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Hull fouling as an invasion vector: can simple models explain a complex problem?

Francisco Sylvester[1,2]*, Odion Kalaci[1], Brian Leung[3,4], Anaïs Lacoursière-Roussel[3], Cathryn Clarke Murray[5], Francis M. Choi[5], Monica A. Bravo[6], Thomas W. Therriault[7] and Hugh J. MacIsaac[1]

[1]*Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario N9B 3P4, Canada;* [2]*Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EHA Buenos Aires, Argentina;* [3]*Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada;* [4]*School of Environment, McGill University, Montreal, Quebec H3A 2A7, Canada;* [5]*Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z3, Canada;* [6]*Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, Nova Scotia B2Y 4A2, Canada; and* [7]*Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia V9T 6N7, Canada*

Summary

1. The most effective way to manage nonindigenous species and their impacts is to prevent their introduction via vector regulation. While ships' ballast water is very well studied and this vector is actively managed, hull fouling has received far less attention and regulations are only now being considered despite its importance for introductions to coastal, marine systems.
2. We conducted comprehensive *in situ* sampling and video recording of hulls of 40 transoceanic vessels to assess propagule and colonization pressure in Vancouver and Halifax, dominant coastal ports in Canada. Concomitant sampling was conducted of harbour fouling communities to compare hull and port communities as part of a vector risk assessment.
3. Although this vector has been operational for a long time, hull and harbour communities were highly divergent, with mean Sørensen's similarity values of 0·03 in Halifax and 0·01 in Vancouver, suggesting invasion risk is high. Propagule pressure (up to 600 000 ind. ship^{-1}) and colonization pressure (up to 156 species ship^{-1}) were high and varied significantly between ports, with Vancouver receiving much higher abundances and diversity of potential invaders. The higher risk of fouling introductions in Vancouver is consistent with historical patterns of successful hull fouling invasions.
4. The extent of hull fouling was modelled using ship history predictors. Propagule pressure increased with time spent in previous ports-of-call and time since last application of antifouling paint, whereas colonization pressure increased with time since last painting and with the number of regions visited by the ship. Both propagule and colonization pressure were negatively related to the time spent at sea and the latitude of ports visited.
5. *Synthesis and applications*. A major challenge for applied invasion ecology is the effective management of introduction vectors. We found that hull fouling has a strong potential for introduction of many species to coastal marine habitats and that management should be considered. Simple variables related to the vessels' hull husbandry, voyage, and sailing patterns may be used to predict and manage hull fouling intensity. The results presented here should interest policy makers and environmental managers who seek to reduce invasion risk, and ship owners seeking to optimize fuel efficiency.

Key-words: biological invasions, hull fouling, introduction vectors, management, models, nonindigenous species, ports, propagule pressure, ships

*Correspondence author. E-mail: fsylvester@ege.fcen.uba.ar

Introduction

The introduction and spread of nonindigenous species (NIS) is a major threat to global biodiversity (Lawler *et al.* 2006; Clavero *et al.* 2009). Given the host of ecological, economic, and health problems associated with NIS introductions, a growing field of study focuses on management policies and procedures (Leppäkoski, Gollasch & Olenin 2002; Ruiz & Carlton 2003). Management efforts appear most successful when they target introduction of new NIS, as successful eradication of established populations is rare (Lodge *et al.* 2006; Bergstrom *et al.* 2009).

In an era of globalization and human population growth, greater trade and associated NIS introductions – both intentional and inadvertent – should be anticipated (Lawler *et al.* 2006; Hulme 2009). International shipping transports ~90% of globally traded goods, and represent perhaps the single largest pathway for transport and introduction of NIS globally (Hewitt, Gollasch & Minchin 2009). Ships provide two principal mechanisms for dispersal of aquatic NIS. Vessels carry ballast water to maintain stability and trim when they are not carrying cargo. This water, usually loaded in the penultimate port-of-call, can support varying abundances (i.e. propagule pressure; see Methods) or diversities (i.e. colonization pressure; see Methods) of species which are subsequently discharged into the recipient port (Carlton 1985). Secondly, externally-exposed vessel surfaces including the hull, tiller, rudder, sea-chest and bulbous nose may become fouled by an assortment of encrusting species or fouling species that may dislodge or reproduce *in situ* in subsequent ports-of-call (e.g. Coutts & Taylor 2004; Ruiz & Smith 2005; Sylvester & MacIsaac 2010).

Recognition of the key role played by ballast water in international dispersal of NIS has resulted in the creation of proposed standards that would limit the permissible density of viable organisms discharged in ships' ballast (IMO (International Maritime Organization) 2004). All international vessels must exchange filled ballast tanks or flush 'empty' ones while crossing the Atlantic Ocean prior to discharging into the Great Lakes, a procedure that appears to substantially reduce the risk of introducing new NIS (Bailey *et al.* unpublished data). In contrast, no international regulations or 'best practices' currently exist that specifically address NIS transported attached to the hull of vessels, with the exception of Australia and New Zealand (Hewitt, Everett & Parker 2009). Following these examples, the IMO has initiated development of hull fouling management guidelines for international merchant vessels although adoption by its members is expected to progress slowly. Currently, however, hull maintenance is a voluntary practice implemented by ship owners with the aim to reduce hydrodynamic drag and fuel consumption. Also, due both to the vast surface area available for colonization under transoceanic vessels and to the existence of refugia niches where antifouling paints are not applied or effective, hull husbandry practices that effectively reduce fouling and improve fuel consumption might still allow sufficient propagules to be transported such that invasion risk remains high (Gollasch 2002; Coutts & Taylor 2004). Faster vessels and shortened transit times, absence of hull maintenance for inactive vessels, development of antifouling resistance by hull fouling species, and a ban in 2008 on one of the most powerful antifouling agents known, tributyltin (TBT), owing to marine toxicity issues may further increase the introduction potential associated with hull fouling (Minchin & Gollasch 2003; Davidson *et al.* 2008; Piola, Dafforn & Johnston 2009).

Although managers and policy makers are slowly turning their focus to hull fouling, logistical and economic challenges associated with sampling have limited hull fouling research. A number of studies have identified variables related to hull fouling propagule pressure (Coutts 1999; Coutts & Taylor 2004; Ruiz & Smith 2005), but few have tried to construct predictive models of risk (Davidson *et al.* 2009; Sylvester & MacIsaac 2010). In this study, we use hull fouling as an example of the potential of vector assessment to provide managers with tools to address risks of biological invasions. We conducted a comprehensive assessment of hull fouling communities associated with 40 international ships arriving to two major ports on the east and west coasts of Canada. Specific objectives of this study were to: (1) assess the potential of hull fouling as an introduction vector; (2) compare propagule and colonization pressure in the ports of Halifax and Vancouver; and (3) develop a hull fouling model to identify factors that may be managed to limit introduction risk.

Materials and methods

Between 2007 and 2009, we surveyed the hulls of 20 commercial trans-oceanic vessels in the Port of Halifax and 20 in Vancouver on the east and west coasts of Canada, respectively. Sample collection and processing methods were similar to those described in a previous study (Sylvester & MacIsaac 2010), and are described here only briefly. We opportunistically sampled vessels representing the prevailing inbound, international traffic to the ports studied. Vessels sampled included bulk, container, general cargo carriers, oil and chemical tankers, roll-on/roll-off cargo vessels, and one cable layer. Divers collected 20 × 20 cm quadrat samples and recorded random video transects from underwater locations of the hull. The combination of abundances in the samples and percentage cover information obtained from video transects was used to estimate total abundance of invertebrates per ship. Control water samples were collected from the dock area and used to adjust species diversity assessments for contamination that may have occurred while the vessel was in port. Basic information including typical sailing speed, and antifouling and travel history for the previous year was collected for all but one vessel. Samples scraped from hulls of 10 vessels (4 in Halifax, 6 in Vancouver) were examined visually at the dock, prior to fixation, to determine if organisms were dead or alive when collected.

To determine whether hull fouling communities differed from those in recipient ports, we conducted extensive sampling of native and non-native benthic fauna in the sampled ports. Harbour sampling was carried out during 2007 through 2009 and comprised dive, settlement plate (subtidal communities), and intertidal sampling. Dive surveys were conducted in 6 locations in the Port of Vancouver and 12 sites in Halifax. At each site, four dock pilings or an equivalent number of transects on a dock wall were examined to a depth of up to 7·5 m for 10 min. When species identifications were not possible by divers *in-situ*, they were obtained through high-resolution pictures or physical samples collected and examined in the laboratory. Settlement plates were suspended from floating structures (1–5 m depth) in each harbour to characterize recruitment. In Halifax, a base with either three to four Petri dishes or three 10 × 10 cm PVC plates were deployed in the harbour plus each of three marinas for 2·5 months. Bases with four Petri dishes attached were deployed in Vancouver; two plates at each of four harbour sites for 3·5 months. Standardized, 4-h long timed walks were used to characterize the species inhabiting intertidal habitats in both Halifax (6 sites) and Vancouver (9 sites). Representative habitats were surveyed in each of three intertidal heights (high, mid, and low) with all macro-organisms encountered recorded.

All samples were sorted and hull fouling invertebrates were counted in the laboratory to estimate abundances. We did not attempt to quantify harbour samples. Organisms were identified to the lowest taxonomic level possible and classified as native, established NIS, or cryptogenic through the use of taxonomic keys, extensive bibliographic search, and through consultation with global taxonomists (see acknowledgements). Hull fouling taxa that were not found in harbour samples were considered non-established NIS for that port. Identifications of ascidians in port waters were confirmed by molecular techniques using the 18S rDNA marker. Algae and nematodes were excluded from analyses. Hull video-transects were used to calculate taxa abundances for the whole ship (see Sylvester & MacIsaac 2010).

In this paper, we use the terms propagule pressure to describe the total number of individuals of a species that is introduced at a given location, propagule number as the number of introduction events, and colonization pressure as the total number of species released (*sensu* Lockwood, Cassey & Blackburn 2009), and introduce the term *combined propagule pressure* to refer to the total number of individuals of all species transported by a vector.

DATA ANALYSIS

To assess colonization pressure associated with hull fouling in Halifax and Vancouver, we estimated species richness by ship and for all ships combined in each port. We used the Chao-2 species richness estimate, calculated using SPADE software (Chao & Shen 2003); significant differences between ports were tested using confidence intervals. Comparisons between vessel and harbour fouling communities were made using Sørensen's Similarity Index (QS). This index was calculated as:

$$QS = \frac{2J}{H + P} \qquad \text{eqn 1}$$

where H and P are the number of fouling species in hull and port communities, respectively, and J is the number of species shared between the two. Additionally, we compared several biotic (e.g. propagule and colonization pressure, sampled number of species, and Sørensen's similarity index between hull and port communities) and abiotic (e.g. number of international port arrivals, average port latitude, total and average port time, number of ports-of-call visited, vessel length, sailing speed, time since last dry-docking, and time since last painting) variables related to the harbour and vessels sampled in Vancouver and Halifax using two-tailed t-tests for samples with unequal variance.

Previous ports-of-call were assigned to the following regions: Atlantic North America; Pacific North America; Gulf of Mexico and Caribbean Sea; Pacific Central America; Atlantic South America; Pacific South America; Europe and North Africa; South Africa and Indian Ocean; Asia; Oceania; Arctic Seas; and Panama (Sylvester & MacIsaac 2010; Fig. 1). We used Pearson's correlation to explore the relationship between the time spent by vessels in ports in a given region over the previous year prior to sampling and the number of species from that region that were found on the hulls. We used the global distribution of the species as a surrogate for the source region.

MODELLING HULL FOULING

We explored simple relationships between average and combined propagule and colonization pressure using ANCOVA, with sampling port as a categorical variable and time since last painting and port residence time over the year prior to sampling as covariates. We fitted simple least square linear regressions to these relations using log(x + 1) transformation of variables to reduce variances and meet statistical assumptions.

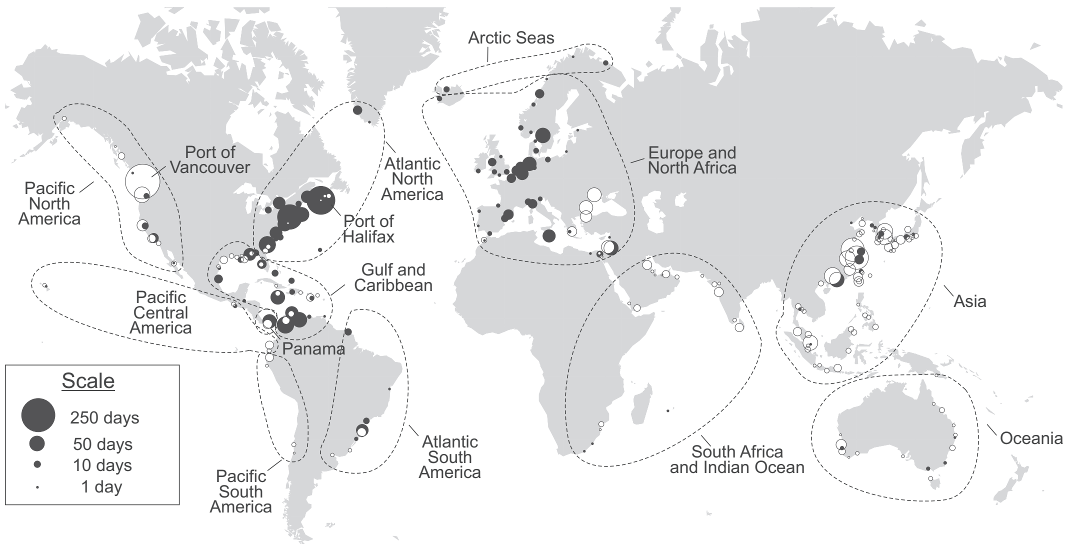

Fig. 1. Ports-of-call visited during the year preceding sampling in Halifax (solid circles) and Vancouver (open circles). The size of the circles indicates the total number of days in port (see scale on map). Dotted balloons group ports-of-call in the same region; regions are indicated.

We modelled sampled species richness, number of individuals, and the metric total estimated number of individuals ship^{-1} using process models of gains and losses. Number of individuals sampled represented the abundance of all invertebrates (i.e. combined propagule pressure) in a quadrat sampled from a patch covered with biofouling, whereas the number of individuals ship^{-1} represented the abundance in a quadrat sampled randomly across the entire hull multiplied by the size of the hull. We generated our models assuming that propagule pressure could be separated into gains and losses: species and individuals accumulated during port stays, and were lost during ship travel. We assumed that the ability of fouling organisms to attach depended upon the antifouling painting, the effectiveness of which is expected to decay over time in a simplified model. The two coasts studied could have different rates of gain resulting from different species pools in their respective source ports. We assumed, however, that loss rate functions would be similar between coasts. Thus, the number of species and individuals in a sample was modelled as:

$$N = \sum_{p=1}^{P} G_p L_p \qquad \text{eqn 2}$$

where N is the number of organisms on a given ship, G_p is the gain of organisms from port p, and L_p the proportion that is subsequently lost. Gain is a function of the number of organisms present (determined by K_1 and K_2), the degree of accumulation (A_p), and the efficacy of antifouling paint (S_p). We hypothesize that accumulation depends on the duration of the stay at port p (D_p), and that S_p depends on the time since the last application of antifouling paint (Q_p). Mathematically:

$$G_p = (K_1 + K_2 x) A_p S_p \qquad \text{eqn 3}$$

where K_1 and K_2 are scalars, x is a dummy variable that allows the sampling ports to differ (0 = Halifax, 1 = Vancouver), and

$$A_p = 1 - e^{-\alpha D_p^{c_1}} \qquad \text{eqn 4}$$

$$S_p = 1 - e^{-\gamma Q^{c_2}} \qquad \text{eqn 5}$$

We hypothesize that loss occurs during travel and may be modified by sailing speed. Loss is given by:

$$L_p = e^{-\left[\beta_1 T_p^{c_3} + \beta_2 V^{c_4} + \beta_3 (VT_p)^{c_5}\right]} \qquad \text{eqn 6}$$

where T_p is travel time since departure from port p, V is typical sailing speed, and VT_p is distance travelled. There may be a lag with respect to how soon organisms start to attach in the port – possibly related to biofilm condition – as well as to when they start to be lost following departure, and an asymptote for gain and loss. These situations were modelled using shape parameters (α, β, γ) and coefficients (c) in each of the eqns 4–6. We compared predicted to observed values across all ships using a Poisson error model for counts of species richness and number of individuals sampled, and a normally distributed error model for number of individuals ship^{-1}. We tested the importance of the components of the model by removing one variable at a time; the change in the model fit was examined using Akaike's Information Criterion (AIC) and bias adjusted AIC values when $n/k < 40$ (Turkheimer, Hinz, & Cunningham 2003; Johnson & Omland 2004).

We conducted a Principal Component Analysis (PCA) to detect relationships that remained unrevealed by the previous models. We used the correlation matrix of variables related to hull fouling propagule pressure, operation patterns (i.e. sailing speed, number of regions visited, number of visits to , latitude of, and time spent in ports-of-call), maintenance (i.e. time since last dry-docking and painting of the hull), and travel history of all ships from this study pooled. Variables that had little relevance or were linearly dependent with other variables analysed were eliminated from the PCA. A significance level of $\alpha = 0{\cdot}05$ was used for all statistical analyses.

Results

The vessels sampled in this study serviced globally distributed ports-of-call, although those in the Gulf of Mexico, Caribbean Sea, Atlantic coast of North America, and Europe constituted the main source of vessels arriving to Halifax, while Asia was by far the most visited source of vessels sampled in Vancouver (Fig. 1). We collected 58 and 109 hull fouling samples, respectively, from vessels in Halifax and Vancouver. Total abundance of organisms sampled was 7262 and 15 787 individuals, and 71 and 141 taxa, respectively (see Appendices S1, S2 in Supporting Information). Barnacles, copepods, bivalves, and amphipods accounted for a large proportion of the individuals and taxa found.

Considerably fewer fouling species, both native and non-native, were found in harbour samples collected in Halifax than Vancouver (Table 1). Similarity between hull and harbour fouling communities was very low overall; Sørensen's similarity values were significantly lower in Vancouver than Halifax (Table 1).

The number of fouling species attributed to a global region was positively correlated with the time vessels spent in ports in that region over the year preceding sampling; this relationship held for vessels sampled in both Halifax ($r^2 = 0{\cdot}50$, $P = 0{\cdot}015$) and Vancouver ($r^2 = 0{\cdot}79$, $P < 0{\cdot}001$). Nine out of 20 variables examined suggested that hull fouling posed a greater introduction risk in Vancouver than Halifax (Table 1). For example, we observed that for all variables related to hull fouling propagule and colonization pressure, Vancouver had similar or higher values than Halifax. Similarly, voyage variables potentially associated with higher hull fouling intensity such as total and average duration of stay in, and the inverse of the latitude of ports visited were significantly greater for vessels visiting Vancouver than Halifax (Table 1, Appendix S3 in Supporting Information).

MODELS

Time in port and time since last application of antifouling paint were significant covariates for propagule and colonization pressure ($P < 0{\cdot}005$; Fig. 2). There were no significant differences between combined and average propagule pressure per ship in the two ports, but colonization pressure was significantly higher in Vancouver than Halifax (ANCOVA, $r = 0{\cdot}70$, $P = 0{\cdot}001$; Fig. 2; Table 1).

Our process models found that the only significant predictors for sampled species richness were mean duration of travel (ΔAIC = 17) and its shape parameter (ΔAIC = 19), time since last painting (ΔAIC = 76), and sampling port (ΔAIC = 83). Thus, the reduced model was:

Table 1. Comparison between vessel and harbour, biotic and abiotic variables characterizing the strength of hull fouling as a vector in the ports of Halifax and Vancouver

Variable	Halifax	Vancouver	Port where vector is strongest
Vessels			
Combined propagule pressure (ind. ship^{-1})	27 713 (49 663)	95 604 (158 832)	n.s.
Average propagule pressure (ind. ship^{-1})	3618 (10 397)	2101 (3285)	n.s.
Colonization pressure (species ship^{-1})	15 (17)	50 (46)	Vancouver
Mean observed species (species ship^{-1})			
Native	0·7 (0·6)	0·3 (0·4)	Halifax
Established NIS	0·2 (0·4)	0·7 (0·7)	Vancouver
Non-established NIS	3·2 (3·3)	6 (3·9)	Vancouver
Total (all ships combined)	34	54	
Time since last painting (*d*)	729 (364)	607 (305)	n.s.
Time since last dry-docking (*d*)	667 (269)	605 (305)	n.s.
Sailing speed (knots)	16·5 (3·4)	15·7 (3·4)	n.s.
Vessel length (*m*)	220 (67)	174 (44)	Halifax
Total port time by region (days y^{-1})			
Most visited	Atlantic North America: 26 (25)	Asia: 48 (26)	Vancouver
2nd most visited	Europe: 23 (20)	Europe: 9 (17)	Halifax
3rd most visited	Gulf: 17 (30)	Pacific North America: 7 (8)	n.s.
Sampling port	Halifax: 5 (6)	Vancouver: 12 (7)	Vancouver
All regions	84 (40)	96 (30)	n.s.
Total number of ports visited (ports y^{-1})	73 (34)	56 (24)	n.s.
Average port stay (*d*)	1 (0·7)	1·7 (1·0)	Vancouver
Average port latitude	37·7 (9·3)	32 (4·6)	Vancouver
Harbour			
International arrivals (ships y^{-1})*	1187 (73)	2987 (188)	Vancouver
Reported fouling species	48	153	
Reported fouling NIS	7	18	
Sørensen's similarity index between hull and port communities	0·03 (0·025)	0·01 (0·01)	Vancouver

Vessel and Sørensen Similarity Index values are means (SD) from 20 vessels unless indicated. Harbour values are total species found. *Mean (SD) for the years 2007, 2008 and 2009. NIS, nonindigenous species. Significant differences between ports (t-test, α = 0·05) are indicated. n.s., non-significant (see Methods).

$$N_{species} = \sum_{p=1}^{P} (K_1 + K_2 x)(1 - e^{-\gamma Q}) e^{-\beta T_p^c} \quad \text{eqn 7}$$

with parameter values: K_1 = 14·38, K_2 = 33·86, γ= 0·000 176, β= $5{\cdot}209 \times 10^{-8}$, and c = 5·8. A plot of expected to observed number of species across ships explained 43% of the total variation, or 57% after removal of one outlying data point (Appendix S4 in Supporting Information). The best predictors for sampled abundance were mean duration of travel (ΔAIC = 9348) and its shape coefficient (ΔAIC = 7054), time since last painting (ΔAIC = 7417) and its shape coefficient (ΔAIC = 3802), and sampling port (ΔAIC = 12 662). The reduced model to predict sampled abundance was:

$$N_{individuals} = \sum_{p=1}^{P} (K_1 + K_2 x)(1 - e^{-\gamma Q^{c_1}}) e^{-\beta T_p^{c_2}} \quad \text{eqn 8}$$

with parameter values: K_1 = 79·91, K_2 = 295·33, γ= $1{\cdot}47 \times 10^{-43}$, c_1 = 16·33, β= $6{\cdot}84 \times 10^{-77}$, and c_2 = 63·55. The model explained 26% of total variation or 38% after removal of one outlier (Appendix S4 in Supporting Information).

For number of individuals ship^{-1}, the significant predictors were duration of stay at port (ΔAIC = 52) and its shape coefficient (ΔAIC = 36), distance travelled (ΔAIC = 36) and its shape coefficient (ΔAIC = 19), time since last painting (ΔAIC = 23) and its shape coefficient (ΔAIC = 24), and sampling port (ΔAIC = 38). The reduced model was:

$$N_{individuals} = \sum_{p=1}^{P} (K_1 + K_2 x)\,(1 - e^{-\alpha D_p^{c_1}})\,(1 - e^{-\gamma Q^{c_2}}) e^{-\beta (V T_p)^{c_3}} \quad \text{eqn 9}$$

with parameter values: K_1 = 92 708, K_2 = $1{\cdot}21 \times 10^6$, α = $5{\cdot}85 \times 10^{-20}$, c_1 = 20·9, γ = $1{\cdot}03 \times 10^{-10}$, c_2 = 3·63, β = $3{\cdot}15 \times 10^{-7}$, and c_3 = 2·39. This model explained 86% of variation in combined propagule pressure across ships, or 64·9% following removal of an outlier (Appendix S4 in Supporting Information).

Variables with the highest factor coordinates in the PCA were vessel combined propagule pressure, port-of-call latitude,

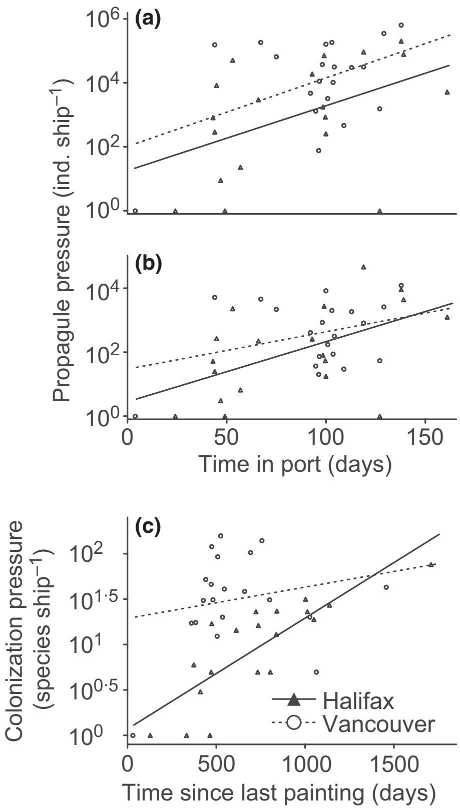

Fig. 2. Combined (a), average propagule pressure (b), and colonization pressure (c) of vessels sampled in Halifax and Vancouver as a function of time in port during the previous year and time since last application of antifouling paint. All relationships are positive and significant for both ports separately and combined, except for average propagule pressure and colonization pressure in Vancouver (b, c). Regression lines for both ports are shown on the graphs. ANCOVA indicated that time in port (a, b) and time since last painting (c) were significant covariates ($P < 0{\cdot}01$); colonization pressure was significantly higher in Vancouver than Halifax ($P = 0{\cdot}001$; c); interactions were non-significant for propagule pressure (a, b) but close to significant for colonization pressure ($P = 0{\cdot}051$; c). Note the logarithmic scale of the *y*-axis.

and duration of stay along PC1, and sailing speed, number of regions visited, and duration of port stays along PC2. The PCA confirmed a strong relationship between total time in port during the previous year, time since last application of antifouling paint, and combined propagule and colonization pressure (Fig. 3). Colonization pressure also was positively related to the number of regions visited over the previous year. Sailing speed had a negative effect on combined propagule pressure along PC2, while a positive effect on colonization pressure is suggested along the same axis; latitude of ports visited had a clear negative effect on both propagule and colonization pressure (Fig. 3). Over 50% of total variability was explained by the first two principal components.

Discussion

Shipping is a major vector for global introductions of marine NIS, with hull fouling typically exceeding ballast water in importance in coastal, marine ecosystems (Hewitt, Gollasch & Minchin 2009). Despite this, there have not been any comparative assessments of hull fouling for different regions, with the exception of a single hull fouling study that compared its data to previous studies (Davidson *et al.* 2009). Here, we conducted the first simultaneous, comprehensive assessment of hull fouling for two major ports. We found a total of 170 fouling taxa, of which 78 were identified to species level, on the hulls of 40 merchant vessels. About 90% of these species have not been recorded in the sampling ports, and are considered non-established NIS. The mismatch between port and hull fouling communities can be partially explained by the different time frames of the hull sampling – typically sampled over a few years – and the assemblage of the harbour communities sampled, which often have been exposed to centuries of hull fouling introductions (Fofonoff *et al.* 2003). It is nonetheless clear that novel NIS are still being carried and that introduction risk is not insubstantial. Unlike in freshwater environments, we cannot assume that salinity mismatch will prevent these species from successfully colonizing or establishing in destination ports (Sylvester & MacIsaac 2010). An alternative view posits that NIS that have not colonized global ports despite centuries of carriage might be considered poor colonizers incapable of successfully establishing populations in new regions.

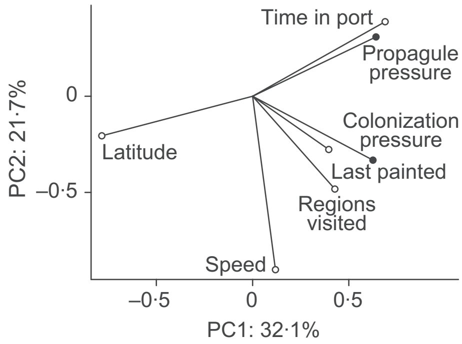

Fig. 3. Principal component analysis of invertebrate communities attached to the hulls of 40 vessels sampled in the ports of Halifax and Vancouver. Response variables included are combined propagule and colonization pressure (solid circles), while independent variables are time since last painted with antifouling agent, typical sailing speed, residence time in port, average latitude of ports, and number of regions visited over the year prior to sampling (open circles). Percentage of total variance explained by the first and second principal components is indicated.

We not only found that Vancouver receives more vessels than Halifax (i.e. propagule number), but also that those vessels transport more hull fouling species (i.e. colonization pressure) at higher abundances (i.e. propagule pressure) than the ones arriving in Halifax. Such marked spatial variation in vector strength is attributable to a number of factors. Propagule source region, for instance, can determine the composition and number of species transported (i.e. colonization pressure). Our results confirm that vessels gather the most hull fouling species from ports that they visit most often. Even if the presence of many cosmopolitan species might have weakened the correlation, the actual relationship remains unchanged. Furthermore, vessels visiting more regions probably gather more species because they are exposed to a greater variety of biological communities.

Propagule pressure was inversely related to the latitude of ports visited. Vessels servicing Vancouver operate at significantly lower latitudes and potentially entrain more taxa and propagules due to longer reproductive seasons, higher temperatures, and increased marine diversity at the ports visited (Hillebrand 2004; Locarnini *et al.* 2010). Hull fouling and harbour communities were very different in both sampling ports, but significantly more so in Vancouver. With a considerably longer history than Vancouver as a major international hub, the Port of Halifax has possibly received many of the species available from its source pool in Europe over the preceding centuries; in contrast, the Port of Vancouver likely remains more dissimilar to its donor sources. Overall these results suggest that Vancouver is more exposed to novel NIS *via* hull fouling than is Halifax, and that this port would be a good candidate to evaluate potential mitigation or control measures to reduce fouling risk.

Among the species found in this study were several NIS of global concern for protection of native diversity. For example, we found one specimen of *Rapana venosa* on a sea-chest cover on a vessel inspected in Vancouver. *R. venosa* is a whelk pest to both natural and cultivated populations of oysters, mussels and other molluscs (ISSG (Invasive Species Specialist Group) 2010). In 1926, it was introduced by oyster stock contamination in Puget Sound, near Vancouver, but failed to invade (U.S. Geological Survey, http://usgs.gov). Although ballast water and hull fouling also have been proposed as introduction vectors for *R. venosa* (Mann, Occhipinti & Harding 2004; Chandler, McDowell & Graves 2008), this study includes the first direct observation of the species as part of hull fouling fauna. Although the risk posed by a single specimen on a sea-chest grating might seem low, other individuals may have been located in the uninspected interior section of the sea-chest (Coutts & Dodgshun 2007).

Other nonindigenous bivalves that we recorded on vessels inspected in Vancouver and Halifax included *Geukensia demissa*, a native of eastern North America, *Mytilus galloprovincialis* from Europe, and *Musculista senhousia* from Asia (Creese *et al.* 1997; Sousa, Gutiérrez & Aldridge 2009; ISSG (Invasive Species Specialist Group) 2010). All three species are non-native to the west coast, while *M. senhousia* and probably *M. galloprovincialis* also are non-native to Halifax. The Asian bivalve *Crassostrea gigas* is an introduced NIS on both coasts of North America that was found on vessels visiting Vancouver (ISSG (Invasive Species Specialist Group) 2010). In fouling communities sampled in Vancouver, we also found *Gammarus tigrinus*, a euryhaline amphipod introduced to both coastal and freshwater habitats across Europe and recently to the North American Great Lakes. These species possess broad environmental tolerances, extensive invasion histories, and records of strong ecological impacts; their global transport is cause for concern considering that neither Canada nor most other countries have policies regarding hull husbandry for vessels approaching their shores, with the exception of bans on use of the potent antifouling agent TBT.

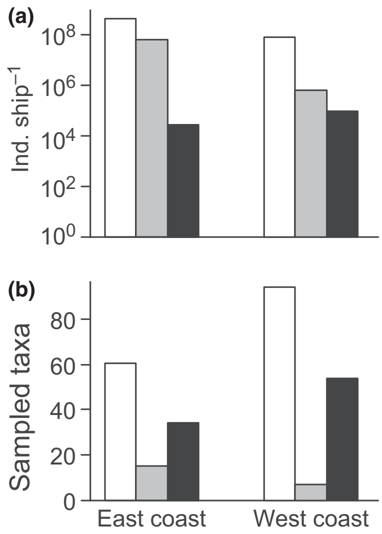

Fig. 4. Estimated propagule pressure (a) and observed colonization pressure (b) transported *via* ballast water (open bars), sediment (grey bars), and hull fouling (solid bars) to ports on the east and west coasts of Canada. Bars in the upper panel are average values across ships, while those in the lower panel are total values for all ships combined. Note the logarithmic scale in the upper panel. Ballast water values are based on 21 (east coast) and 26 ships (west coast), ballast sediment on 60, and hull fouling on 20 ships on each coast. Ballast water and sediment sampling was conducted in several ports on the east and west coast of Canada including Halifax and Vancouver during 2006–2008 (ballast water) and 2007–2009 (ballast sediment). Hull fouling data are from this study, whereas other data is courtesy of C. DiBacco, L. Nasmith (ballast water) and E. Briski (ballast sediment).

Hull fouling transports only a moderate number of propagules to Halifax and Vancouver relative to those transported in ballast sediment and, especially, ballast water (Fig. 4). Nevertheless, hull fouling appears to be a stronger subvector in terms of the number of species transported (Fig. 4). As well, there are broad spatial differences between these three subvectors in terms of both propagule and colonization pressure. For example, the total number of individuals and species transported *via* hull fouling is higher in Vancouver than Halifax, while ballast water (for number of individuals) and sediment (for both variables) exhibit the opposite pattern (Fig. 4). This suggests that the strength and potential for successful introduction differs for the three subvectors in different ports. Previous studies in Australia, New Zealand, the North Sea, and San Francisco Bay have revealed that hull fouling is as, or more important than, ballast water to the introduction of NIS to novel habitats (see Hewitt, Gollasch & Minchin 2009). While the IMO has proposed standards for ballast water effluent, at present no standards exist for hull fouling. This discrepancy should be addressed in future national or international management strategies.

MANAGING RISK

We have identified several variables potentially important for the management of the hull fouling vector. The effectiveness of antifouling paints decreases with age, allowing the gradual establishment of an increasingly rich fouling assemblage (Coutts 1999). We found that vessels with paint up to 375 and 427 days old in Halifax and Vancouver, respectively, were relatively clean, but that heavy fouling occurs thereafter. Since many merchant vessels go for periods up to 3 years between paint reapplication, shortening this time has management potential although it would increase maintenance and opportunity costs for the vessel. Noticeably, the relation between species gain and age of antifouling paint is significant in Halifax but not so in Vancouver (Fig. 2c), suggesting that the rate of species colonization of painted surfaces varies spatially (and likely temporally). If we assume that the performance of antifouling paint is maintained across ports, the different fouling patterns we observed between Halifax and Vancouver could be attributable to a varying ability of different taxa to foul painted surfaces across source regions (Floerl, Pool & Inglis 2004; Piola, Dafforn & Johnston 2009). Alternatively, these divergent patterns might originate from variable performance over time of the different antifouling paints, which cannot be accounted for in our simplified models.

Long stays at port increase opportunities for organisms to attach to hull surfaces (Davidson *et al.* 2009; Sylvester & MacIsaac 2010). Typically, ships would endeavour to keep port time to a minimum to maximize operational efficiency, which should have the added benefit of reducing fouling accumulation. While management of port residence time is unlikely, it is possible for managers to assess risk of vessels introducing NIS based upon their recent history of prolonged stays in port or at anchor. Given the downturn in the global economy over the past three years, there are presently thousands of vessels at anchor in tropical (e.g. Singapore) and other ports that could be accumulating massive fouling communities. These vessels will pose an enormous invasion risk when economic conditions improve and they recommence typical commercial activities, even though much of the built-up community is expected to be sloughed off when the vessel achieves cruising speed (Davidson *et al.* 2008; Floerl & Coutts 2009).

Extended periods at sea may lower biofouling by creating low food and high flow conditions that are stressful for fouling organisms (Ruiz & Smith 2005). Consistent with previous studies, sailing speed has a negative effect on propagule pressure (Davidson *et al.* 2009; Coutts *et al.* 2010) but there was no observed effect, or perhaps even a positive effect, on colonization pressure (Fig. 3). By washing away organisms, moderate speeds may impede monopolization of suitable niches on the hull by single species, creating opportunities for other species to colonize (Davidson *et al.* 2008). Additional research is required to determine the trade-off between these factors in order to provide the best management advice.

Conclusions

Hull fouling on commercial vessels has a strong potential for marine introductions. The time interval between applications of antifouling paint, duration of stays at port versus time at sea, sailing speed, and ports visited may be used to predict the extent and intensity of biofouling on these vessels. Our study illustrates how research that assesses spatial variation in propagule pressure and in vector traits can be used to inform management. Although drawn from a study on hull fouling, this conclusion is applicable to a wide range of invasion vectors. Future research should model specific vector management strategies to assess their effectiveness (Hulme 2009).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Hull-fouling invertebrate specimens identified to species. Sampling port: H = Halifax, V = Vancouver, HV = both. Habitat: M = marine, E = estuarine, F = freshwater, B = brackish water. Invasive status: E-NIS = established NIS; NE-NIS = non-established NIS; NIS = nonindigenous species. Invasive status is indicated only for taxa found in each port. Where necessary, the port where live specimens were found is indicated in parentheses.

Appendix S2. Hull-fouling specimens not identified to species. NIS = taxon has NIS, NE-taxa = non-established taxa; rest of the codes as per Appendix 1.

Appendix S3. Supplementary information on hull fouling communities and vessels sampled in the ports of Halifax and Vancouver. Coast codes for vessels: EC = east coast, WC = west coast.

Appendix S4. Plot of observed values vs. values predicted by process models of gains and losses for sampled species richness (a), number of individuals (b), and number of individuals ship^{-1} (c). Species $r^2 = 0{\cdot}43$, individuals $r^2 = 0{\cdot}26$, and individuals ship^{-1} $r^2 = 0{\cdot}86$; the last model was not predictive for 31 of 39 points which did not follow the overall pattern.

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