



RESEARCH ARTICLE

Climate change and vessel traffic create networks of invasion in marine protected areas

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Abstract

1. Establishment of protected areas to maintain biodiversity requires identification, prioritization and management of stressors that may undermine conservation goals. Nonindigenous species and climate change are critical ecosystem stressors that need greater attention in the context of spatial planning and management of protected areas. Risk of invasion into protected areas needs to be quantified under current and projected climate conditions in conjunction with prioritization of key vectors and vulnerable areas to enable development of effective management strategies.
2. We assessed the likelihood of invasion across networks of marine protected areas (MPAs) to determine how invaded MPAs may compromise MPA networks by sharing nonindigenous species. We evaluated invasion risk in 83 MPAs along Canada's Pacific coast for eight nonindigenous species based on environmental suitability under current and future (average conditions from 2041 to 2070) climate conditions and association with shipping and boating pathways. We applied species distribution models and network analysis of vessel tracking data for 805 vessels in 2016 that connected MPAs.
3. The probability of occurrence within MPAs and the proportion of MPA area that is suitable to the modelled species significantly increased under future climate conditions, with six species reaching over 90% predicted occurrence across MPAs and over 70% of suitable area within MPAs. Vessel traffic created four network clusters of 61 highly connected MPAs that spanned the coastline. Occupancy of over 90% of the MPAs within the clusters was predicted for most species.
4. *Synthesis and applications.* Our results indicate a high likelihood of marine protected area (MPA) network invasion based on current and future environmental conditions and vectors of spread, and the potential for extensive nonindigenous species distributions within MPAs. Our approach highlights how interacting stressors can exacerbate MPA susceptibility to nonindigenous species, adding further challenges for protected area management. Management planning that invests in understanding connectivity and vector processes (human behaviours)

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is more likely to derive effective policies to stem the flow of nonindigenous species under both current and future conditions. In particular, biosecurity measures including vessel biofouling regulations and MPA- and MPA network-specific plans for prevention, monitoring and mitigation of nonindigenous species are needed.

KEYWORDS

automatic identification systems, biosecurity regulations, conservation areas, invasive alien species, network analysis, ship and boat vectors, species distribution models, species range shifts

1 | INTRODUCTION

The Convention on Biological Diversity Aichi Targets call for a global increase in 'ecologically representative and well-connected systems of protected areas' alongside management and mitigation of ecosystem stressors including invasive, nonindigenous species and climate change (Targets 9–11). Marine protected areas (MPAs) covered 6 million km² in 2018 and increased to 29 million km² by January 2020, with a goal of 36 million km² protected by the end of 2020 (UNEP-WCMC, IUCN, & NGS, 2018, 2020). Nonindigenous species invasions may be effectively reduced by protection of relatively pristine areas and restriction of human activities (Gallardo et al., 2017). MPAs may also buffer the effects of climate change more than unprotected areas by maintaining diverse and abundant biota (creating functional redundancy) and preventing carbon loss by avoiding habitat disturbance (Roberts et al., 2017). Despite these benefits, MPAs are still susceptible to ocean warming and to invasions from unmanaged pathways and species redistribution. The protected status of MPAs make them key focal areas for understanding the impacts of stressors, and MPA legislation, regulations and policies provide managers with the tools to regulate some of these stressors.

Nonindigenous species are prevalent in MPAs globally (Iacarella, Saheed, Dunham, & Ban, 2019), and some have had large impacts on protected communities (Coma et al., 2011; Gallagher et al., 2017; Kaplan et al., 2018). However, vectors of nonindigenous species are rarely considered in spatial planning or restricted in MPA management plans (Giakoumi et al., 2016; Iacarella, Saheed, et al., 2019; Mačić et al., 2018). Ships and boats are the most prevalent vectors in marine systems through organism entrainment in ballast water and biofouling (Molnar, Gamboa, Revenga, & Spalding, 2008; Williams et al., 2013). Whether a nonindigenous species will establish upon introduction depends on propagule pressure (number of individuals released and number of release events), environmental suitability and biotic interactions with the resident community (Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005).

Shifts in environmental suitability from climate change will alter the composition of native and nonindigenous species currently present in protected areas, as well as the likelihood of future invasions. Warmer temperatures have caused nonindigenous species outbreaks (Walther et al., 2009) and can alter impact potential (Hellmann, Byers, Bierwagen, & Dukes, 2008). The rate and

prevalence of range expansions and contractions are predicted to vary across biomes and taxa. For nonindigenous species, freshwater and terrestrial invertebrate ranges are expected to expand globally, whereas ranges of invasive birds and amphibians are expected to contract (Bellard et al., 2013). In marine systems, global models predict range expansions to dominate over contractions with invasions generally adding species to communities without extirpation (García Molinos et al., 2015). Climate-induced changes in environmental suitability will interact with changes in shipping and other pathways to provide new opportunities for the introduction and spread of nonindigenous species (Ricciardi et al., 2017). For many MPAs, there is little understanding of the strength of invasion pathways, how invasions will change under future climate conditions and how this will vary by species. Consequently, many MPAs lack effective management strategies for nonindigenous species invasions.

Marine spatial planning designs benefit from high connectivity among MPAs by ensuring larval, nutrient and energy flow (Balbar & Metaxas, 2019). However, high connectivity for nonindigenous species in the form of self-dispersal or human-mediated vectors can lead to many MPAs in a network becoming susceptible to the impacts of an invader. At the individual MPA level, invasion risk should be considered from proximal sources and vectors moving from unprotected, invaded areas into MPAs as nonindigenous species may enter an MPA from a multitude of sources and locations (Iacarella, Burke, et al., 2020). A systematic analyses of these various sources and locations is beyond the scope of this study, rather we focus here on investigating the potential that upon entry, an invader may be further spread to other MPAs within a network provided network connections. We evaluate the likelihood of domestic, secondary spread of nonindigenous species among MPAs by measuring two components of establishment potential: environmental suitability and anthropogenic vector strength via ships and boats. We predict environmental suitability under current and future climate conditions for eight nonindigenous species that are currently present along the coast of British Columbia (BC), Canada and pair this with analysis of vessel traffic patterns to characterize networks of invasion potential across MPAs. We expect that MPAs that have high environmental suitability and strong vessel connections among MPAs are likely to share nonindigenous species. We suggest that when managing MPA networks, either as pre-designated networks or networks based on connection strength, the nonindigenous species that are predicted to be able to invade

many of the MPAs within the network (and have high impacts) are those that should be prioritized. Our results identify nonindigenous species, vessel connections and MPA networks that can be targeted by management efforts using protected area legislation (e.g. mandated cleaning practices before entry or prior to departing). This provides first-step measures of the three components of invasions—species, pathways and sites—that must form prioritization assessments for decision making to achieve Aichi Targets (McGeoch et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Environmental suitability in MPAs

Eight nonindigenous, noncultured species were selected for analysis of environmental suitability based on high likelihood of invasion and impact (i.e. risk) in Canada's Pacific coast waters (Drolet

et al., 2016) and adequate geospatial records for model fitting. All of these nonindigenous species are currently present in the study area, and include *Styela clava* (tunicate), *Botryllus schlosseri* (tunicate), *Didemnum vexillum* (tunicate), *Botrylloides violaceus* (tunicate), *Carcinus maenas* (crab), *Ocenebrellus inornatus* (snail), *Caprella mutica* (amphipod) and *Sargassum muticum* (seaweed; hereafter referred to by genus; Table 1). Tunicates comprise half of the modelled species as they represent high risk species with a demonstrated propensity to foul vessel hulls (Clarke Murray, Pakhomov, & Therriault, 2011; Clarke Murray et al., 2014; Therriault & Herborg, 2007). Although they are often found on artificial structures, they can invade natural substrates and impact native benthic communities (Kaplan et al., 2018; Simkanin, Davidson, Dower, Jamieson, & Therriault, 2012).

Species occurrence records were collected from the scientific and technical literature, online databases and Fisheries and Oceans Canada monitoring programmes for the Pacific coast from Baja California, Mexico to the Gulf of Alaska (24–62°N and

TABLE 1 Primary introduction and spread details of nonindigenous species included in environmental suitability analysis for British Columbia, Canada (Fofonoff et al., 2018; Molnar et al., 2008; see Appendix S3 for maps of distributions)

Nonindigenous species	Origin	Introduction vectors	Impacts	Larval settlement	Self-dispersal potential	Year first obs., distribution in BC
<i>Styela clava</i>	Asia	Shipping, aquaculture	Modifies native habitat; competes for food and space resources	Immediate to <1 day (anchiplanic)	Limited	1994, limited to southern extent
<i>Botryllus schlosseri</i>	Europe	Shipping, aquaculture	Modifies native habitat; overgrows and competes with attached, filter-feeding organisms	Immediate to <1 day (anchiplanic)	Limited	1998, widespread
<i>Didemnum vexillum</i>	Japan	Shipping, aquaculture	Modifies native habitat by forming dense mats along seabed; changes benthic community composition	Immediate to <1 day (anchiplanic)	Limited	2003, limited to southern extent
<i>Botrylloides violaceus</i>	Asia	Shipping, aquaculture	Competes for space resources; becomes a permanent member of the community, but not likely to replace present native species	Immediate to <1 day (anchiplanic)	Limited	1992, widespread
<i>Carcinus maenas</i>	Europe	Shipping, aquaculture, live seafood trade, aquarium trade	Voracious predator that has caused declines in crab and bivalve species	25–90 days (anchiplanic)	Moderate distance as larvae and megalopa	1999, limited to exposed southern extent, actively spreading north
<i>Ocenebrellus inornatus</i>	Asia	Aquaculture	Outcompetes native predatory sea snails	None, crawl away larvae (aplantic)	Limited	1935, limited to southern extent
<i>Caprella mutica</i>	Siberia	Shipping, aquaculture	Competes for food and space resources	None, free-swimming juvenile	Long-distance by rafting on drifting algae, localized free-swimming	2006, widespread
<i>Sargassum muticum</i>	Asia	Shipping, aquaculture	Modifies native habitat by forming dense monospecific stands; strong competitor for space and light	Immediate	Long-distance drifting vegetation	1955, widespread

111–155°W; see Appendix S1 for species sample sizes and data sources). Some of the tunicates, such as *Botryllus*, may represent different clades of the same species complex (e.g. Nydam, Giesbrecht, & Stephenson, 2017). The models may over- or underestimate environmental suitability of these species if genetic differences between clades results in different environmental tolerances. However, in the absence of confirmed data on genetic structure or reported differences in tolerances along the west coast of North America, we treated all possible clades within each species complex together as a single species. Species records and present-day seasonal, sea surface temperature and salinity climatologies were used to fit species distribution models at a resolution of 0.04° (3.8 × 3.8 km) in MAXENT (v. 3.4.1; Phillips, Dudik, & Schapire, 2017), which is designed specifically for presence-only data (Elith et al., 2011). All models were fit using 30-fold random cross validation to assess uncertainty and estimate confidence intervals, except 19-fold random cross validation was used for *Ocinebrellus* owing to fewer observational records. Future environmental suitability was similarly modelled using temperature and salinity projections from the BC ROMS model (RCP 8.5, 2041–2070; Peña, Fine, & Masson, 2018). Environmental suitability was predicted for waters shallower than 200 m, the estimated maximum survivable depth for the modelled nonindigenous species (Herborg, O'Hara, & Therriault, 2009; Locke, Hanson, Ellis, Thompson, & Rochette, 2007; Therriault & Herborg, 2008).

Eighty-three of 195 MPAs within BC were compiled as those that have (a) a management plan or draft/interim plan (excluded 49), (b) a purpose statement or zoning plan within these documents that identified a marine conservation value (excluded 61) and (c) a spatial extent within waters shallower than 200 m (excluded 2). MPA spatial

extents were trimmed to contain only depths ≤200 m to match environmental suitability models. MPAs were then spatially overlaid with species distribution models and assigned gridded occurrence probability values (ArcGIS v. 10.4; Figure 1). Seven MPAs with low model coverage (i.e. in inlets; future climate models with ≤17% cover) were excluded, retaining 76 for environmental suitability analysis. Any spatial extent within MPAs that was missing model coverage was not considered in the environmental suitability analysis (10 of 76 MPAs had 75%–99% coverage for current and future climate models, the remainder had 100% coverage); we determined that extrapolation would be inaccurate as model coverage was primarily missing from MPA extents that were further inland and often associated with freshwater input. For both climate models, 16 MPAs intersected one gridded occurrence probability value ('cell'), 46 intersected 2–14 cells and 14 intersected 14–315 cells (Appendix S2, Figure S1).

Environmental suitability for each MPA, k , was calculated as (a) the probability of occurrence of species j in at least one cell l and (b) the proportion of MPA k area that is suitable for species j . The probability of at least one occurrence was calculated as 1 – the product of the probabilities of cell-level non-occurrence (Williams & Araújo, 2002):

$$p_{jk} = 1 - \prod_{l=1}^L (1 - p_{jkl}), \quad (1)$$

where p_{jk} is the probability species j is present in MPA k , and p_{jkl} are the gridded probabilities of occurrence estimated by the species distribution models. For example, the probability of occurrence in Figure 1 is $1 - [(1 - 0.18) \times [1 - 0.17] \times [1 - 0.18] \times [1 - 0.21)] = 0.56$. The total expected number of nonindigenous species that can occur

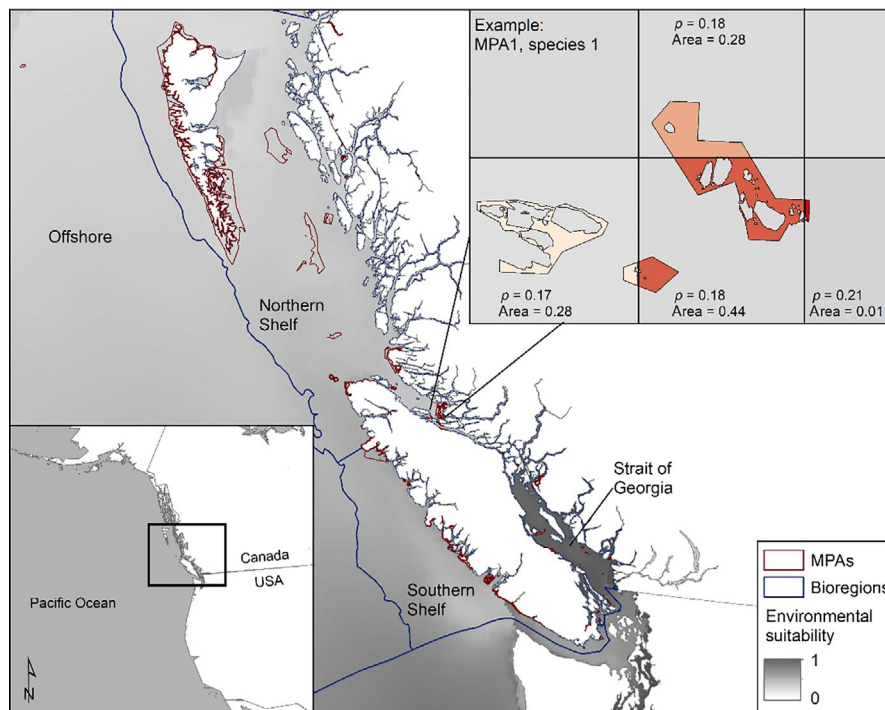


FIGURE 1 Marine bioregions of British Columbia, Canada and marine protected areas (MPAs) included in the study. Inset: Occurrence probability values (' p ') for areas of an MPA that overlap species distribution model cells (3.8 × 3.8 km). The area of the MPA that falls within a cell is calculated as the proportion of the total MPA area

in MPA k ($E(S_k)$) is, then, the sum of the probabilities of occurrence in at least one cell for each species (Calabrese, Certain, Kraan, & Dormann, 2014):

$$E(S_k) = \sum_{j=1}^J p_{jk}. \quad (2)$$

Similarly, the number of MPAs in which species j is expected to be able to occur ($E(M_j)$) was the sum of the probabilities of occurrence for each MPA:

$$E(M_j) = \sum_{k=1}^K p_{jk}. \quad (3)$$

We applied nonparametric bootstrapping with replacement ($n = 2,000$) to Maxent model replicates and used the randomly selected models for Equations 2 and 3 to obtain mean and 95% confidence interval estimates of nonindigenous species richness and occurrence across MPAs by species respectively. Lastly, the proportion of MPA k area that is suitable for species j was calculated as the sum of cell probabilities multiplied by the proportion of MPA k area that they cover:

$$H_{jk} = \sum_{l=1}^L (p_{jl} \times a_l), \quad (4)$$

where a_l is the proportion of the area of MPA k filled by cell l . For example in Figure 1, the proportion of area that is suitable is $(0.18 \times 0.28) + (0.17 \times 0.28) + (0.18 \times 0.44) + (0.21 \times 0.01) = 0.18$. The means of cell probabilities across model replications for each species were used for this calculation.

2.2 | Vessel traffic connections

We identified how vessel traffic links MPAs and contributes to across-MPA invasion risk for MPA network-level management prioritization. Vessel traffic connections between the 83 MPAs were determined using hourly automatic identification system data for 2016 (MarineTraffic; <https://www.marinetraffic.com>). We focused on vessel traffic within MPAs, not outside and found in preliminary analyses that vessel densities were similarly high within MPAs as within comparable, outside buffer extents (Appendix S2, Figure S2). For the 805 vessels that entered at least two MPAs (of an original 8,142), shortest-path overwater routes were interpolated using a network grid of 1-km-sided triangles and coastline. Route segments that connected points within MPAs were intersected by the MPAs to determine the route length within and outside. Duration within MPAs and vessel speed was calculated for each connection created by a vessel moving between two MPAs. Only connections with vessel speeds ≤ 20.5 m/s were retained as this is the maximum speed reported for the tracked vessel types (Clarke Murray et al., 2011). Vessel duration within MPAs was calculated as the

total duration within two connected MPAs across multiple connections made by vessels, which was used to identify MPAs that are highly connected to each other. We chose vessel duration as a measure of connection strength given that more time in MPAs increases risk of nonindigenous species vector colonization and introduction (Carlton & Hodder, 1995; Minchin & Gollasch, 2003), whereas the invasion risk created by the number of vessels that enter an MPA is dependent on their duration within the MPA. Other vessel characteristics such as hull fouling surface area, history of antifouling treatments, ballast and bilge tank size and uptake/release activities also mediate invasion risk; however, these components require detailed information that is more conducive to an individual MPA risk analysis. MPA vessel traffic network clusters (i.e. highly connected MPAs) were identified by weighting paired MPA connections based on vessel durations and analysing MPA community structure using fast greedy modularity optimization ('IGRAPH' in R; Clauset, Newman, & Moore, 2004; Csardi & Nepusz, 2006). The number of MPAs in which each nonindigenous species was expected to occur was applied to the clusters using Equation 3; none of the seven MPAs with low species distribution model coverage were retained in the cluster analysis as they also had low vessel traffic.

2.3 | Statistical analysis

Linear regressions were run to test: (a) the interactive and additive effects of species and climate (current, future) on the probability of occurrence within an MPA and the proportion of MPA area that is suitable; and (b) the interactive effects of bioregion (Strait of Georgia, Southern Shelf and Northern Shelf including one northern offshore MPA) and proportion of an MPA that is nearshore (<20 m depth) on the proportion of an MPA that is suitable for each species and climate combination separately. Bioregion and proportion of nearshore area were selected as two descriptors of MPAs that can be used to explore how environmental suitability varies across MPAs coastwide. Top models were selected by evaluating all possible predictor combinations based on Akaike information criterion (AIC) and AIC weights ('MuMIn' package in R; Bartón, 2009); the second best-fit model was selected in cases where $\Delta AIC < 2$. Additive effects of climate and bioregion were also tested on average temperature and salinity within MPAs. Tukey contrasts were used to determine significant differences between factor levels and interaction terms. All analyses were done in R (R Development Core Team, 2018).

3 | RESULTS

The expected richness and probability of occurrence for nonindigenous species was generally high across MPAs under current conditions and increased under future conditions (Figure 2, see Appendix S3 for species-specific maps). Across MPAs and species, probability of

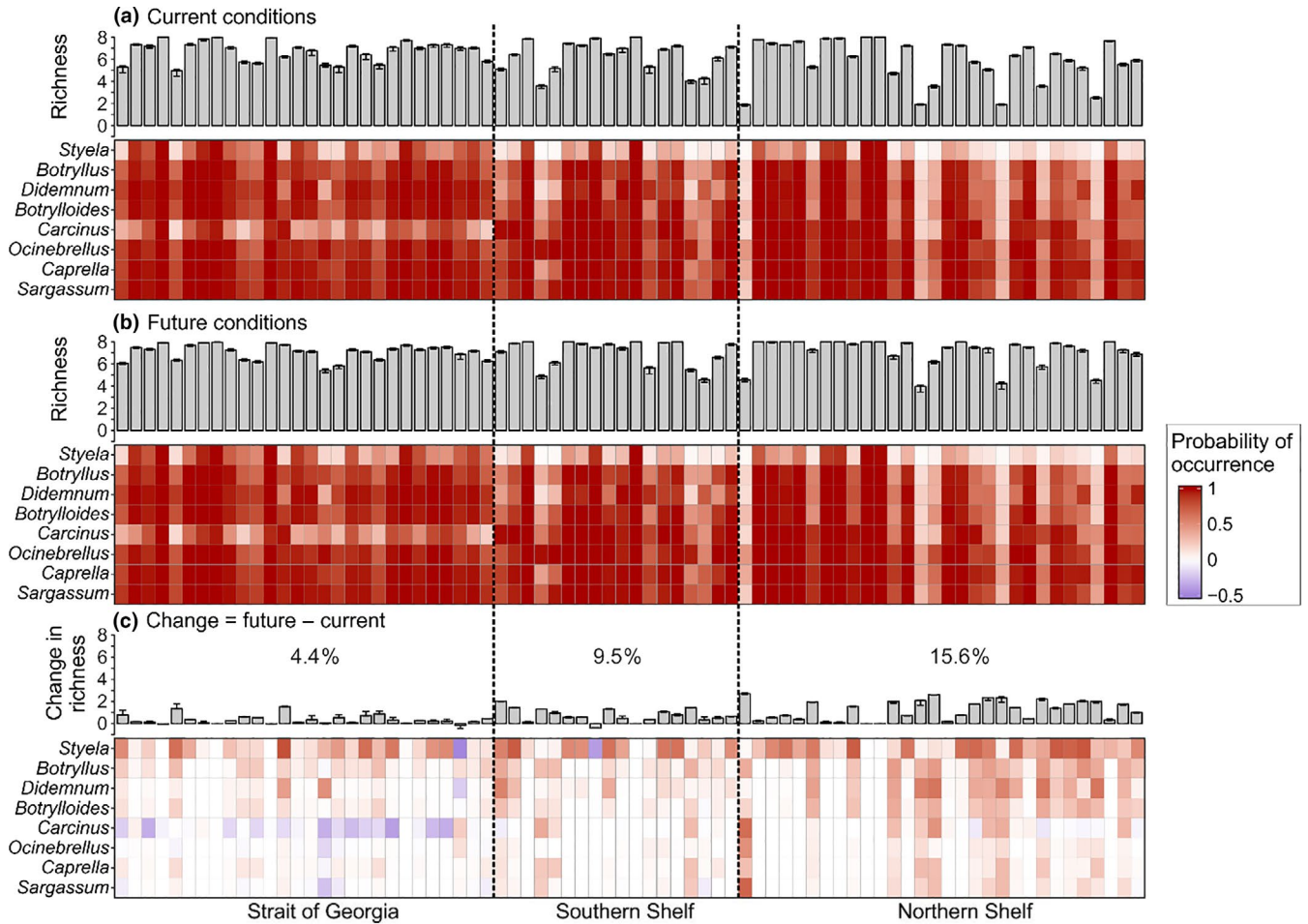


FIGURE 2 Expected richness (bars) and probability of occurrence (matrix) in marine protected areas for eight nonindigenous species by bioregion. Environmental suitability was estimated for (a) current climate conditions, (b) future (average conditions from 2041 to 2070) conditions and (c) the change from current to future conditions. Richness bars are the mean of bootstrapped species distribution models \pm 95% CIs, and mean change within bioregions is in text

occurrence increased in 82% of cases (497 of 608) and decreased in only 14% of cases (84 of 608). MPAs with maximal expected richness (7–8 species) increased by 24% from 35 to 53 MPAs (of 76) under future conditions; richness declined slightly for five MPAs (-0.13 ± 0.14 ; Figure 2; Appendix S2, Figure S3). Overall, nonindigenous species richness increased the most in the Northern Shelf bioregion (15.6%), followed by the Southern Shelf (9.5%) and Strait of Georgia (4.4%).

Species and climate had an interactive effect on the probability of occurrence within an MPA (Top model, $F_{15,1200} = 29.08$, $p < 0.001$, adj. $r^2 = 0.26$) and the proportion of MPA area that is suitable ($F_{15,1200} = 48.29$, $p < 0.001$, adj. $r^2 = 0.37$; Figure 3). *Caprella* had the highest environmental suitability values, whereas *Styela* had the lowest (Tukey contrasts, $p < 0.001$), followed by *Carcinus* ($p < 0.002$; Figure 3). The proportion of MPA area that is suitable was mediated by bioregion for all species and climate projections (Table 2); nonindigenous species had greater environmental suitability in MPAs within the Strait of Georgia, except for *Carcinus* which had higher suitability in the Southern Shelf (Appendix S2, Figure S4). The proportion of nearshore area within

MPAs had additive or interactive effects with bioregion for all species except for *Caprella*; however, the direction and strength of the effect varied by species (Appendix S2, Figure S4). Surface water temperature within MPAs increased under future climate conditions (Tukey contrasts, $p < 0.001$) and was higher in the Strait of Georgia than the other bioregions ($p < 0.001$; Full model, $F_{3,604} = 96.60$, $p < 0.001$, adj. $r^2 = 0.32$). Salinity did not change significantly with future climate ($p > 0.05$), but was higher in the Northern Shelf ($p < 0.001$; $F_{3,604} = 27.70$, $p < 0.001$, adj. $r^2 = 0.12$; Appendix S2, Figure S5).

Vessel traffic connected 61 of the original 83 MPAs (73%) and created four clusters of highly connected MPAs (Figure 4). All the clusters contained MPAs that extended across the BC coastline. The probability of occurrence of modelled species was generally 80%–90% across MPAs within vessel clusters, with fewer suitable MPAs for *Styela* (Figure 5). Probability of occurrence within clusters increased the most under future conditions for *Styela*, followed by the other three modelled tunicates. For *Carcinus*, probability of occurrence increased in the two clusters that cover the Southern Shelf bioregion and the Central Coast

FIGURE 3 Environmental suitability within marine protected areas (MPAs) for eight modelled nonindigenous species under current (light grey) and future (dark grey) climate conditions. The probability of occurrence within an MPA (a) and proportion of MPA area that is suitable (b) increases under future climate conditions. Bars are the mean across replicate models and MPAs \pm 95% CIs; “*” indicate nonindigenous species that have significantly lower values than all others ($p \leq 0.002$)

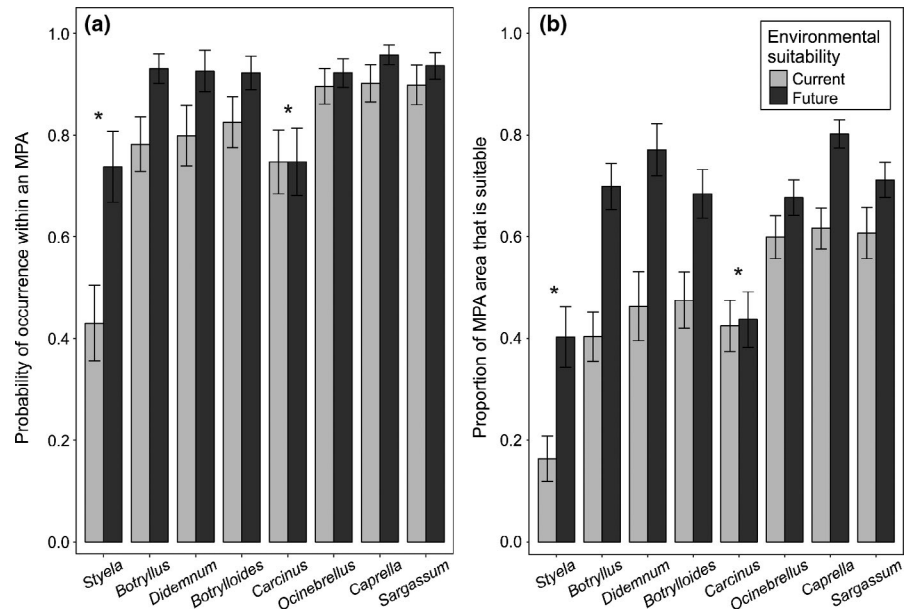


TABLE 2 Regression model terms for the additive (+) and interactive (‘:’) effect of bioregion (Strait of Georgia, Southern Shelf, Northern Shelf) and proportion of the marine protected area (MPA) that is nearshore (<20 m depth; significant slopes provided, ‘m’) on the proportion of MPA area that is suitable for nonindigenous species, separately by species and climate projections. Significance of model terms (‘NS’ for $p > 0.05$), top model test statistics, adjusted r^2 and Akaike information criterion weight (‘AIC_w’) are provided

Nonindigenous species	Climate	Bioregion	Nearshore	Bioregion: Nearshore	Top model statistics	Adj. r^2	AIC _w
<i>Styela clava</i>	Current	$p < 0.001$	NS	NS	$F_{2,73} = 67.16, p < 0.001$	0.64	0.36
	Future	+	+	$p = 0.04$; Southern Shelf, $m = -0.29$	$F_{5,70} = 34.89, p < 0.001$	0.69	0.60
<i>Botryllus schlosseri</i>	Current	$p < 0.001$	$p = 0.01, m = 0.05$	NS	$F_{3,72} = 286.00, p < 0.001$	0.92	0.72
	Future	+	+	$p = 0.005$; Southern Shelf, $m = -0.18$; Northern Shelf, $m = 0.15$	$F_{5,70} = 41.29, p < 0.001$	0.73	0.93
<i>Didemnum vexillum</i>	Current	$p < 0.001$	NS	NS	$F_{2,73} = 97.77, p < 0.001$	0.72	0.68
	Future	$p < 0.001$	$p = 0.05, m = -0.13$	NS	$F_{3,72} = 9.68, p < 0.001$	0.26	0.44
<i>Botrylloides violaceus</i>	Current	$p < 0.001$	$p = 0.04, m = 0.06$	NS	$F_{3,72} = 209.70, p < 0.001$	0.89	0.26
	Future	+	+	$p = 0.004$; Southern Shelf, $m = -0.24$; Northern Shelf, $m = 0.13$	$F_{5,70} = 38.37, p < 0.001$	0.71	0.94
<i>Carcinus maenas</i>	Current	+	+	$p = 0.01$; Northern Shelf, $m = 0.24$	$F_{5,70} = 13.80, p < 0.001$	0.46	0.83
	Future	+	+	$p = 0.03$; Northern Shelf, $m = 0.30$	$F_{5,70} = 27.66, p < 0.001$	0.64	0.84
<i>Ocinebrellus inornatus</i>	Current	$p < 0.001$	$p = 0.03, m = 0.09$	NS	$F_{3,72} = 34.32, p < 0.001$	0.57	0.50
	Future	+	+	$p = 0.03$; Northern Shelf, $m = 0.24$	$F_{5,70} = 11.07, p < 0.001$	0.40	0.85
<i>Caprella mutica</i>	Current	$p < 0.001$	NS	NS	$F_{2,73} = 134.80, p < 0.001$	0.78	0.64
	Future	$p < 0.001$	NS	NS	$F_{2,73} = 46.71, p < 0.001$	0.55	0.46
<i>Sargassum muticum</i>	Current	$p < 0.001$	$p = 0.04, m = 0.06$	NS	$F_{3,72} = 174.30, p < 0.001$	0.87	0.65
	Future	$p < 0.001$	NS	NS	$F_{2,73} = 56.81, p < 0.001$	0.60	0.38

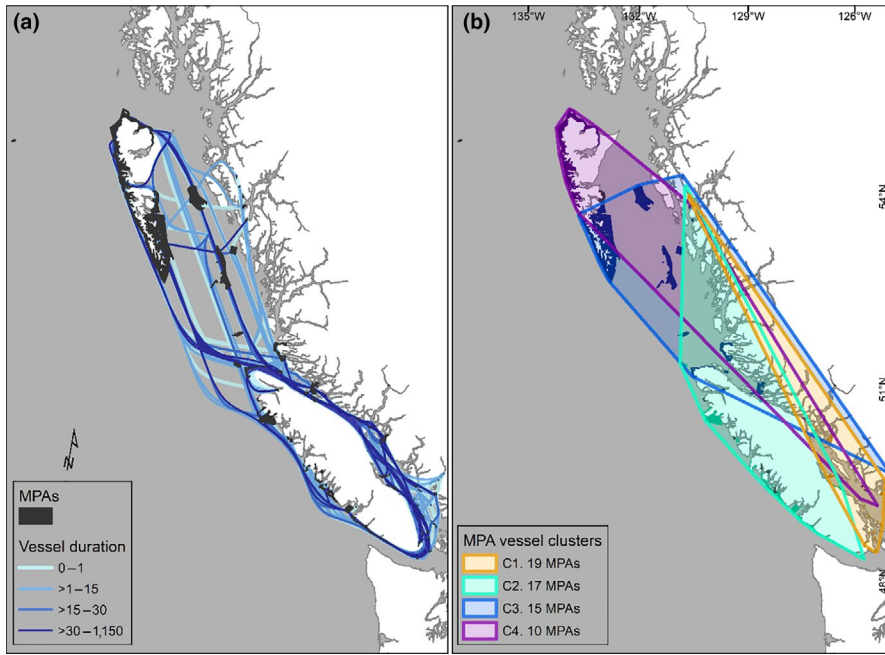


FIGURE 4 Vessel traffic connections between marine protected areas (MPAs) are vectors of nonindigenous species across the coast of British Columbia, Canada. (a) Connections between MPAs colour-coded by duration (days) within the MPAs and (b) MPAs that are highly linked by vessel traffic are indicated as clusters ('C1'-'C4')

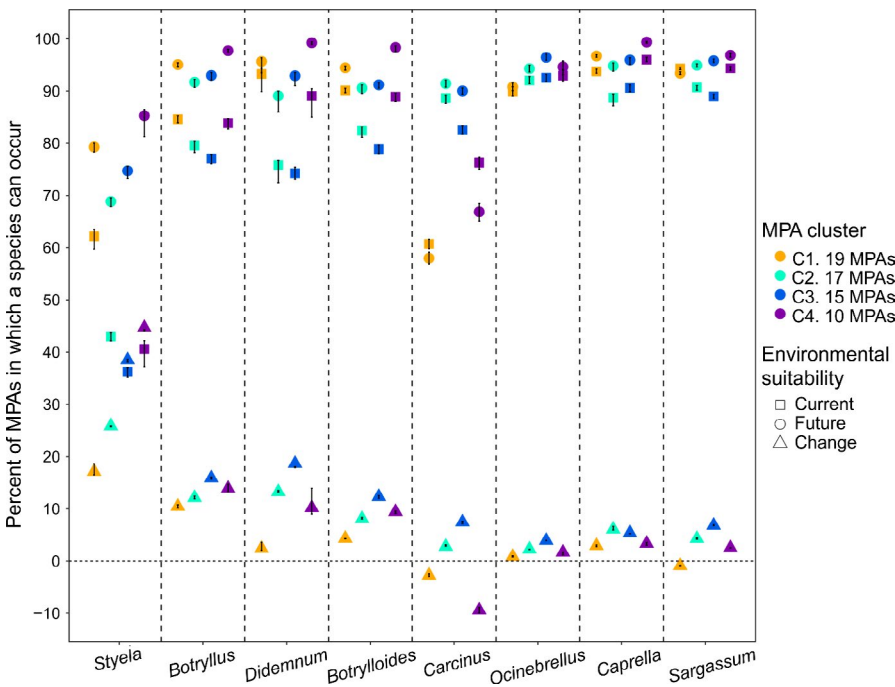


FIGURE 5 Percent of marine protected areas (MPAs) in which a nonindigenous species is expected to occur among those highly connected by vessel traffic ('C1'-'C4') under current (squares) and future (circles) climate conditions, and the change (triangle) from current to future conditions. Symbols are the mean of bootstrapped species distribution models \pm 95% CIs

of BC (i.e. clusters 2 and 3), and decreased in the other two (Figures 4 and 5).

4 | DISCUSSION

Our results show that MPA networks have a high potential for invasion based on environmental suitability and major vectors of spread—shipping and boating. Invasions into MPAs are expected to increase under future climate conditions, a finding that is consistent with predicted trends for marine systems globally (García Molinos

et al., 2015). Given the trajectory of climate conditions, only vigilant vector awareness and management can potentially mitigate these predictions, particularly for species with limited ability for self-dispersal such as tunicates. We recommend that monitoring and management efforts target MPA networks that are highly connected by vessel traffic and show projected increases in environmental suitability under future climates for nonindigenous species of concern. In our study area, the most susceptible and connected MPAs for invasive tunicates were generally within the Strait of Georgia and Northern Shelf bioregions (Figures 4 and 5). *Carcinus maenas*—an invader with notably high impact potential—is also expected to be able

to invade MPAs further north in the Northern Shelf bioregion in the future. MPAs in Canada's Pacific coast waters have a high proportion of area that is suitable to the modelled nonindigenous species under future conditions (70%–80%; Figure 3b). This indicates that upon introduction, a substantial amount of the MPA network will be susceptible to the invader. Outcomes of invasions can be difficult to predict, but a small number of high impact invaders can have significant consequences, and the likelihood of further invasion and impacts often increases in areas with higher nonindigenous species richness (Braga, Gómez-Aparicio, Heger, Vitule, & Jeschke, 2018; Simberloff & Von Holle, 1999).

Some MPAs world-wide have already experienced significant impacts of invaders that threaten their conservation status. For instance nonindigenous species dominate a protected coral reef community in the Mediterranean Sea, comprising up to 44% of fish density and 100% of epi-benthic molluscs among sites (Rilov et al., 2018). In an Atlantic coast MPA, *Didemnum* drives native epi-benthic biodiversity loss (Kaplan et al., 2018). *Carcinus* is currently present in seagrass meadows within MPAs in the Southern Shelf of BC, where it can decimate seagrass cover and alter fish communities as shown in BC and other Canadian waters (Appendix S2; Howard, Francis, Côté, & Therriault, 2019; Matheson et al., 2016). All the nonindigenous species included in this study have the potential to impact protected communities through resource competition (i.e. *Styela*, *Botryllus*, *Didemnum*, *Botrylloides*, *Caprella*), habitat modification (*Didemnum*, *Carcinus*, *Sargassum*) or predation (*Carcinus*, *Ocinebrellus*, *Caprella*; Table 1; Fofonoff, Ruiz, Steves, Simkanin, & Carlton, 2018; Molnar et al., 2008).

Upon primary introduction and establishment in a new region—generally via shipping and historically via aquaculture vectors for marine systems (Molnar et al., 2008; Williams et al., 2013)—invaders often exhibit stepping stone dispersal between areas with suitable habitat. Such spread may be achieved through self-dispersal, although for many invaders this is highly limited by larval settlement rates and mobility (Table 1). Invaders with high dispersal capability but minimal range expansions are likely restricted by environmental suitability or biotic interactions. For instance *Carcinus* has moderate to high dispersal capability but its distribution in the Northeastern Pacific has been limited in part by environmental conditions (Compton, Leathwick, & Inglis, 2010) and by biotic resistance from native crab species (Hunt & Yamada, 2003; Jensen, McDonald, & Armstrong, 2007); our results show that the current temperature and salinity boundary will shift northwards allowing expansion under future conditions, whereas the Strait of Georgia may become too warm. Conversely, *Botrylloides* and *Botryllus* tunicates are widespread in BC but have low self-dispersal capability due to larvae that remain in the plankton from a few hours to a few days after spawning (i.e. anchiplanic); these species were likely spread through human-mediated secondary vectors including shipping and boating (e.g. Clarke Murray et al., 2011; Simkanin, Davidson, Falkner, Sytsma, & Ruiz, 2009; Ulman et al., 2019), movements of maritime structures such as oil rigs and docks (Iacarella, Davidson, & Dunham, 2019) and aquaculture translocations (Haydar & Wolff, 2011). Ship and boat traffic is a particularly strong vector within regions owing

to the large number of vessels and their frequency of movements (as shown here; Iacarella, Burke, et al., 2020), the entrainment potential in biofouling, ballast and bilge water (Clarke Murray et al., 2011; Fletcher et al., 2017; Ulman et al., 2019) and the lack of regulatory oversight within domestic waters (Briski, Wiley, & Bailey, 2012; Simkanin et al., 2009). Comprehensive risk assessments at the species and MPA level would need to consider self-dispersal capability and other vectors and source locations (Iacarella, Burke, et al., 2020). However, understanding invasion potential across MPA networks for a suite of species and primary vectors, as shown here, provides spatial planning and management direction at a larger scale and can be used to prioritize limited resources.

Our study focused on nonindigenous species that have already established in some parts of coastal BC and are representative of a variety of functional groups that may be afforded introduction opportunities in the future. International vessel traffic is a likely transfer mechanism for incoming novel introductions and is expected to increase over time. Global shipping traffic is projected to rise by 240%–1,209% from 2014 to 2050 based on economic growth models (Sardain, Sardain, & Leung, 2019). In our study region, a recently approved pipeline expansion will increase tanker traffic between Asia and the Port of Vancouver by seven-fold (DFO, 2018). Regional scale traffic for ships and recreational boats is also on an upward trajectory, although predictions for the magnitude of these changes are not currently available. We determined likelihood of secondary spread from vessel traffic connections from 1 year of tracking data, but vessel intensity will likely be higher in future scenarios. Higher propagule pressure from international shipping will increase the likelihood of uptake by local vectors, and potential expansion of environmental suitability with climate change will further facilitate establishment and spread.

Our results can provide an indication of risk for future invasions via secondary spread, as well as range expansions in response to climate change. Further prioritization at the individual MPA level may identify native species and habitats that are most susceptible to impacts by these different nonindigenous species, and may determine a cumulative risk across nonindigenous species for each MPA. As with all species distribution modelling efforts, our predictions do not account for the ability of species to spread into areas with conditions that differ from those where they are currently found or for adaptation (Compton et al., 2010); thus our estimates of environmental suitability may be conservative. The inclusion of substrate type and bottom water conditions as environmental model parameters—currently only available over limited spatial extents within our modelling domain—would also contribute to a better understanding of susceptibility within areas and how factors such as nearshore area extent influence environmental suitability, particularly for benthic invaders. Our environmental suitability predictions indicate the likelihood of survival for nonindigenous species in surface waters or shallow benthos, which may not survive or establish in deeper areas; this is a key area for development of future modelling efforts.

The Convention on Biological Diversity Aichi Target 9 calls for identification and prioritization of invasive species and pathways, and management of the determined priorities by 2020. McGeoch et al. (2016) propose that prioritization must also include determining sites that are susceptible to invasion (defined as 'high exposure and high invasion probability') and sensitive to invasion ('severe consequences of impact', e.g. protected areas). Applying species distribution and vector models is a promising method for prioritizing species, pathways and sites. However, very few studies have done this to-date (McGeoch et al., 2016). Previous studies that identified susceptible sites based on environmental suitability (or climate) and vector strength did so for *Dreissena polymorpha* (zebra mussels) transported between lakes by recreational boaters (Stewart-Koster, Olden, & Johnson, 2015) and for plant seeds attached to visitors to Antarctica (Chown et al., 2012). The only other study, to our knowledge, that has measured invasion risk across protected areas was conducted using species distribution models for invaders in terrestrial and MPAs in Europe; vectors were not measured, but human accessibility was a key factor in protected area invasions (Gallardo et al., 2017). Our study provides a first-step approach to evaluating the three components of prioritization (species, pathways, sites) with the treatment of MPAs as equally vulnerable to invasion (i.e. having high conservation value) and determination of which were most likely to be invaded across a suite of nonindigenous species with different life-history traits and based on networks created by the most pervasive vectors.

Management of prioritized invasion risks occurs at international, national and site levels. International regulations and codes of practice for international ships' ballast water and aquaculture have greatly reduced the risk of new invasions via these vectors (Williams et al., 2013). However, biofouling of ships and boats is largely unregulated and remains a concern for primary and secondary invasions (Briski et al., 2012; Davidson, Scianni, Minton, & Ruiz, 2018; Ulman et al., 2019); thus, new invaders are likely to come from biofouling communities such as those modelled here. Some nations impose biosecurity measures such as biofouling compliance regulations for incoming vessels (Davidson et al., 2018; Ministry for Primary Industries, 2018), as well as trade bans on high impact invaders, albeit with mixed success of the latter (Patoka et al., 2018). Managers may also include nonindigenous species prevention, monitoring and mitigation measures in MPA and MPA network management plans. The Mediterranean MPA network has developed a common framework for prevention and early detection of invasions for managers to conduct in their MPAs (Otero, Cebrian, Francour, Galil, & Savini, 2013). In addition, California's MPA network management plan includes a commitment to integrate MPAs into ongoing nonindigenous species monitoring with the aim to detect invasions that may impact MPAs (California Department of Fish and Wildlife, 2016). Prevention and mitigation activities are currently uncommon in MPAs globally, though there are some notable exceptions, including the use of MPA zoning regulations to ban fishing nets in areas infested with invasive *Caulerpa taxifolia* alga to reduce further spread (Industry & Investment NSW,

2009), as well as targeted removal of *Carcinus maenas* and *Pterois* lionfish species (Iacarella, Saheed, et al., 2019). Limiting artificial structures such as docks within and nearby MPAs can also reduce vessel traffic (Iacarella, Burke, et al., 2020) and stepping-stone dispersal of biofouling species associated with these surfaces (Bishop et al., 2017). Managing invasions at an MPA network level is a promising approach to use in concert with individual MPA risk assessments as it affords risk management and prioritization across many MPAs and utilizes distinct boundaries from which vectors can be regulated with protected area legislation. It is paramount to act on these issues now as climate change and increasing invasion pathways threaten to compromise protected areas and impact other relatively pristine areas in the near future.

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AUTHORS' CONTRIBUTIONS

J.C.I., D.A.L., T.W.T. and C.D.B. designed methodology; J.C.I., D.A.L. and L.B. processed and analysed the data; J.C.I. led the writing of the manuscript. All authors conceived the ideas, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2v6wwpzjc> (Iacarella, Lyons, et al., 2020).

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REFERENCES

- Balbar, A. C., & Metaxas, A. (2019). The current application of ecological connectivity in the design of marine protected areas. *Global Ecology and Conservation*, 17, e00569. <https://doi.org/10.1016/j.gecco.2019.e00569>
- Bartón, K. (2009). *Mu-MIn: Multi-model inference*. R Package Version 0.12.2/r18. Retrieved from <http://R-Forge.R-project.org/projects/mumin/>
- Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., & Courchamp, F. (2013). Will climate change promote future invasions? *Global Change Biology*, 19, 3740–3748. <https://doi.org/10.1111/gcb.12344>
- Bishop, M. J., Mayer-Pinto, M., Airoldi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., ... Dafforn, K. A. (2017). Effects of ocean sprawl on ecological connectivity: Impacts and solutions. *Journal of Experimental Marine Biology and Ecology*, 492, 7–30. <https://doi.org/10.1016/j.jembe.2017.01.021>
- Braga, R. R., Gómez-Aparicio, L., Heger, T., Vitule, J. R. S., & Jeschke, J. M. (2018). Structuring evidence for invasional meltdown: Broad support

- but with biases and gaps. *Biological Invasions*, 20, 923–936. <https://doi.org/10.1007/s10530-017-1582-2>
- Briski, E., Wiley, C. J., & Bailey, S. A. (2012). Role of domestic shipping in the introduction or secondary spread of nonindigenous species: Biological invasions within the Laurentian Great Lakes. *Journal of Applied Ecology*, 49, 1124–1130. <https://doi.org/10.1111/j.1365-2664.2012.02186.x>
- Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, 23, 99–112. <https://doi.org/10.1111/geb.12102>
- California Department of Fish and Wildlife. (2016). *California Marine Life Protection Act master plan for marine protected areas*. Adopted by the California Fish and Game Commission on August 24, 2016. Retrieved from <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=133535&inline>
- Carlton, J. T., & Hodder, J. (1995). Biogeography and dispersal of coastal marine organisms: Experimental studies on a replica of a 16th-century sailing vessel. *Marine Biology*, 121, 721–730. <https://doi.org/10.1007/BF00349308>
- Chown, S. L., Huiskes, A. H. L., Gremmen, N. J. M., Lee, J. E., Terauds, A., Crosbie, K., ... Bergstrom, D. M. (2012). Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 4938–4943. <https://doi.org/10.1073/pnas.1119787109>
- Clarke Murray, C., Gartner, H., Gregr, E., Chan, K., Pakhomov, E. A., & Therriault, T. W. (2014). Spatial distribution of marine invasive species implicates the recreational boating pathway. *Diversity and Distributions*, 20, 824–836. <https://doi.org/10.1111/ddi.12215>
- Clarke Murray, C., Pakhomov, E. A., & Therriault, T. W. (2011). Recreational boating: A large unregulated vector transporting marine invasive species. *Diversity and Distributions*, 17, 1161–1172. <https://doi.org/10.1111/j.1472-4642.2011.00798.x>
- Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E*, 70, 066111. <https://doi.org/10.1103/PhysRevE.70.066111>
- Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: A null model for biological invasions. *Biological Invasions*, 8, 1023–1037. <https://doi.org/10.1007/s10530-005-3735-y>
- Coma, R., Serrano, E., Linares, C., Ribes, M., Díaz, D., & Ballesteros, E. (2011). Sea urchins predation facilitates coral invasion in a marine reserve. *PLoS ONE*, 6, e22017. <https://doi.org/10.1371/journal.pone.0022017>
- Compton, T. J., Leathwick, J. R., & Inglis, G. J. (2010). Thermogeography predicts the potential global range of the invasive European green crab (*Carcinus maenas*). *Diversity and Distributions*, 16, 243–255. <https://doi.org/10.1111/j.1472-4642.2010.00644.x>
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, 1–9.
- Davidson, I. C., Scianni, C., Minton, M. S., & Ruiz, G. M. (2018). A history of ship specialization and consequences for marine invasions, management and policy. *Journal of Applied Ecology*, 55, 1799–1811. <https://doi.org/10.1111/1365-2664.13114>
- DFO. (2018). *Technical review: Potential effectiveness of mitigation measures to reduce impacts from project-related marine vessels on Southern Resident Killer Whales*. DFO Canadian Science Advisory Secretariat Science Response 2018/050. Retrieved from <https://waves-vagues.dfo-mpo.gc.ca/Library/4073982x.pdf>
- Drolet, D., DiBacco, C., Locke, A., McKenzie, C. H., McKindsey, C. W., Moore, A. M., ... Therriault, T. W. (2016). Evaluation of a new screening-level risk assessment tool applied to non-indigenous marine invertebrates in Canadian coastal waters. *Biological Invasions*, 18, 279–294. <https://doi.org/10.1007/s10530-015-1008-y>
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Fletcher, L. M., Zaiko, A., Atalah, J., Richter, I., Dufour, C. M., Pochon, X., ... Hopkins, G. A. (2017). Bilge water as a vector for the spread of marine pests: A morphological, metabarcoding and experimental assessment. *Biological Invasions*, 19, 2851–2867. <https://doi.org/10.1007/s10530-017-1489-y>
- Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). *National exotic marine and estuarine species information system*. Retrieved from <http://invasions.si.edu/nemesis/>
- Gallagher, M. C., Culloty, S. C., Davenport, J., Harman, L., Jessopp, M. J., Kerrigan, C., ... McAllen, R. (2017). Short-term losses and long-term gains: The non-native species *Austrominius modestus* in Lough Hyne Marine Nature Reserve. *Estuarine, Coastal and Shelf Science*, 191, 96–105. <https://doi.org/10.1016/j.ecss.2017.04.020>
- Gallardo, B., Aldridge, D. C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P., ... Vilà, M. (2017). Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, 23, 5331–5343. <https://doi.org/10.1111/gcb.13798>
- García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., ... Burrows, M. T. (2015). Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, 6, 83–88. <https://doi.org/10.1038/nclimate2769>
- Giakoumi, S., Guilhaumon, F., Kark, S., Terlizzi, A., Claudet, J., Felling, S., ... Katsanevakis, S. (2016). Space invaders; biological invasions in marine conservation planning. *Diversity and Distributions*, 22, 1220–1231. <https://doi.org/10.1111/ddi.12491>
- Haydar, D., & Wolff, W. J. (2011). Predicting invasion patterns in coastal ecosystems: Relationship between vector strength and vector tempo. *Marine Ecology Progress Series*, 431, 1–10. <https://doi.org/10.3354/meps09170>
- Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, 22, 534–543. <https://doi.org/10.1111/j.1523-1739.2008.00951.x>
- Herborg, L. M., O'Hara, P., & Therriault, T. W. (2009). Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*. *Journal of Applied Ecology*, 46, 64–72. <https://doi.org/10.1111/j.1365-2664.2008.01568.x>
- Howard, B. R., Francis, F. T., Côté, I. M., & Therriault, T. W. (2019). Habitat alteration by invasive European green crab (*Carcinus maenas*) causes eelgrass loss in British Columbia, Canada. *Biological Invasions*, 12, 3607–3618. <https://doi.org/10.1007/s10530-019-02072-z>
- Hunt, C. E., & Yamada, S. B. (2003). Biotic resistance experienced by an invasive crustacean in a temperate estuary. *Biological Invasions*, 5, 33–43. <https://doi.org/10.1023/A:1024011226799>
- Iacarella, J. C., Burke, L., Davidson, I. C., DiBacco, C., Therriault, T. W., & Dunham, A. (2020). Unwanted networks: Vessel traffic heightens the risk of invasions in marine protected areas. *Biological Conservation*, 245, 108553. <https://doi.org/10.1016/j.biocon.2020.108553>
- Iacarella, J. C., Davidson, I. C., & Dunham, A. (2019). Biotic exchange from movement of 'static' maritime structures. *Biological Invasions*, 21, 1131–1141. <https://doi.org/10.1007/s10530-018-1888-8>
- Iacarella, J. C., Lyons, D. A., Burke, L., Davidson, I. C., Dunham, A., Therriault, T. W., & DiBacco, C. (2020). Data from: Climate change and vessel traffic create networks of invasion in marine protected areas. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.2v6wwpzcj>
- Iacarella, J. C., Saheed, D., Dunham, A., & Ban, N. C. (2019). Non-native species are a global issue for marine protected areas. *Frontiers in Ecology and the Environment*, 17, 495–501. <https://doi.org/10.1002/fee.2100>
- Industry & Investment NSW. (2009). *New South Wales control plan for the noxious marine alga Caulerpa taxifolia*. Orange, NSW: Department of

- Industry and Investment. Retrieved from https://www.dpi.nsw.gov.au/_data/assets/pdf_file/0004/637177/NSW-control-plan-caule-rpa-taxifolia.pdf
- Jensen, G. C., McDonald, P. S., & Armstrong, D. A. (2007). Biotic resistance to green crab, *Carcinus maenas*, in California bays. *Marine Biology*, 151, 2231–2243. <https://doi.org/10.1007/s00227-007-0658-4>
- Kaplan, K. A., Hart, D. R., Hopkins, K., Gallager, S., York, A., Taylor, R., & Sullivan, P. J. (2018). Invasive tunicate restructures invertebrate community on fishing grounds and a large protected area on Georges Bank. *Biological Invasions*, 20, 87–103. <https://doi.org/10.1007/s10530-017-1517-y>
- Locke, A., Hanson, J. M., Ellis, K. M., Thompson, J., & Rochette, R. (2007). Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Stela clava* Herdman): Potential mechanisms for invasions of Prince Edward Island estuaries. *Journal of Experimental Marine Biology and Ecology*, 342, 69–77. <https://doi.org/10.1016/j.jembe.2006.10.016>
- Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, 20, 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Mačić, V., Albano, P. G., Alpanidou, V., Claudet, J., Corrales, X., Essl, F., ... Katsanevakis, S. (2018). Biological invasions in conservation planning: A global systematic review. *Frontiers in Marine Science*, 5, 178. <https://doi.org/10.3389/fmars.2018.00178>
- Matheson, K., McKenzie, C. H., Gregory, R. S., Robichaud, D. A., Bradbury, I. R., Snelgrove, P. V. R., & Rose, G. A. (2016). Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. *Marine Ecology Progress Series*, 548, 31–45. <https://doi.org/10.3354/meps11674>
- McGeoch, M. A., Genovesi, P., Bellingham, P. J., Costello, M. J., McGrannachan, C., & Sheppard, A. (2016). Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. *Biological Invasions*, 18, 299–314. <https://doi.org/10.1007/s10530-015-1013-1>
- Minchin, D., & Gollasch, S. (2003). Fouling and ships' hulls: How changing circumstances and spawning events may result in the spread of exotic species. *Biofouling*, 19(Suppl. 1), 111–122. <https://doi.org/10.1080/0892701021000057891>
- Ministry for Primary Industries. (2018). *Guidance document for the craft risk management standard for biofouling. GD CRMS-BIOFOUL*. Wellington, New Zealand: Ministry for Primary Industries. Retrieved from <https://www.mpi.govt.nz/dmsdocument/11671/direct>
- Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6, 485–492. <https://doi.org/10.1890/070064>
- Nydam, M. L., Giesbrecht, K. B., & Stephenson, E. E. (2017). Origin and dispersal history of two colonial Ascidian clades in the *Botryllus schlosseri* species complex. *PLoS ONE*, 12, e0169944. <https://doi.org/10.1371/journal.pone.0169944>
- Otero, M., Cebrian, E., Francour, P., Galil, B., & Savini, D. (2013). *Monitoring marine invasive species in Mediterranean marine protected areas (MPAs): A strategy and practical guide for managers*. Malaga, Spain: IUCN. Retrieved from <https://portals.iucn.org/library/sites/library/files/documents/2013-008.pdf>
- Patoka, J., Magalhães, A. L. B., Kouba, A., Faulkes, Z., Jerikho, R., & Vitule, J. R. S. (2018). Invasive aquatic pets: Failed policies increase risks of harmful invasions. *Biodiversity and Conservation*, 27, 3037–3046. <https://doi.org/10.1007/s10531-018-1581-3>
- Peña, A., Fine, I., & Masson, D. (2018). Towards climate change projections of biogeochemical conditions along the British Columbia coast. In C. J. Jang & E. Curchitser (Eds.), *Report of Working Group 29 on Regional Climate Modeling* (pp. 114–124). PICES Sci. Rep. No. 54.
- Phillips, S. J., Dudík, M., & Schapire, R. E. (2017). *Maxent software for modeling species niches and distributions (Version 3.4.1)*. Retrieved from http://biodiversityinformatics.amnh.org/open_source/maxent
- R Development Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ricciardi, A., Blackburn, T. M., Carlton, J. T., Dick, J. T. A., Hulme, P. E., Iacarella, J. C., ... Aldridge, D. C. (2017). Invasion science: A horizon scan of emerging challenges and opportunities. *Trends in Ecology & Evolution*, 32, 464–474. <https://doi.org/10.1016/j.tree.2017.03.007>
- Rilov, G., Peleg, O., Yeruham, E., Garval, T., Vichik, A., & Raveh, O. (2018). Alien turf: Overfishing, overgrazing and invader domination in south-eastern Levant reef ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 351–369. <https://doi.org/10.1002/aqc.2862>
- Roberts, C. M., O'Leary, B. C., McCauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., ... Castilla, J. C. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 6167–6175. <https://doi.org/10.1073/pnas.1701262114>
- Sardain, A., Sardain, E., & Leung, B. (2019). Global forecasts of shipping traffic and biological invasions to 2050. *Nature Sustainability*, 2, 274–282. <https://doi.org/10.1038/s41893-019-0245-y>
- Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, 1, 21–32. <https://doi.org/10.1023/A:1010086329619>
- Simkanin, C., Davidson, I., Dower, J. F., Jamieson, G., & Therriault, T. W. (2012). Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. *Marine Ecology*, 33, 499–511. <https://doi.org/10.1111/j.1439-0485.2012.00516.x>
- Simkanin, C., Davidson, I., Falkner, M., Sytsma, M., & Ruiz, G. (2009). Intra-coastal ballast water flux and the potential for secondary spread of non-native species on the US West Coast. *Marine Pollution Bulletin*, 58, 366–374. <https://doi.org/10.1016/j.marpolbul.2008.10.013>
- Stewart-Koster, B., Olden, J. D., & Johnson, P. T. J. (2015). Integrating landscape connectivity and habitat suitability to guide offensive and defensive invasive species management. *Journal of Applied Ecology*, 52, 366–378. <https://doi.org/10.1111/1365-2664.12395>
- Therriault, T. W., & Herborg, L. M. (2007). *Risk assessment for two solitary and three colonial tunicates in both Atlantic and Pacific Canadian waters*. DFO Canadian Science Advisory Secretariat Research Document 2007/063. <https://waves-vagues.dfo-mpo.gc.ca/Library/333997.pdf>
- Therriault, T. W., & Herborg, L. M. (2008). Predicting the potential distribution of the vase tunicate *Ciona intestinalis* in Canadian waters: Informing a risk assessment. *ICES Journal of Marine Science*, 65, 788–794. <https://doi.org/10.1093/icesjms/fsn054>
- Ulman, A., Ferrario, J., Forcada, A., Seebens, H., Arvanitidis, C., Occhipinti-Ambrogi, A., & Marchini, A. (2019). Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. *Journal of Applied Ecology*, 56, 2620–2629. <https://doi.org/10.1111/1365-2664.13502>
- UNEP-WCMC, IUCN, & NGS. (2018). *Protected planet report 2018*. Cambridge, UK; Gland, Switzerland; Washington, DC: UNEP-WCMC, IUCN & NGS. Retrieved from https://livereport.protectedplanet.net/pdf/Protected_Planet_Report_2018.pdf
- UNEP-WCMC, IUCN, & NGS. (2020). *Protected planet live report 2020*. Cambridge, UK; Gland, Switzerland; Washington, DC: UNEP-WCMC, IUCN & NGS. Retrieved from <https://livereport.protectedplanet.net/>

- Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., ... Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, 24, 686–693. <https://doi.org/10.1016/j.tree.2009.06.008>
- Williams, P. H., & Araújo, M. B. (2002). Apples, oranges, and probabilities: Integrating multiple factors into biodiversity conservation with consistency. *Environmental Modeling & Assessment*, 7, 139–151. <https://doi.org/10.1023/A:1015657917928>
- Williams, S. L., Davidson, I. C., Pasari, J. R., Ashton, G. V., Carlton, J. T., Crafton, R. E., ... Zabin, C. J. (2013). Managing multiple vectors for marine invasions in an increasingly connected world. *BioScience*, 63, 952–966. <https://doi.org/10.1525/bio.2013.63.12.8>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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