



ELSEVIER

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Policy analysis

Unwanted networks: Vessel traffic heightens the risk of invasions in marine protected areas

Josephine C. Iacarella^{a,*}, Lily Burke^a, Ian C. Davidson^{b,c}, Claudio DiBacco^d,
Thomas W. Therriault^e, Anya Dunham^e

^a Fisheries and Oceans Canada, Institute of Ocean Sciences, 9860 W. Saanich Rd., Sidney, BC V8L 4B2, Canada

^b Cawthron Institute, 98 Halifax Street East, Nelson, 7010, New Zealand

^c Smithsonian Environmental Research Centre, 647 Contee Wharf Road, Edgewater, MD 21037, USA

^d Fisheries and Oceans Canada, Bedford Institute of Oceanography, 1 Challenger Dr., Dartmouth, NS B2Y 4A2, Canada

^e Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Rd., Nanaimo, BC V9T 6N7, Canada

ARTICLE INFO

Keywords:

Automatic identification systems (AIS)
Conservation areas
Invasive alien species
Marine vector pathways
Network analysis

ABSTRACT

Invasive species pose a significant threat to a primary objective of marine conservation, protecting native biodiversity. To-date, research quantifying invasion risk to marine protected areas (MPAs) is limited despite potential negative consequences. As a first step towards identifying invasion risk to MPAs via vessel ballast or biofouling, we evaluated vessel traffic patterns by applying graph-theoretic concepts for 1346 vessels that connected invaded areas ('invasion nodes') along the Northeast Pacific coast to MPAs within Canadian waters in 2016. We found that 29% of MPAs overlapped with invasion nodes and 70% were connected to invasion nodes via vessel traffic. Recreational vessels were most prevalent within invasion and MPA nodes, made the most connections between invasion nodes and MPAs, and spent the most time within nodes. Vessel connections increased in summer and with spatial extent and dock area at invasion and MPA nodes, as well as for MPAs with minimal regulatory protection. Results from this work highlight risk posed by vessels as a vector for non-indigenous species spread and present an opportunity to develop improved management measures to help protect MPAs. Such an approach can be applied to vector interactions with protected areas across biomes for targeted invasion management.

1. Introduction

Protected areas are a primary focus of conservation efforts following the international agreement to protect 10% of ocean waters and 17% of terrestrial and inland waters by 2020 (Aichi Target #11; Sustainable Development Goal #14). In the Post-2020 Global Biodiversity Framework, there are calls to further increase the percentage of protected areas, including 30% of marine areas by 2030 (Woodley et al., 2019). A protected area is, "a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature..." (IUCN Definition, 2008). There are many stressors that must be addressed to achieve long-term conservation, the most significant of which are land- and sea-use change (i.e. agriculture, coastal development), exploitation (i.e. harvesting, logging, fishing), climate change, and pollution (i.e. nonindigenous species, marine plastics, waste, emissions) (IPBES, 2019). Some of these stressors can be directly managed or mitigated

with protected area regulations.

Nonindigenous species are a major threat to native biodiversity (Blackburn et al., 2019) and have had large impacts on terrestrial and marine protected communities that compromise the conservation goals of the protected area (Coma et al., 2011; Foxcroft et al., 2017; Kaplan et al., 2018). Invasions are considered a management concern by many marine protected area (MPA) experts (Iacarella et al., 2019a), yet are often overlooked in protected area planning and regulation. Less than 5% of spatial planning designs for protected areas across biomes consider nonindigenous species (Giakoumi et al., 2016; Mačić et al., 2018) and only 26% of experts working in MPAs globally are aware of a section on nonindigenous species in their management plans (Iacarella et al., 2019a).

Restricting nonindigenous species incursion and spread is much more likely to succeed than eradication following establishment (Simberloff et al., 2013). Nonindigenous species have many pathways of introduction and spread, but often fit a "hub-and-spoke" model of

* Corresponding author.

E-mail address: Josephine.Iacarella@dfo-mpo.gc.ca (J.C. Iacarella).

<https://doi.org/10.1016/j.biocon.2020.108553>

Received 13 November 2019; Received in revised form 11 March 2020; Accepted 29 March 2020

Available online 15 April 2020

0006-3207/ Crown Copyright © 2020 Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

initial introduction and establishment at transport hubs, followed by secondary spread via vectors and self-dispersal (Carlton, 1996). Propagule dispersal of invertebrates, plants, and algae in the marine realm is largely limited by larval duration and currents, and long-distance dispersal is often driven by human-mediated transport and stepping-stone events (Pérez-Portela et al., 2013; Manel et al., 2019). Commercial shipping and recreational boating create the most potent transport mechanisms through ballast water and biofouling, followed by aquaculture-related movement and the seafood and aquarium trades (Molnar et al., 2008; Williams et al., 2013). Some MPA management plans limit vessel-related activities including fishing and waste discharge, but vessel traffic transiting into and within MPAs is largely free from vector management provisions, leaving MPAs vulnerable to invasions. Conversely, no-entry or vector-regulated MPAs, such as areas within the Great Barrier Reef, protect against impacts and reduce invasion potential (Frisch and Rizzari, 2019).

Protected areas have different focal goals and governing bodies which may affect the prevalence of invasion vectors and the ability to manage them. For instance, parks are often zoned based on a defined value that can be recreation- or conservation-focused and have matching allowable uses that influence the type and amount of traffic they experience (e.g. B.C. Parks, 2012). These allowable uses and associated infrastructure are likely to affect invasion risk. In Canada, there is currently no centralized or coordinated effort to mitigate invasion risk into MPAs. Here, we examine vessel traffic as an invasion risk factor for MPAs as a first step towards quantifying the magnitude of the problem and identifying areas that would benefit from management.

We apply graph-theoretic concepts to vessel traffic data for the Northeast Pacific coast of North America to evaluate connections made by vessels from invaded areas spanning the west coast of Canada and adjacent US waters to MPAs within Canada. Graph-theory has previously been used to identify high risk areas for spread of freshwater and terrestrial invaders (Glen et al., 2013; Stewart-Koster et al., 2015) and is effective for identifying at-risk protected areas. Our analysis of vessel movement patterns focuses on secondary spread of non-indigenous species that have already invaded the study region via a variety of primary vectors. We identify the types of vessels and invaded areas that lead to higher risk of invasion into MPAs, the attributes that promote risk, and the MPAs that are at higher risk. Our analytical methods and application of results relate to several areas of conservation planning across biomes: considering invasion risk in protected area design, optimizing resource allocation for management of risks, and implementing communication strategies to promote vector- or location-based management.

2. Methods

We applied a graph-theoretic framework to analyze connections made by vessel routes ('edges') from invaded areas ('invasion nodes') to marine protected areas ('MPA nodes') (Fig. 1; Pavlopoulos et al., 2011). Geospatial datasets were collated for invasion nodes and vessel traffic across the Northeast Pacific coast from 47 to 59°N (Washington, USA, across British Columbia, Canada to Southeast Alaska, USA) and for MPAs within British Columbia waters. Invasion and MPA nodes were identified prior to vessel traffic analysis.

2.1. Invasion and MPA nodes

We identified invaded areas using geospatial records from Washington to Southeast Alaska for all nonindigenous and non-cultured invertebrates, plants, and algae ($n = 1696$ records for 132 species from 1888 to 2016; see Appendix, Table A1 for species list); data on abundances were not available, and are difficult to estimate for many biofouling species that are observed on settlement plates. Presence records were aggregated within 20 km of each other ('aggregate points' tool

required ≥ 3 locations within 20 km; ArcGIS v. 10.4) to create invaded areas; aggregated areas varied in size depending on distances between locations (Appendix A, 'Invasion nodes'; Iacarella et al., 2019b). We selected the areas within the top 80th percentile of nonindigenous species richness (7–59 species; $n = 25$) to represent invasion nodes that create the most risk of uptake by shipping vectors. Two outlying locations (i.e. those not nearby two other locations) in Southeast Alaska were within the top 80th percentile so circles with 20 km radii were drawn around them to capture an estimated invaded area (Appendix, 'Invasion nodes', Fig. A2). Our focus on the highest risk invaded areas reduced our overall estimation of vessel traffic into MPAs, but enabled analyses and results that highlight priorities for management under limited resource scenarios. All nonindigenous species included have the potential to be entrained in vessel ballast water or biofouling (Gartner et al., 2016; Ruiz et al., 2011).

MPAs within British Columbia were identified from the Conservation Areas Reporting and Tracking System geodatabase (<https://www.ccea.org/carts>) which collates all protected areas in Canada. We focused our study on 83 of 195 MPAs that had (1) a management plan or draft/interim plan (excluded 49), (2) a purpose statement or zoning plan within these documents that identified a marine conservation value (excluded 61), and (3) a spatial extent within waters no deeper than 200 m as the estimated maximum survivable depth for most nonindigenous species currently present on the Northeast Pacific coast (excluded 2) (Appendix, Fig. A3). MPA spatial extents were trimmed to contain only depths ≤ 200 m for vessel traffic analysis.

2.2. Vessel route creation and analysis

Hourly Automatic Identification System (AIS) data were obtained from MarineTraffic (<https://www.marinetraffic.com>) for 2016 from Washington to Southeast Alaska. The initial dataset of 10 million observations for 8142 vessels was first reduced by overlaying vessel points with invasion and MPA nodes using ArcGIS and retaining vessels that intersected both node types. For these vessels, shortest-path overwater routes were interpolated using a network grid of 1 km-sided triangles and coastline. Route segments that connected points within invasion and MPA nodes were intersected by the relevant nodes to determine the route length within and outside of nodes (Fig. 1b; Appendix, 'Vessel traffic route creation and analysis'). We calculated duration within invasion and MPA nodes using the timestamps associated with each route segment and the proportion of the route that lay within the node (e.g. if 50% of a route segment from sequential vessel points A - B was within a node and the time difference between A - B was one hour, then we estimated a duration of 0.5 h within the node).

Durations within invasion and MPA nodes were calculated for each edge connection created by a vessel moving from an invasion node to an MPA. Edges were given weightings equal to the sum of the duration within the invasion node and MPA node they connected as a first step approximation of invasion risk given that more time in nodes increases risk of nonindigenous species vector colonization and introduction (Carlton and Hodder, 1995; Minchin and Gollasch, 2003). Biofouling entrainment may take more time than biofouling release; however, we treated vessel duration in invaded areas and MPAs equally and additively since the time needed for uptake versus release is not known and will differ based on the type of uptake (e.g. fouling, ballast, bilge water), as well as the species, their life history stages, and their abundances. Other elements of invasion risk such as species richness at the invaded area, vessel speed, or distance traveled between invasion and MPA nodes were not included in the weighting as this would require a detailed understanding of how these context-dependent factors contribute to risk (see Discussion). Each case of a vessel entering an invasion or MPA node was treated as a separate contribution to invasion risk such that multiple edges connecting the same invasion and MPA nodes within 2016 were created when vessels traveled into and out of

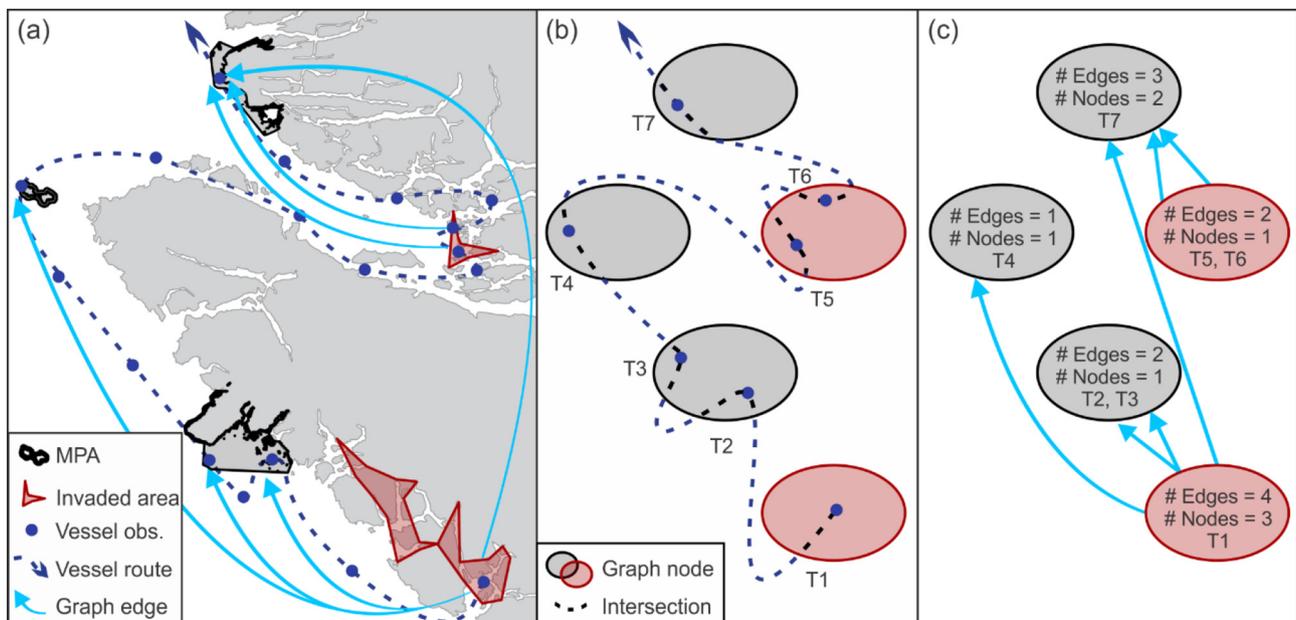


Fig. 1. (a) Map and (b, c) graph-theoretic illustration of invasion risk from vessel routes between invasion and marine protected area (MPA) nodes. Nodes are connected by edges representing vessel routes that traveled from invasion nodes to marine protected areas (a, c). Multiple edge connections can be made by vessel routes traveling into and out of nodes repeatedly. Route intersections (b) were used to determine the duration of time spent within nodes (T).

nodes repeatedly (Fig. 1). Node strength was calculated for each node (NS_k) as the mean of the duration within connected invasion and MPA nodes across multiple connections made by vessels (i.e. sum of edge weights):

$$NS_k = \frac{\sum_1^n (t_k + t_n)}{n}$$

where t_k is the time spent in the focal node k , t_n is the time spent in the paired node, and n is the number of edge connections made to the focal node k . Note, t_k and t_n had to be > 0 to be included in the analysis.

2.3. Statistical analysis

Predictors of vessel connection attributes included vessel category ($n = 6$), season (warm/cold), invasion and MPA node area, and dock area within 5 km to capture nearby marinas for all invasion and MPA nodes (see Appendix, ‘Statistical analysis: additional details for factors’). The presence or absence of the top five major ports in the region (Vancouver, Prince Rupert, Nanaimo, Seattle, Tacoma) was also tested on vessel connection attributes for invasion nodes only; four overlapped with invaded areas (all but Tacoma), whereas none overlapped with MPAs. In addition, the effect of MPA protection strength was tested for MPA nodes only. MPA protection strength was based on park zoning regulations and permitted uses: ‘minimal’ protection included high recreational-value parks (i.e. intensive use and little to no human use restrictions), ‘mixed’ included parks with multiple zones of various uses, and ‘strong’ included highly regulated and low-use wilderness areas, reserves, and Canadian *Oceans Act* MPAs; fisheries closures were also included as nodes, but not in the analysis of MPA protection strength (Appendix, ‘Statistical analysis: additional details for factors’, Table A2, Fig. A3).

Count variables of the number of vessels within an invasion or MPA node, edges connecting a node, and nodes connected to a node (i.e. the number of MPA nodes an invasion node is connected to and vice versa) were assessed using negative binomial regressions to account for a high number of zeroes. Zero-values occurred when an invasion or MPA node was not connected to other nodes for a particular vessel category or season. Total time across vessels and average time per vessel spent within invasion and MPA nodes were tested using linear regressions

with a $\log_{10}(x + 1)$ transformation to improve normality and meet the assumption of homogeneity of variances (Fligner-Killeen, $p > .05$). All invasion and MPA nodes ($n = 108$) were used for the count variables (except in the major port and MPA strength analysis), and only nodes that had a minimum of one vessel entry ($n = 83$) were included for the time variables to reduce zeroes. Global models included vessel category, season, node area, and dock area additively and interactions between (a) vessel category and dock area and (b) vessel category and season. 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).

Separate regressions were run on vessel response variables to test (1) the effect of the presence of major ports in invasion nodes for merchant, passenger, and tug vessels combined and (2) the effect of MPA strength for recreational vessels in MPA nodes; these vessels are expected to be most affected by ports and MPA protection levels, respectively (for instance, the main vessels that transit the Port of Vancouver are container ships, carrier ships, tankers, cruise ships, and tug boats). For these two tests, the influence of invasion and MPA node area was accounted for by adding an offset to the negative binomial regressions of count variables and dividing time variables by node area for the linear regressions. Tukey contrasts were used to determine significant differences between factor levels. All analyses were done in R (R Development Core Team, 2018).

3. Results

We evaluated routes of 1346 vessels that were found to connect invasion nodes along the Northeast Pacific coast to marine protected areas within Canadian waters in 2016. Most of the vessels were recreational ($n = 796$), followed by fishing ($n = 214$), tug ($n = 134$), merchant ($n = 89$), government and research ($n = 57$), and passenger ($n = 57$). Over the duration of a year, tug vessels traveled the greatest cumulative distance (4,347,287 km) and passenger vessels traveled the greatest average distances per vessel (36,263 km \pm 8203, mean \pm 95% CI) (Appendix, Table A3). Recreational (2578 km \pm 140) and fishing vessels (8547 km \pm 2209) traveled the shortest average distances per vessel and tended to have the slowest average and maximum speeds (Appendix, Fig. A4).

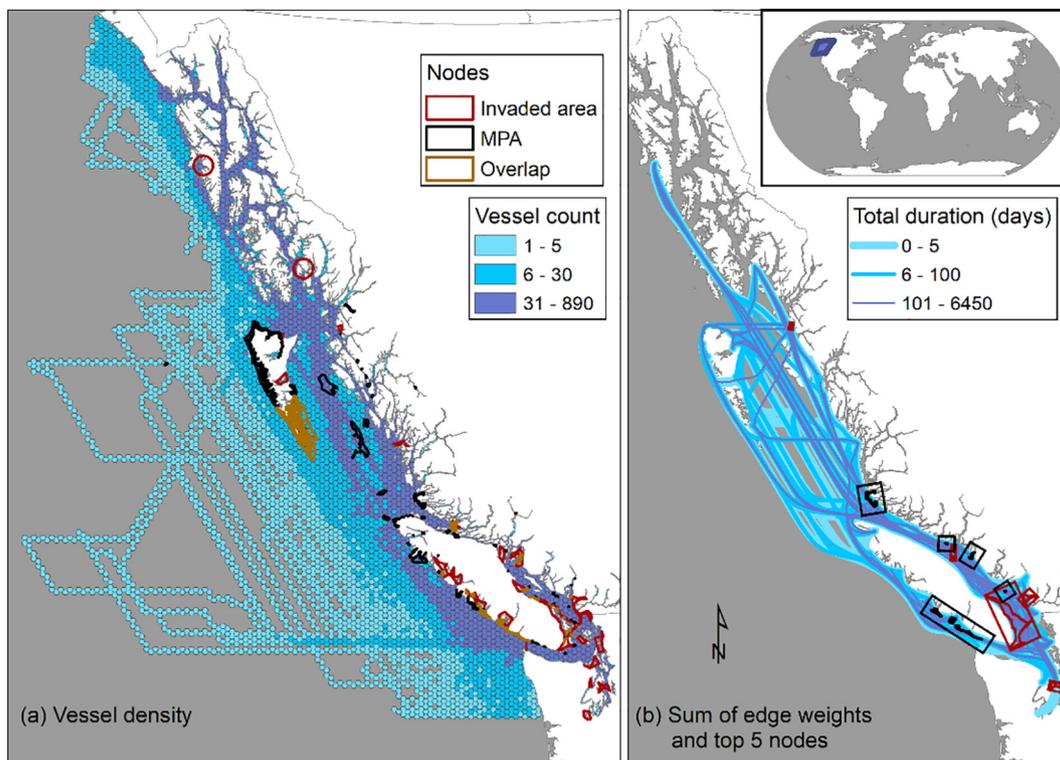


Fig. 2. (a) Vessel traffic density for 1346 vessels that intersected invasion and MPA nodes across the NE Pacific coast in 2016 and (b) sums of edge weights connecting all node pairs – as defined by the total duration in the connected nodes – show the magnitude of vessel connections. The top 5 highest risk nodes (i.e. node strength based on average of edge weight sums) are outlined by rectangles in (b) and included invasion nodes, south to north, near Seattle (USA), Vancouver, Victoria/Nanaimo, Campbell River, and Prince Rupert (Canada) and MPAs of Strait of Georgia and Howe Sound Glass Sponge Reef closure (Sechelt), Desolation Sound Marine Park, Rock Bay Marine Park, Ugwiwey/Cape Caution Conservancy, and on the west coast, Pacific Rim National Park Reserve. MPAs that spatially overlap invasion nodes are indicated (“overlap”) in (a).

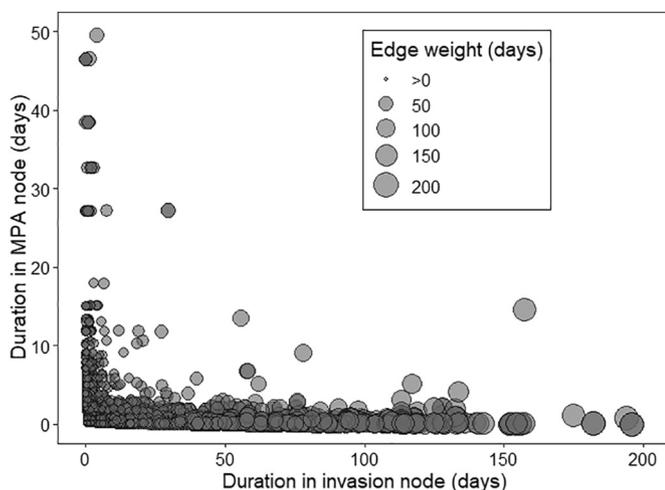


Fig. 3. Duration vessels spent within invasion and MPA nodes for each edge connection made between the two nodes. Symbols are size-coded by the duration across the two nodes (i.e. edge weight).

High vessel densities and edge weightings were concentrated around Vancouver Island and nearshore along the coastline (Fig. 2; Appendix, Fig. A5). The top five highest risk invasion nodes and at-risk MPAs (i.e. those with the highest node strength) were in the Salish Sea (Puget Sound, Washington and Strait of Georgia, British Columbia), except for one invasion node near Prince Rupert in northern British Columbia and one MPA on the outer coast of Vancouver Island. Fifty-eight of the 83 MPAs (70%) were found to have vessel connections with invasion nodes, and 24 MPAs (29%), including 6 strongly protected

ones, overlapped invasion nodes (Appendix, Table A2). Vessels tended to spend more time in invasion nodes than in MPAs, with a number of outlying vessel connections that included durations of up to 200 days in invasion nodes and 50 days in MPAs (Fig. 3).

Best-fit model predictors of vessel connections and duration within invasion and MPA nodes included vessel category, season, node area, dock area, and an interaction between vessel category and season (Table 1). Recreational vessels were the most prevalent within nodes and connected the most invasion nodes to MPAs, whereas tug vessels made the most connecting edges from invasion nodes to MPAs while transiting through (Fig. 4a1-c1). The total and average time vessels spent within invasion and MPA nodes was greatest for recreational vessels followed by fishing vessels (Fig. 4d1-e1). All vessel connection attributes increased during the warm season ($p < .001$; Fig. 4a2-e2) and with node and dock area (Table 1; Appendix, Fig. A6). The total and average time per area that merchant, passenger, and tug vessels spent in invasion nodes with a major port ($n = 4$) was significantly greater than in invasion nodes without ports ($n = 21$; total time: $t = 4.912, p < .001$; average time: $t = 3.228, p = .002$; Fig. 5d1-e1), but the number of vessels and connections to MPAs per area of invasion nodes was similar with and without ports ($p > .05$) (Fig. 5a1-c1). MPAs with minimal protection strength had a significantly higher number of vessel entries (minimal vs. mixed, $z = 2.719, p = .018$; minimal vs. strong, $z = 3.094, p = .006$) and connections to invasion nodes per area of MPA (minimal vs. mixed, $z = 2.405, p = .043$) (Fig. 5a2-c2), though the amount of time per area vessels spent within MPAs did not differ among protection levels ($p > .05$; Fig. 5d2-e2).

4. Discussion

Our results show that vessel traffic creates a high number of

Table 1

Top three models for the number of vessels, edges, and nodes that were connected to invasion and marine protected area nodes, as well as total time across vessels ($\log_{10}[x + 1]$ in seconds) and average time per vessel ($\log_{10}[x + 1]$ in seconds) within nodes. Global model terms included additive parameters of vessel category ($n = 6$), season ($n = 2$), node area (km^2), dock area (km^2), and interactions (“:”) between vessel category and dock area, and vessel category and season. Retention of categorical model terms are indicated as ‘+’ and slopes are provided for continuous model terms. Parameter degrees of freedom (“df”), Akaike information criterion (“AIC”), difference in AIC (“ Δ ”), and AIC weight (“ AIC_w ”) is provided.

Response variable	Vessel	Season	Node area	Dock area	Vessel: Dock area	Vessel: Season	df	AIC	Δ	AIC_w
No. vessels	+	+	0.001	9.59	-	+	15	6581.30	0	0.95
	+	+	0.001	9.52	-	-	10	6588.18	6.88	0.03
	+	+	0.001	6.76	+	+	20	6590.26	8.96	0.01
No. edges	+	+	0.0008	8.41	-	+	15	9020.36	0	0.89
	+	+	-	10.05	-	+	14	9025.52	5.16	0.07
	+	+	0.0009	8.35	-	-	10	9027.24	6.88	0.03
No. nodes	+	+	0.0007	7.50	-	-	10	5337.17	0	0.66
	+	+	0.0007	7.59	-	+	15	5338.53	1.36	0.33
	+	+	0.0007	6.47	+	-	15	5346.02	8.86	0.008
Total time	+	+	0.001	13.00	-	-	10	4595.35	0	0.59
	+	+	0.001	13.00	-	+	15	4596.15	0.80	0.40
	+	+	0.001	12.42	+	-	15	4604.07	8.72	0.008
Average time	+	+	0.001	7.00	-	-	10	4128.89	0	0.75
	+	+	0.001	7.00	-	+	15	4131.23	2.34	0.23
	+	+	0.001	7.35	+	-	15	4138.47	9.58	0.006

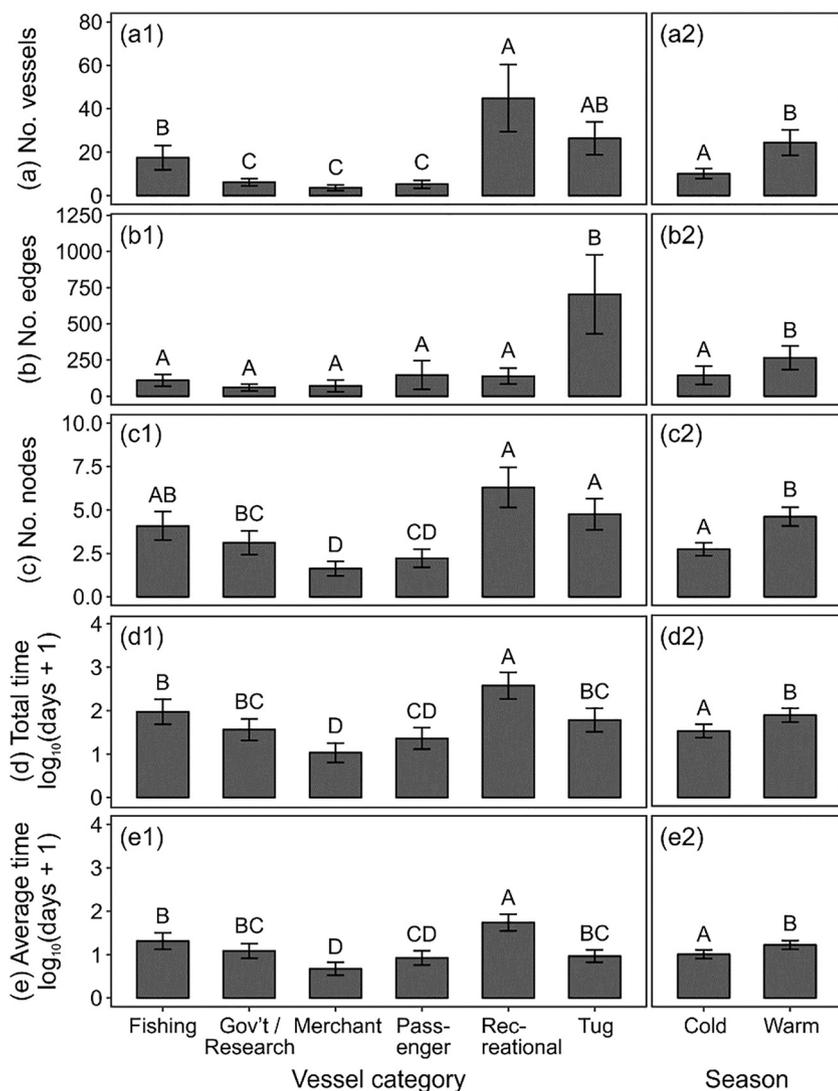


Fig. 4. Top model factors that mediated attributes of vessel traffic connecting invasion nodes to MPAs. Differences were found among vessel categories (a1 – e1) and season (a2 – e2; ‘cold’ connections were made within fall and any spring/summer/fall connection with winter, ‘warm’ connections were made from spring to fall). Measured attributes included the number of vessels within and connecting an invasion or MPA node (a1 – a2), the number of edges connecting nodes (b1 – b2), the number of other nodes a node is connected to (c1 – c2), the total time ($\log_{10}(x + 1)$ in days) vessels spend in a node (d1 – d2), and the average time ($\log_{10}(x + 1)$ in days) vessels spend in a node (e1 – e2). Different letters indicate significant differences between factor levels within each graph panel ($p < .05$; ‘NS’ is not significant), and error bars are 95% confidence intervals.

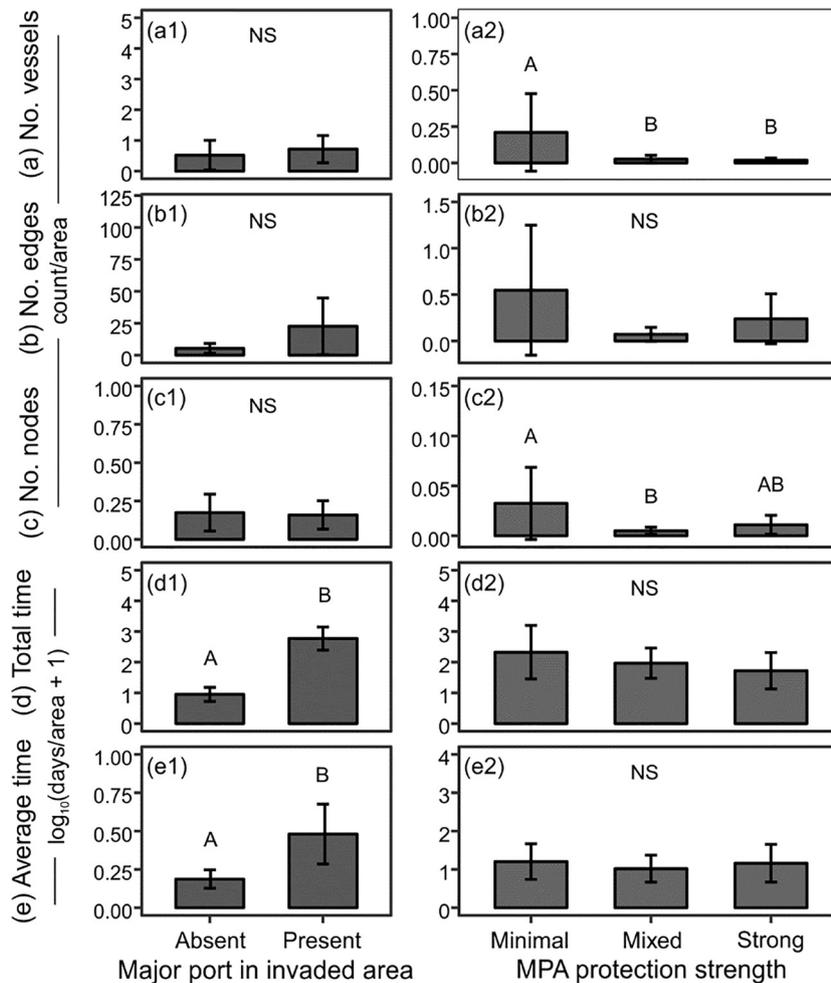


Fig. 5. Vessel traffic attributes divided by node area for merchant, passenger, and tug vessels in invasion nodes with and without a major port (a1 – e1) and for recreational vessels in MPA nodes with different levels of protection strength (a2 – e2). Different letters indicate significant differences between factor levels within each graph panel ($p < .05$; 'NS' is not significant), and error bars are 95% confidence intervals.

connections between invaded areas and marine protected areas and that these connections are greater for MPAs with minimal protection levels. Vessels sometimes spend significant amounts of time in invaded areas, potentially accumulating nonindigenous species in ballast water (including bilge, holding tanks, etc.) or as biofouling, and then transit to MPAs where nonindigenous species may be released. In particular, we found more connections between invaded areas and MPAs and longer visit durations for recreational vessels, during warm seasons when nonindigenous species are most abundant, and for invasion and MPA nodes of greater spatial extent and dock coverage. Consideration of these high-risk vessel and node characteristics is largely lacking in current MPA planning, monitoring, and management decisions, despite broad agreement that invasions would compromise the management goals for most protected areas (Iacarella et al., 2019a). However, MPAs with mixed (multiple zones) and strong regulatory protection strengths have lower invasion risk than minimally protected MPAs owing to fewer vessel entries and connections (Fig. 5). Invasion risk from vessel traffic is therefore reduced by limiting resource extraction and recreational use of MPAs even though this was not the focus of the regulations. Analyses of patterns of nonindigenous species and vector intersections and how they link to protected areas is an effective first step that can be applied across biomes to prioritize management efforts.

We considered the time vessels spent within invaded areas and MPAs – highest for recreational vessels in our study area – as a fundamental contributor to invasion risk, though there are other mediating factors. Vessels traveling at higher speeds (> 9 m/s) may dislodge or

fragment biofouling while in transit, especially organisms that are not hard or encrusting (Coutts et al., 2010; Clarke Murray et al., 2012). If a boat docks in an invaded area and accumulates biofouling, then travels quickly through an MPA, dislodgement or fragmentation may lead to invasion. Longer durations in MPAs increase the potential for biofouling to spawn (Minchin and Gollasch, 2003). The distance and abiotic conditions of a voyage may also affect biofouling survival and attachment, though nonindigenous species have been found to survive extended inter-ocean voyages across steep salinity and temperature gradients (Davidson et al., 2008). Organisms in ballast, bilge, or holding tank water of commercial and recreational vessels (e.g. Campbell et al., 2016) are not exposed to these external conditions and will likely survive provided they are picked up and dropped off in similar conditions. Bilge water of recreational vessels is often overlooked as a transfer mechanism, but has been shown to carry a rich and viable community (Fletcher et al., 2017). Whether or not a nonindigenous species will then establish will depend on the abiotic and biotic characteristics of the receiving environment and the propagule pressure of individuals released. Further risk-analyses may incorporate vessel type details including the amount of underwater surface available for fouling, carrying capacity of ballast, bilge, or holding tank water, and husbandry practices/frequencies (e.g. antifouling coatings, etc.) (Sylvester et al., 2011). In addition, the abundance and richness of nonindigenous species at invaded areas, or locations of high impact invaders, would contribute to weighting risk from different invaded areas. These factors all mediate the probability of species uptake and

release, and apply similarly to vectors and invaders in other biomes. Moving forward, we need to develop a better understanding of the relative contribution of these factors and how they can be applied in risk analyses and to determine management effectiveness.

We focused our analyses on secondary spread from vessel traffic that transits from invaded areas with high nonindigenous species richness to MPAs to help target management actions. Ten of the 24 MPAs that overlapped invaded areas did not have identified vessel connections from other invaded areas in 2016 (we did not include vessel connections between overlapping areas as pathways in the analysis; Appendix, Table A2). The origin of invasion in these areas may be from traffic in previous years, other marine vectors (e.g. aquaculture, marine infrastructure), or primary introduction from oceangoing ships. Our results underestimate invasion potential in MPAs by not considering primary introduction or other vectors. However, primary and secondary vectors, and vector types, are managed at different scales and by different governing bodies. Our results can guide management of localized vessel traffic, particularly for recreational boats which are a major source of nonindigenous species spread owing to their prevalence on the water (as shown here) and lack of management or regulation to promote biosecurity behaviours (Clarke Murray et al., 2011; Ferrario et al., 2017; Ulman et al., 2019).

4.1. Regulatory measures to prevent invasions and facilitate conservation

Vector management can be implemented nationally at three levels: primary introductions into domestic waters, subsequent spread across domestic waters, and spread into MPAs. IMO-mandated and nationally enforced ballast water/sediment management for international ships provide effective reduction of freshwater organism concentrations in flux (Casas-Monroy et al., 2018). However, there is a strong need for mandated biofouling management for all vessels. IMO guidelines on biofouling management for shipping are currently voluntary, and invasions from biofouling remain a significant issue despite modern antifouling coatings and the operational incentive to remove biofouling drag (Sylvester et al., 2011; Davidson et al., 2016). New Zealand and California are at the forefront of managing vessel biofouling by establishing biofouling compliance programs for incoming vessels (California Code of Regulations, 2017; Ministry for Primary Industries, 2018). Overseas arrivals of commercial and recreational boats are regulated by New Zealand's 'Craft Risk Management Standard' for biofouling, which applies a more stringent management threshold on any type of vessel intending to remain in New Zealand waters for > 20 days (Ministry for Primary Industries, 2018).

Managing secondary spread within national waters is also valuable once nonindigenous species have established, yet has received little attention relative to primary introductions. Domestic ballast water transfer is often permitted (Verna and Harris, 2016) and movement of biofouled vessels and maritime structures is largely unrestricted (Ferrario et al., 2017; Iacarella et al., 2019b). Recreational vessels are particularly high-risk invasion vectors as they have extensive biofouling and strongly link invaded areas to MPAs, as shown here, yet they are not broadly considered in marine regulations or guidelines (Clarke Murray et al., 2011; Ferrario et al., 2017; Ulman et al., 2019). Managing secondary spread at the national level would benefit MPAs as well as other areas of conservation and ecotourism value and can be largely achieved by requiring vessel cleaning prior to departing home marinas (clean-before-you-go). The spread of freshwater zebra mussels has been stemmed in North America and Europe in this way by mandating inspections and cleaning of boats transiting between lakes (Lalaguna and Marco, 2008; Zook and Phillips, 2012).

In addition to national-level vector management, MPAs benefit from customized regulations to meet their conservation goals. With notable exceptions, most global MPAs have no prevention measures in place to reduce invasion risk, and experts report ballast water and hull fouling as the most common vectors of spread of sessile invertebrates, plants,

and algae into MPAs (Iacarella et al., 2019a). MPA managers can develop policies to enforce ballast, bilge, and holding tank water and biofouling management for all incoming vessel traffic. This approach has been adopted for two MPAs to-date – the Papahānaumokuākea Marine National Monument (USA) and the Galapagos Marine Reserve (Campbell et al., 2015; Moser et al., 2016). Analogous vector policies exist in terrestrial and freshwater protected areas; for instance, some protected areas in New Zealand and USA mandate cleaning of shoes, clothing, and vehicles prior to entry to reduce propagule pressure from nonindigenous species (Genovesi and Monaco, 2013). When resources are limited, MPA managers may focus enforcement on particular vessel types and other characteristic risk-profiling features that increase invasion risk, as shown in this study. For instance, zoning recreational use within MPAs via mandate or reduced infrastructural amenity is likely to reduce recreational vessel traffic to important areas. Other management actions such as restricting anchorage and fishing in MPAs would reduce the time vessels spend within these areas and consequently reduce the likelihood of nonindigenous species transfer. Such restrictions could be enacted seasonally to reduce risk at sensitive times of year (i.e. warm months when vessels and organisms are more prevalent) or for particular MPAs identified as over-exposed to connections with invasion hubs. Our analysis showed that MPAs with strong protection measures or containing limited use zones were less connected to invaded areas than MPAs with high recreational use values. Managing for conservation values by limiting human uses can inherently reduce invasion risk by minimizing vectors. Studies on plant invasions into terrestrial protected areas have also found that heavy use of the landscape surrounding protected areas (i.e. high human population densities, agricultural land) increases invasions; management recommendations include limiting human uses within and surrounding protected areas (Pauchard and Alaback, 2004; Spear et al., 2013).

In addition to much needed policies, public awareness and effective communication strategies are key in helping prevent the spread of nonindigenous species (Campbell et al., 2017), particularly for recreational boaters who may dock within invaded areas and make trips to MPAs. Managers are increasingly relying on citizen self-regulation to mitigate the spread of invaders (Campbell et al., 2017), with a major focus in North America on educational campaigns that target inland recreational boaters. Such efforts have increase public awareness and some cleaning practices, though outreach messages must be tailored and paired with other management strategies to achieve sufficient vector mitigation (Cole et al., 2016; Seekamp et al., 2016). From our study results, we suggest that invaded areas (departure points) and MPAs be identified with signs and information on the importance of cleaning out ballast, bilge, and holding tank water and removing biofouling using best-practices. To-date protected areas, invasions, and human activities that connect the two have largely been managed as distinct entities, yet effective long-term conservation will require integrated policies and coordinated efforts to reduce invasions and their impacts.

CRedit authorship contribution statement

Josephine C. Iacarella: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing - original draft. **Lily Burke:** Data curation, Investigation, Methodology. **Ian C. Davidson:** Conceptualization, Funding acquisition, Methodology, Writing - original draft. **Claudio DiBacco:** Conceptualization, Funding acquisition, Methodology, Writing - original draft. **Thomas W. Theriault:** Conceptualization, Data curation, Funding acquisition, Methodology, Writing - original draft. **Anya Dunham:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing - original draft.

Acknowledgements

We thank Michael Grilliot for contributing to vessel data analysis, Jessica Nephin, Cole Fields, and Katie Gale for coding and GIS support, and the anonymous reviewers for feedback. Funding was provided by Fisheries and Oceans Canada (DFO) Strategic Program for Ecosystem-based Research and Advice and Fisheries and Oceans Canada (DFO) National Conservation Plan (JCI, LB, and AD) and the Smithsonian Institution (ICD).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108553>.

References

- Bartón, K., 2009. Mu-Min: multi-model inference. R package version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>.
- Blackburn, T.M., Bellard, C., Ricciardi, A., 2019. Alien versus native species as drivers of recent extinctions. *Front. Ecol. Environ.* 17, 203–207.
- California Code of Regulations, 2017. Biofouling Management to Minimize the Transfer of Nonindigenous Species from Vessels Arriving at California Ports. California Code of Regulations.
- Campbell, M.L., Keith, I., Hewitt, C.L., Dawson, T.P., Collins, K., 2015. Evolving marine biosecurity in the Galapagos Islands. *Manag. Biol. Invasion* 6, 227–230.
- Campbell, T., Verboomen, T., Montz, G., Seilheimer, T., 2016. Volume and contents of residual water in recreational watercraft ballast systems. *Manag. Biol. Invasion* 7, 281–286.
- Campbell, M.L., Bryant, D.E.P., Hewitt, C.L., 2017. Biosecurity messages are lost in translation to citizens: implications for devolving management to citizens. *PLoS One* 12, e0175439. <https://doi.org/10.1371/journal.pone.0175439>.
- Carlton, J.T., 1996. Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* 78, 97–106.
- Carlton, J.T., Hodder, J., 1995. Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. *Mar. Biol.* 121, 721–730.
- Casas-Monroy, O., Linley, R.D., Chan, P.-S., Kydd, J., Vanden Byllaardt, J., Bailey, S., 2018. Evaluating efficacy of filtration + UV-C radiation for ballast water treatment at different temperatures. *J. Sea Res.* 133, 20–28.
- Clarke Murray, C., Pakhomov, E.A., Theriault, T.W., 2011. Recreational boating: a large unregulated vector transporting marine invasive species. *Divers. Distrib.* 17, 1161–1172.
- Clarke Murray, C., Theriault, T.W., Martone, P.T., 2012. Adapted for invasion? Comparing attachment, drag and dislodgment of native and nonindigenous hull fouling species. *Biol. Invasions* 14, 1651–1663.
- Cole, E., Keller, R.P., Garbach, K., 2016. Assessing the success of invasive species prevention efforts at changing the behaviors of recreational boaters. *J. Environ. Manag.* 184, 210–218.
- 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>.
- Coutts, A.D.M., Piola, R.F., Hewitt, C.L., Connell, S.D., Gardner, J.P.A., 2010. Effect of vessel voyage speed on survival of biofouling organisms: implications for translocation of non-indigenous marine species. *Biofouling* 26, 1–13.
- Davidson, I.C., McCann, L.D., Fofonoff, P.W., Sytsma, M.D., Ruiz, G.M., 2008. The potential for hull-mediated species transfers by obsolete ships on their final voyages. *Divers. Distrib.* 14, 518–529.
- Davidson, I., Scianni, C., Hewitt, C., Everett, R., Holm, E., Tamburri, M., Ruiz, G., 2016. Mini review: assessing the drivers of ship biofouling management – aligning industry and biosecurity goals. *Biofouling* 32, 411–428.
- Ferrario, J., Caronni, S., Occhipinti-Ambrogi, A., Marchini, A., 2017. Role of commercial harbours and recreational marinas in the spread of non-indigenous fouling species. *Biofouling* 33, 651–660.
- Fletcher, L.M., Zaiko, A., Atalah, J., Richter, I., Dufour, C.M., Pochon, X., Wood, S.A., Hopkins, G.A., 2017. Bilge water as a vector for the spread of marine pests: a morphological, metabarcoding and experimental assessment. *Biol. Invasions* 19, 2851–2867.
- Foxcroft, L.C., Pyšek, P., Richardson, D.M., Genovesi, P., MacFadyen, S., 2017. Plant invasion science in protected areas: progress and priorities. *Biol. Invasions* 19, 1353–1378.
- Frisch, A.J., Rizzari, J.R., 2019. Parks for sharks: human exclusion areas outperform no-take marine reserves. *Frontiers Ecol. Environ.* 17, 145–150.
- Gartner, H.N., Clarke Murray, C., Frey, M.A., Nelson, J.C., Larson, K.J., Ruiz, G.M., Theriault, T.W., 2016. Non-indigenous invertebrate species in the marine fouling communities of British Columbia, Canada. *BiolInvasions Rec* 5, 205–212.
- Genovesi, P., Monaco, A., 2013. Guidelines for addressing invasive species in protected areas. In: Foxcroft, L.C., Pyšek, P., Richardson, D.M., Genovesi, P. (Eds.), *Plant Invasions in Protected Areas: Patterns, Problems and Challenges*. Springer, Berlin, pp. 487–506.
- Giakoumi, S., Guilhaumon, F., Kark, S., Terlizzi, A., Claudet, J., Felling, S., Cerrano, C., Coll, M., Danovaro, R., Frascchetti, S., Koutsoubas, D., Ledoux, J.-B., Mazor, T., Mérigot, B., Micheli, F., Katsanevakis, S., 2016. Space invaders; biological invasions in marine conservation planning. *Divers. Distrib.* 22, 1220–1231.
- Glen, A.S., Pech, R.P., Byrom, A.E., 2013. Connectivity and invasive species management: towards an integrated landscape approach. *Biol. Invasions* 15, 2127–2138.
- Iacarella, J.C., Saheed, D., Dunham, A., Ban, N.C., 2019a. Non-native species are a global issue for marine protected areas. *Frontiers Ecol. Environ.* 17, 495–501.
- Iacarella, J.C., Davidson, I.C., Dunham, A., 2019b. Biotic exchange from movement of ‘static’ maritime structures. *Biol. Invasions* 21, 1131–1141.
- IPBES, 2019. In: Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneeth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichihli, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razaque, J., Reyers, B., Roy Chowdhury, R., Shin, Y.J., Visseren-Hamakers, L.J., Willis, K.J., Zayas, C.N. (Eds.), *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES secretariat, Bonn, Germany.
- 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. *Biol. Invasions* 20, 87–103.
- Lalaguna, C.D., Marco, A.A., 2008. The zebra mussel invasion in Spain and navigation rules. *Aquat. Invasions* 3, 315–324.
- Mačić, V., Albano, P.G., Almpantidou, V., Claudet, J., Corrales, X., Essl, F., Evagelopoulou, A., Giovos, I., Jimenez, C., Kark, S., Marković, O., Mazaris, A.D., Ólafsdóttir, G., Panayotova, M., Petović, S., Rabitsch, W., Ramdani, M., Rilov, G., Tricarico, E., Fernández, T.V., Sini, M., Trygonis, V., Katsanevakis, S., 2018. Biological invasions in conservation planning: a global systematic review. *Front. Mar. Sci.* 5. <https://doi.org/10.3389/fmars.2018.00178>.
- Manel, S., Loiseau, N., Andreollo, M., Fietz, K., Goñi, R., Forcada, A., Lenfant, P., Kininmonth, S., Marcos, C., Marques, V., Mallol, S., Pérez-Ruzafa, A., Breusing, C., Puebla, O., Mouillot, D., 2019. Long-distance benefits of marine reserves: myth or reality? *Trends Ecol. Evol.* 34, 342–354.
- 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), 111–122.
- Ministry for Primary Industries, New Zealand, 2018. Guidance Document for the Craft Risk Management Standard for Biofouling. GD CRMS-BIOFOUL. Ministry for Primary Industries, Wellington.
- Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers Ecol. Environ.* 6, 485–492.
- Moser, C.S., Wier, T.P., Grant, J.F., First, M.R., Tamburri, M.N., Ruiz, G.M., Miller, A.W., Drake, L.A., 2016. Quantifying the total wetted surface area of the world fleet: a first step in determining the potential of ships’ biofouling. *Biol. Invasions* 18, 265–277.
- Parks, B.C., 2012. BC Parks Zoning Framework: A Management Planning Tool. British Columbia. <http://www.env.gov.bc.ca/bcparks/planning/docs/zoning-framework.pdf>.
- Pauchard, A., Alaback, P.B., 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Conserv. Biol.* 18, 238–248.
- Pavlopoulos, G.A., Scerif, M., Moschopoulos, C.N., Soldatos, T.G., Kossida, S., Aerts, J., Schneider, R., Bagos, P.G., 2011. Using graph theory to analyze biological networks. *BioData Min* 4, 10. <http://www.biodatamining.org/content/4/1/10>.
- Pérez-Portela, R., Arranz, V., Rius, M., Turon, X., 2013. Cryptic speciation or global spread? The case of a cosmopolitan marine invertebrate with limited dispersal capabilities. *Sci. Rep.* 3, 3197.
- R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ruiz, G.M., Fofonoff, P.W., Steves, B., Foss, S.F., Shiba, S.N., 2011. Marine invasion history and vector analysis of California: a hotspot for western North America. *Divers. Distrib.* 17, 362–373.
- Seekamp, E., McCreary, A., Mayer, J., Zack, S., Charlebois, P., Pasternak, L., 2016. Exploring the efficacy of an aquatic invasive species prevention campaign among water recreationists. *Biol. Invasions* 18, 1745–1758.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what’s what and the way forward. *Trends Ecol. Evol.* 28, 58–66.
- Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.A., 2013. Human population density explains alien species richness in protected areas. *Biol. Conserv.* 159, 137–147.
- 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. *J. Appl. Ecol.* 52, 366–378.
- Sylvester, F., Kalaci, O., Leung, B., Lacoursière-Roussel, A., Clarke Murray, C., Choi, F.M., Bravo, M.A., Theriault, T.W., MacIsaac, H.J., 2011. Hull fouling as an invasion vector: can simple models explain a complex problem? *J. Appl. Ecol.* 48, 415–423.
- 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. *J. Appl. Ecol.* 56, 2620–2629.
- Verna, D.E., Harris, B.P., 2016. Review of ballast water management policy and associated implications for Alaska. *Mar. Policy* 70, 13–21.
- Williams, S.L., Davidson, I.C., Pasari, J.R., Ashton, G.V., Carlton, J.T., Crafton, R.E., Fontana, R.E., Grosholz, E.D., Whitman Miller, A., Ruiz, G.M., Zabin, C.J., 2013. Managing multiple vectors for marine invasions in an increasingly connected world. *Bioscience* 63, 952–966.
- Woodley, S., Locke, H., MacKinnon, K., Sandwith, T., Smart, J., 2019. A review of evidence for area-based conservation targets for the Post-2020 Global Biodiversity Framework. *PARKS: The International Journal of Protected Areas and Conservation* 25 (2), 31–46.
- Zook, B., Phillips, S., 2012. Uniform Minimum Protocols and Standards for Watercraft Interception Programs for Dreissenid Mussels in the Western United States (UMPS II). Pacific States Marine Fisheries Commission, Oregon, USA.