area was largest for the 1D approach (Table 2). Dispersal area differed by only 5% between the 2D and 3D approaches for the bryozoan but was nearly twice as large for the 2D than 3D approach for the sea urchin. The Jaccard index was greatest between the 2D and 3D approaches for both the bryozoan and sea urchin (Table 3). Maximum in-water distance was similar for the 1D and 2D

Table 2. Species dispersal metrics for the 3 modelling approaches (1D, 2D, 3D) applied. For maximum in-water distance for the 3D approach, the mean \pm SD over 10 runs is shown. See Section 2 for a full description of each approach

Taxon	Area (km^2)			Maximum in-water distance (km)		
	1D	2D	3D	1D	2D	3D
Laminarian kelps	1071	655	3297	8	8	45 \pm 14
<i>Membranipora membranacea</i>	64 281	18 757	19 820	250	242	307 \pm 49
<i>Strongylocentrotus droebachiensis</i>	171 745	87 920	45 969	797	792	641 \pm 42

Table 3. Jaccard index of study taxa based on pairwise comparison of modelling approaches (1D, 2D, 3D) applied. See Section 2 for a full description of each approach

Taxon	1D and 2D	1D and 3D	2D and 3D
Laminarian kelps	0.61	0.32	0.20
<i>Membranipora membranacea</i>	0.20	0.16	0.43
<i>Strongylocentrotus droebachiensis</i>	0.25	0.13	0.30

approaches for all 3 taxa, varying by <3%. Maximum in-water distance was largest for the 3D approach for kelps and the bryozoan, whereas it was smallest for the sea urchin (Table 2).

The number of connections from the ESI to other coastal MPAs was consistent across approaches for species with short CPD (kelps), but variable for those with medium–long CPD (bryozoan and sea urchin; Table 4). For laminarian kelps, all 3 approaches predicted retention of propagules within the ESI and

no dispersal to adjacent MPAs. Retention of propagules within the ESI decreased with increasing CPD (Table 4). Some connections to MPAs northeast of the ESI were predicted by the 1D and 2D approaches, but not by the 3D approach. Conversely, a greater proportion of trajectories and therefore more connections with MPAs to the southwest were predicted by the 2D and 3D approaches than the 1D approach. The most notable differences among approaches were for the sea urchin, where the number of connections varied from 10 to 17. Like the bryozoan, most connections were southwest of the ESI, along the main direction of the Nova Scotia Current, particularly for the 2D and 3D approaches. Connections were more consistent between the 3D and 2D approaches than with the 1D approach (Table 4).

Dispersal patterns over time revealed differences in the number of propagules within each MPA throughout the CPD (Fig. S5). In general, there was a consistent supply of propagules to MPAs closer to the source MPA (the ESI) at all time points, with most propagules dispersing to MPAs southwest of their release location.

Table 4. Connectivity matrix from the Eastern Shore Islands into other existing and potential future coastal marine protected areas (MPAs). Columns represent each taxon and approach (1D, 2D, 3D), and values represent the connection strength. For the 1D and 2D approaches, a binary value (1 or 0) indicates whether the dispersal area and MPA polygons intersect (0 = no connection, 1 = connection in **bold**). For the 3D approach, **bold** cells indicate a connection, and the value in the cell represents the mean proportion of particle tracks (\pm SD) that passed through the MPA, averaged over the competent propagule duration (CPD) and across all runs (10 runs per taxon). See Table 1 for CPD values for each taxon. NWA: national wildlife area

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

The number of propagules within MPAs generally decreased as distance from the source MPA (the ESI) increased, with fewer than 100 propagules per model run ending up in the farthest reached MPAs.

4. DISCUSSION

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

4.1. Comparison of dispersal estimates among approaches

Kelps were the only taxon for which dispersal area and maximum in-water distance predicted using the 3D approach were greater than those predicted for the 1D and 2D approaches. This is likely because the linear approximation of particle displacement assumed by the 1D and 2D approaches oversimplifies the dynamics that affect particle dispersal, namely changing velocity fields with x , y , and z , and horizontal diffusion. However, as CPD increases, dispersal trajectories in 3D tend to scale sub-linearly compared to the 1D and 2D approaches. The ESI region is composed of 282 nearshore islands, which introduce eddies, drag, and small-scale variation in currents supporting retention of propagules (Jeffery et al. 2020, Feng et al. 2022). However, millions of propagules were tracked with the 3D approach and therefore subjected to many flow fields, potentially explaining the broader dispersal area observed. Our

measurements for maximum in-water distance (km to 10s of km) were similar to that estimated based on genetic structure of *Laminaria digitata* in the English Channel, using microsattellites (Billot et al. 2003, Couceiro et al. 2013), and spore dispersal for the giant kelp *Macrocystis pyrifera* at the San Clemente artificial reef (Reed et al. 2004) and the Carpinteria sand flat, both in California, USA (Gaylord et al. 2006). Because we do not account for the sexual reproduction phase of gametophytes in our simulations, our dispersal estimates should be interpreted as maximum dispersal potential. In *M. pyrifera*, tissue containing spores, called sori, is found at the base of the plant, whereas for the 2 dominant kelp species in Nova Scotia, *Saccharina latissima* and *L. digitata*, sori form at the distal end of the thallus and spores are released further from the substratum, possibly promoting wider spore dispersal (Billot et al. 2003). Additionally, canopy kelps can generate drag to flows at a magnitude equal to and opposing the horizontal pressure gradient force, resulting in a decrease in tidal currents by 40–80% in the interior of the kelp bed (Wu et al. 2017). Therefore, it is possible that propagules from canopy kelps disperse shorter distances than propagules from prostrate kelps. For a short-distance disperser such as kelps, habitat size and quality are typically the target metrics for protection, translating to the design principle of MPA size. To ensure an MPA is large enough to encapsulate the dispersal ability of a species with a short CPD, the 1D approach provides an adequate proxy.

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

East Australian Current (Roughan et al. 2011, 2022). Propagules of yellow tang *Zebrasoma flavescens* tracked off the island of Hawaii dispersed northward of their release locations following the dominant cyclonic eddy in the region (Christie et al. 2010).

4.2. Relative benefits of approaches

The benefits associated with the outputs of each of the 3 approaches for estimating dispersal are proportional to the cost of their calculation, in terms of time and resources. For instance, the input data and computation power needed to produce predictions for the 1D approach have the lowest cost but also a low benefit as the least data-informed, only accounting for CPD, spawning locations, and average current speed. Goetze et al. (2021) applied a similar distance-based metric (50 km radius) to assess the number of connections to each marine reserve in Australia, a distance suggested by Almany et al. (2009), as a between-reserve distance for maintaining demographic connectivity of corals and fish populations in this region. Alternatively, the cost to develop and run a fine-scale oceanographic model that can be used to estimate dispersal area (the 3D approach) is in the order of hundreds of thousands of dollars (Table S6). Those models combine modelled (and validated) data on ocean currents resolved at fine spatial scales (<1 km, depending on the local oceanography), knowledge of ontological and life history details, in addition to the life history information applied for the 1D approach. There are, however, proportional benefits to this investment, as outputs from the 3D approach capture individual propagule locations throughout their CPD, which can be used to produce a density map or connectivity matrix. Using a graph theoretic approach, connectivity metrics that quantitatively inform whether a population is a source, sink, stepping-stone, or central population can be extracted from a connectivity matrix. Several studies employ this methodology to discern spatial dependencies in various regions and answer both scientific and management-based questions (Trembl et al. 2008, Thomas et al. 2014, Álvarez-Romero et al. 2018, Ospina-Alvarez et al. 2020). Even though their geographic focus is rapidly expanding, many of these studies are still focussed on certain regions where biophysical model infrastructure exists. For example, in Canada, such oceanographic models at resolutions that are appropriate for nearshore systems (e.g. FVCOM models) currently exist for Nova Scotia and the Gulf of Maine (Feng et al. 2022), the Discovery Islands

(Foreman et al. 2012), Queen Charlotte Strait (Lin & Bianucci 2023), and Placentia Bay (Ma et al. 2012). Lastly, the 2D approach can be calculated with an intermediate-level cost of tens of thousands of dollars (Table S7) and benefit, compared to the 1D and 3D approaches. Time series of ocean currents are coupled with life history information on CPD, spawning locations, and a general spawning window, to produce a polygon describing dispersal area. This output is more data informed than that of the 1D approach because components of velocity in cross-shore and alongshore directions are applied to predict dispersal in 4 directions, 90° apart, independently.

4.3. Management implications

In our case study, we applied the 4 recommendations proposed by Balbar & Metaxas (2019) for incorporating connectivity into the design of MPAs. First, we identified 3 candidate taxa, with a range of life history characteristics, for which to consider dispersal patterns and estimate connectivity in the case study. We prioritized our efforts on keystone and foundation species, which is an effective strategy for making efficient use of resources for measuring dynamic processes such as dispersal (Jahnke et al. 2017, Alegría-Ortega et al. 2021). Second, we identified the role of the proposed ESI MPA in supporting connectivity, which varied depending on the dispersal ability of the taxa. We found that the ESI will (1) serve as a source area, primarily for MPAs downstream along the dominant current direction, for medium–long CPD dispersers and (2) be self-sustaining for short CPD dispersers. Identifying the role each MPA plays in supporting connectivity has also recently been adapted as a rule of thumb for operationalizing connectivity into MPA network design (Cannizzo et al. 2021). Third, we evaluated patterns of dispersal on the spatial scale of the potential future MPAs on the Atlantic coast of Nova Scotia. At spatial scales of management (>10s km), patterns of connectivity were most similar between the 2 more complex approaches, supporting application of the simplest of the 2 to the design or post hoc analysis of networks of MPAs. We applied the approaches to predict the number of connections from one source MPA to other potential future MPAs in an existing configuration. This post hoc assessment can be conducted prior to or after designation, depending on the research question. Alternatively, the approaches can be applied to the design process to help determine the size and spacing of MPAs, as was the case with the sim-

plest approach for the design of the network of MPAs along the coast of California (Carr et al. 2010, Moffitt et al. 2011). Fourth, we improved our regional knowledge of connectivity patterns. There have been recent advancements, both in Canada (Friesen et al. 2019, Kenchington et al. 2019, Cristiani et al. 2021) and internationally (Assis et al. 2021), in improving our understanding of regional patterns of connectivity to better inform management decisions.

Deciding which tool or approach to use to estimate patterns of dispersal and connectivity can be viewed as an optimization problem, where the goal is to maximize predictive ability, defined here as the ability to detect patterns at a defined spatial and temporal scale, given a set of limited resources. For example, the Atlantic coast of Nova Scotia is a region with a complex coastline, a series of coastal islands, prominent tides, and varied bathymetry, all of which influence current velocity over small spatial (10–100s m) and temporal scales (minutes to hours). Under these circumstances, the simplest approach does not capture the complexity of the system, making the other 2 approaches more appropriate, except for species with a short CPD, such as kelps. The approach of intermediate complexity can be used to identify patterns at the scale of management units with fewer resources than the most complex approach. Research questions that aim to identify patterns of dispersal and connectivity on evolutionary timescales should apply genetic methods, such as isolation-by-distance and gene flow, instead of the 3 approaches in this study. The 2D approach was developed for species for which dispersal is driven by ocean currents (e.g. planktonic spores and generally passive larvae), and may not be suitable for highly migratory species and those for which complex behaviours play a dominant role in dispersal patterns (e.g. larval fish). Additionally, the 2D approach is best suited for coastal regions with a dominant unidirectional offshore current and may not be suitable in the open ocean (e.g. ocean gyres) or where large-scale currents vary over distances smaller than the average dispersal capability of the species of interest. For conservation practices, the simpler approaches we used for estimating dispersal area can be applied to other coastal MPAs with unidirectional current regimes to identify their role in supporting connectivity for species or functional groups with different life history characteristics.

While research that addresses fundamental questions often prioritizes predictive ability, applied research for management is generally limited by resources, such as human capacity, limited time horizons, and limited availability of data, often resulting

in the application of ‘rules of thumb’ to inform size and spacing of MPAs in a network in place of more data-informed approaches (e.g. Carr et al. 2010). In our case study, the intermediate approach provides a compromise in terms of the cost of inputs and benefit of outputs and can be applied to regions where coastally resolved ocean models have not been developed, but time series data on ocean currents are available. The lower relative cost of the intermediate approach can facilitate faster decision making, particularly in light of global warming. This is important because delaying management action can result in greater habitat loss prior to MPA designation (Camaclang et al. 2022). However, understanding the relative importance of each site in a network can inform the best strategy for sequentially designating a series of MPAs to best achieve metapopulation persistence (Kininmonth et al. 2019).

4.4. Conclusions

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

Open research statement. The digital elevation model and spatial layer of relative wave exposure at 35 m resolution were obtained from DFO (O’Brien et al. 2022). The physio-

graphic coastline classification map was based on Greenlaw et al. (2013). Hindcast ocean current data were obtained from DFO (Feng et al. 2022). R code to produce the random forest model is available on request. R code for dispersal area is available as an R package called 'rcove' at <http://github.com/abalbar/rcove> and is archived on Zenodo (doi: 10.5281/zenodo.10059205).

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LITERATURE CITED

- Addison JA, Hart MW (2004) Analysis of population genetic structure of the green sea urchin (*Strongylocentrotus droebachiensis*) using microsatellites. *Mar Biol* 144:243–251
- Addison JA, Hart MW (2005) Colonization, dispersal, and hybridization influence phylogeography of North Atlantic sea urchins (*Strongylocentrotus droebachiensis*). *Evolution* 59:532–543
- Aiken CM, Navarrete SA, Castillo MI, Castilla JC (2007) Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. *Mar Ecol Prog Ser* 339:13–24
- Alegría-Ortega A, Sanín-Pérez MJ, Quan-Young LI, Londoño-Mesa MH (2021) Genetic structure of *Orbicella faveolata* population reveals high connectivity among a marine protected area and Varadero Reef in the Colombian Caribbean. *Aquat Conserv* 31:764–776
- Almany GR, Connolly SR, Heath DD, Hogan JD and others (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351
- Álvarez-Romero JG, Munguía-Vega A, Beger M, del Mar Mancha-Cisneros M and others (2018) Designing connected marine reserves in the face of global warming. *Glob Change Biol* 24:e671–e691
- Assis J, Failler P, Fragkopoulou E, Abecasis D and others (2021) Potential biodiversity connectivity in the network of marine Protected Areas in Western Africa. *Front Mar Sci* 8:765053
- Balbar AC (2023) abalbar/rcove: Alpha Release (v0.1.0). Zenodo. <https://doi.org/10.5281/zenodo.10059205>
- Balbar AC, Metaxas A (2019) The current application of ecological connectivity in the design of marine protected areas. *Glob Ecol Conserv* 17:e00569
- Beger M, Metaxas A, Balbar AC, McGowan JA and others (2022) Demystifying ecological connectivity for actionable spatial conservation planning. *Trends Ecol Evol* 37:1079–1091
- Billot C, Engel CR, Rousvoal S, Kloareg B, Valero M (2003) Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel. *Mar Ecol Prog Ser* 253:111–121
- Blackford C, Krkošek M, Fortin MJ (2021) A data-limited modeling approach for conserving connectivity in marine protected area networks. *Mar Biol* 168:86
- Briton F, Cortese D, Duhaut T (2018) High-resolution modeling of ocean circulation can reveal retention spots important for biodiversity conservation. *Aquat Conserv* 28:882–893
- Bryan-Brown DN, Brown CJ, Hughes JM, Connolly RM (2017) Patterns and trends in marine population connectivity research. *Mar Ecol Prog Ser* 585:243–256
- Buchwald R, Scheibling RE, Simpson AGB (2018) Detection and quantification of a keystone pathogen in a coastal marine ecosystem. *Mar Ecol Prog Ser* 606:79–90
- Camaclang AE, Chadès I, Martin TG, Possingham HP (2022) Predicting the optimal amount of time to spend learning before designating protected habitat for threatened species. *Methods Ecol Evol* 13:722–733
- Cannizzo ZJ, Lausche B, Wenzel L (2021) Advancing marine conservation through ecological connectivity: building better connections for better protection. *Parks Stewardship Forum* 37:477–487
- Carr MH, Saarman E, Caldwell MR (2010) The role of 'rules of thumb' in science-based environmental policy: California's Marine Life Protection Act as a case study. *Stanford J Law Sci Pol* 2:1–17, <https://law.stanford.edu/wp-content/uploads/2018/05/carr.pdf> (accessed 10 May 2022)
- Carr MH, Robinson SP, Wahle C, Davis G and others (2017) The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquat Conserv* 27:6–29
- CBD (Convention on Biological Diversity) (2022) Kunming–Montreal Global biodiversity framework. CBD/COP/15/L.25. Convention on Biological Diversity, Montreal
- Cecino G, Trembl EA (2021) Local connections and the larval competency strongly influence marine metapopulation persistence. *Ecol Appl* 31:e02302
- Chambers JC, Allen CR, Cushman SA (2019) Operationalizing ecological resilience concepts for managing species and ecosystems at risk. *Front Ecol Evol* 7:241
- Chapman ARO (1984) Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *J Exp Mar Biol Ecol* 78:99–109
- Christie MR, Tissot BN, Albins MA, Beets JP and others (2010) Larval connectivity in an effective network of marine protected areas. *PLOS ONE* 5:e15715
- Couceiro L, Robuchon M, Destombe C, Valero M (2013) Management and conservation of the kelp species *Laminaria digitata*: using genetic tools to explore the potential exporting role of the MPA 'Parc naturel marin d'Iroise.' *Aquat Living Resour* 26:197–205
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466
- Cristiani J, Rubidge E, Forbes C, Moore-Maley B, O'Connor MI (2021) A biophysical model and network analysis of invertebrate community dispersal reveals regional pat-

- terns of seagrass habitat connectivity. *Front Mar Sci* 8: 717469
- ✦ D'Aloia CC, Daigle RM, Côté IM, Curtis JMR, Guichard F, Fortin MJ (2017) A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. *Biol Conserv* 216: 93–100
- ✦ Daigle RM, Metaxas A, deYoung B (2014) Fine-scale distribution and spatial variability of benthic invertebrate larvae in an open coastal embayment in Nova Scotia, Canada. *PLOS ONE* 9:e106178
- ✦ Dakos V, Quinlan A, Baggio JA, Bennett E, Bodin Ö, Burnsilver S (2015) Principle 2 – Manage connectivity. In: Biggs R, Schlüter M, Schoon ML (eds) *Principles for building resilience: sustaining ecosystem services in social-ecological systems*. Cambridge University Press, p 80–104
- ✦ Eckman JE, Duggins DO, Sewell AT (1989) Ecology of understory kelp environments. I. Effects of kelps on flow and particle transport near the bottom. *J Exp Mar Biol Ecol* 129:173–187
- ✦ Feehan CJ, Scheibling RE (2014) Disease as a control of sea urchin populations in Nova Scotian kelp beds. *Mar Ecol Prog Ser* 500:149–158
- ✦ Feng T, Stanley RRE, Wu Y, Kenchington E, Xu J, Horne E (2022) A high-resolution 3-D circulation model in a complex archipelago on the coastal Scotian shelf. *J Geophys Res Oceans* 127:e2021JC017791
- ✦ Filbee-Dexter K, Scheibling RE (2017) The present is the key to the past: linking regime shifts in kelp beds to the distribution of deep-living sea urchins. *Ecology* 98: 253–264
- ✦ Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152
- ✦ Foreman MGG, Stucchi DJ, Garver KA, Tuele D and others (2012) A circulation model for the Discovery Islands, British Columbia. *Atmos-Ocean* 50:301–316
- ✦ Friesen SK, Martone R, Rubidge E, Baggio JA, Ban NC (2019) An approach to incorporating inferred connectivity of adult movement into marine protected area design with limited data. *Ecol Appl* 29:e01890
- ✦ Gaylord B, Reed DC, Raimondi PT, Washburn L (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. *Ecol Monogr* 76:481–502
- ✦ Goetze JS, Wilson S, Radford B, Fisher R and others (2021) Increased connectivity and depth improve the effectiveness of marine reserves. *Glob Change Biol* 27:3432–3447
- ✦ Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Greenlaw M, Gromack A, Basquill SP, Mackinnon D and others (2013) A physiographic coastline classification of the Scotian Shelf bioregion and environs: the Nova Scotia coastline and the New Brunswick Fundy Shore. DFO Can Sci Advis Sec Res Doc 2012/051. Fisheries and Oceans Canada, Ottawa
- ✦ Hijmans RF (2023) raster: Geographic Data Analysis and Modeling. R package version 3.6-21. <https://rspatial.org/raster>
- ✦ Hilty J, Worboys GL, Keeley A, Woodley S and others (2020) Guidelines for conserving connectivity through ecological networks and corridors. Best Practice Protected Area Guidelines Series No. 30. International Union for the Conservation of Nature, Gland
- ✦ Himmelman JH (1978) Reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*. *Can J Zool* 56:1828–1836
- ✦ Jahnke M, Casagrandi R, Melià P, Schiavina M, Schultz ST, Zane L, Procaccini G (2017) Potential and realized connectivity of the seagrass *Posidonia oceanica* and their implication for conservation. *Divers Distrib* 23:1423–1434
- ✦ Jeffery NW, Heaslip SG, Stevens LA, Stanley RRE (2020) Biophysical and ecological overview of the Eastern Shore Islands area of interest (AOI). Res Doc 2019/025. Canadian Science Advisory Secretariat, Fisheries and Oceans Canada. <https://waves-vagues.dfo-mpo.gc.ca/library-bibliotheque/40885045.pdf> (accessed 13 September 2022)
- ✦ Kelly JR, Scheibling RE, Balch T (2011) Invasion-mediated shifts in the macrobenthic assemblage of a rocky subtidal ecosystem. *Mar Ecol Prog Ser* 437:69–78
- ✦ Kenchington E, Wang Z, Lirette C, Murillo FJ, Guijarro J, Yashayaev I, Maldonado M (2019) Connectivity modelling of areas closed to protect vulnerable marine ecosystems in the northwest Atlantic. *Deep Sea Res I* 143: 85–103
- ✦ Kininmonth S, Weeks R, Abesamis RA, Bernardo LPC and others (2019) Strategies in scheduling marine protected area establishment in a network system. *Ecol Appl* 29: e01820
- ✦ Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. *Landsc Ecol* 28:165–185
- ✦ Krumhansl KA, Scheibling RE (2011) Detrital production in Nova Scotian kelp beds: patterns and processes. *Mar Ecol Prog Ser* 421:67–82
- ✦ Lagabrielle E, Crochelet E, Andrello M, Schill SR, Arnaud-Haond S, Alloncle N, Ponge B (2014) Connecting MPAs — eight challenges for science and management. *Aquat Conserv* 24:94–110
- ✦ Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecol Appl* 13: 71–89
- ✦ Lequeux BD, Ahumada-Sempol MA, López-Pérez A, Reyes-Hernández C (2018) Coral connectivity between equatorial eastern Pacific marine protected areas: a biophysical modeling approach. *PLOS ONE* 13:e0202995
- ✦ Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282–297
- ✦ Lin Y, Bianucci L (2023) Seasonal variability of the ocean circulation in Queen Charlotte Strait, British Columbia. *Atmos-Ocean* doi:10.1080/07055900.2023.2184321
- ✦ Ma Z, Han G, deYoung B (2012) Modelling temperature, currents and stratification in Placentia Bay. *Atmos-Ocean* 50:244–260
- ✦ Meidel SK, Scheibling RE (1998) Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. *Mar Biol* 131:461–478
- ✦ Metaxas A, Saunders M (2009) Quantifying the 'bio-' components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. *Biol Bull* 216:257–272
- ✦ Moffitt EA, Wilson White J, Botsford LW (2011) The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. *Biol Conserv* 144:306–318
- ✦ O'Brien JM, Wong MC, Stanley RRE (2022) A relative wave

- exposure index for the coastal zone of the Scotian Shelf–Bay of Fundy Bioregion. figshare. <https://doi.org/10.6084/m9.figshare.c.5433567>
- Ospina-Alvarez A, de Juan S, Alós J, Basterretxea G and others (2020) MPA network design based on graph theory and emergent properties of larval dispersal. *Mar Ecol Prog Ser* 650:309–326
- Pearce CM, Scheibling RE (1991) Effect of macroalgae, microbial films, and conspecifics on the induction of metamorphosis of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *J Exp Mar Biol Ecol* 147:147–162
- Pebesma E (2018) Simple features for R: standardized support for spatial vector data. *R J* 10:439–446
- Pineda J, Hare JA, Sponaugle SU (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:22–39
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Real R, Vargas JM (1996) The probabilistic basis of Jaccard's index of similarity. *Syst Biol* 45:380–385
- Reed DC, Schroeter SC, Raimondi PT (2004) Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J Phycol* 40:275–284
- Roughan M, Macdonald HS, Baird ME, Glasby TM (2011) Modelling coastal connectivity in a Western Boundary Current: seasonal and inter-annual variability. *Deep Sea Res II* 58:628–644
- Roughan M, Cetina-Heredia P, Ribbat N, Suthers IM (2022) Shelf transport pathways adjacent to the East Australian Current reveal sources of productivity for coastal reefs. *Front Mar Sci* 8:789687
- Saunders M, Metaxas A (2007) Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada. *Mar Ecol Prog Ser* 344:95–106
- Saunders MI, Metaxas A (2010) Physical forcing of distributions of bryozoan cyphonautes larvae in a coastal embayment. *Mar Ecol Prog Ser* 418:131–145
- Scheibling R (1986) Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia* 68:186–198
- Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. *Can J Fish Aquat Sci* 56:2300–2314
- Schill SR, Raber GT, Roberts JJ, Treml EA, Brenner J, Halpin PN (2015) No reef is an island: integrating coral reef connectivity data into the design of regional-scale marine protected area networks. *PLOS ONE* 10:e0144199
- Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. *Biol Bull* 216:373–385
- Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ (2013) Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol Evol* 3:4016–4038
- Smith J, Metaxas A (2018) A decision tree that can address connectivity in the design of Marine Protected Area networks (MPAn). *Mar Policy* 88:269–278
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Strathmann R (1978) Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. *J Exp Mar Biol Ecol* 34:23–27
- Thomas CJ, Lambrechts J, Wolanski E, Traag VA, Blondel VD, Deleersnijder E, Hanert E (2014) Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef. *Ecol Model* 272:160–174
- Tremblay MJ (2002) Large epibenthic invertebrates in the Bras d'Or Lakes. *Proc N S Inst Sci* 42:101–126
- Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modelling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landsc Ecol* 23:19–36
- van Etten J (2017) R Package gdistance: distances and routes on geographical grids. *J Stat Softw* 76:1–21
- Ward M, Saura S, Williams B, Ramirez-Delgado JP and others (2020) Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nat Commun* 11:4563
- Watanabe S, Scheibling RE, Metaxas A (2010) Contrasting patterns of spread in interacting invasive species: *Membranipora membranacea* and *Codium fragile* off Nova Scotia. *Biol Invasions* 12:2329–2342
- Wickham H, Averick M, Bryan J, Chang W and others (2019) Welcome to the tidyverse. *J Open Source Softw* 4:1686
- Wilson KL, Tittensor DP, Worm B, Lotze HK (2020) Incorporating climate change adaptation into marine protected area planning. *Glob Change Biol* 26:3251–3267
- Wu Y, Hannah CG, O'Flaherty-Sproul M, Thupaki P (2017) Representing kelp forests in a tidal circulation model. *J Mar Syst* 169:73–86

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