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BIODIVERSITY RESEARCH

Recreational boating: a large unregulated vector transporting marine invasive species

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ABSTRACT

Aim Recreational boating is arguably the largest unregulated vector for the introduction and spread of marine invasive species. Hull fouling communities have been recognized to harbour non-indigenous species (NIS), but presence should not be equated with transport. In this study, we characterize the presence of NIS in hull fouling communities, determine if host vessels transport these species and evaluate the importance of recreational boating as a vector for introduction and spread.

Location Coastal British Columbia (BC), Canada.

Methods Dive surveys in BC marinas were conducted to record the presence of NIS and to estimate their per cent cover. In addition, a boater questionnaire survey was used to determine common travel and maintenance practices. These results were combined to investigate the potential for recreational boats to transport NIS.

Results Nine NIS, including the highly invasive ascidians *Styela clava* and *Botrylloides violaceus*, and the macroalga *Sargassum muticum*, were found in hull fouling communities on recreational boats. Overall, per cent cover was generally low; however, niche areas were commonly fouled, even on active and otherwise clean boats. Fouling of niche areas was not related to either antifouling paint age or travel frequency, and fouling levels were highly variable among individual boats both within marinas and across regions.

Main conclusions Recreational boating is a major vector contributing to the spread of marine invasive species. Our results indicate that recreational boats represent a high-risk vector both for primary introduction and secondary spread of marine NIS and should be subject to vector management regulations.

Keywords

Biological invasions, dive survey, hull fouling, marine invasion, niche area, non-indigenous species, questionnaire, recreational boat.

INTRODUCTION

Globally, non-indigenous species (NIS) are introduced intentionally or unintentionally to new locations by a variety of vectors (Elton, 1958; Ruiz *et al.*, 2000; Wonham *et al.*, 2001; Wilson *et al.*, 2009). Over the past 30 years, efforts to control and manage introductions have focused on traditional and well-studied vectors such as ballast water and aquaculture imports. For example, the International Council for the Exploration of the Sea (ICES) voluntary Code of Practice on the Introductions and Transfers of Marine Organisms in the 1970s reduced the number of species introduced intentionally for aquaculture or other purposes (International Council for the Exploration of the Sea, 2005). Today, new introductions must undergo a rigorous evaluation before approvals are granted. Similarly, the International Maritime Organization (IMO) implemented mid-ocean exchange regulations in 1997 to reduce introductions by ballast water (International Maritime Organization, 2009a). In 2004, IMO adopted the International Convention for the Control and Management of Ships' Ballast Water and Sediments. This regulation requires the implementation of a ballast water management programme

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for each ship that meets certain standards on the density of propagules (10 viable organisms per cubic metre) in ballast tanks (International Maritime Organization, 2009b). Despite ongoing debate about the effectiveness of this measure (Zhang & Dickman, 1999; Sutherland *et al.*, 2001), the intent is clear: that by reducing the number of potential propagules the risk of invasion is reduced.

In contrast, a vast number of other vectors remain completely unmanaged. Small recreational watercraft hull fouling may be the largest unregulated vector for the introduction and spread of marine invasive species. Further, current restrictions on antifouling compounds like tributyl tin (TBT) are likely increasing the rate of invasion via this vector (Evans *et al.*, 2000; Nehring, 2001; Lewis *et al.*, 2004). The IMO ban of the highly effective, and yet extremely toxic, TBT-containing antifouling paints was adopted in 2001 (International Maritime Organization, 2011). Following this ban, there has been an increase in hull fouling which recently has caused resurgence in the importance of this vector for NIS transport (Fofonoff *et al.*, 2003).

Small recreational boats can travel long distances, and their relatively low speeds (compared to commercial ships) make them ideal vectors for fouling species (Minchin *et al.*, 2006). Pleasure craft have been implicated in the introduction of algae including *Undaria pinnatifida* (Hay, 1990; Farrell & Fletcher, 2006) and *Codium fragile* spp. *tomentosoides* (Carlton & Scanlon, 1985; Bird *et al.*, 1993; Trowbridge, 1995; Chapman, 1999) and several mussel species including *Mytilopsis sallei* (Field, 1999), *Perna viridis* (Power *et al.*, 2004), *Dreissena polymorpha* and *Dreissena rostriformis bugensis* (Padilla *et al.*, 1996; Buchan & Padilla, 1999; Johnson *et al.*, 2001). Further, the bryozoans *Waterispora subtorquata* and *Bugula neritina* are cosmopolitan invaders and well-known hull fouling species (Floerl & Inglis, 2005). They have a known tolerance to antifouling paint compounds which allows them to facilitate the transport of other invasive species by negating the need to make direct contact with the vessel's hull. Intolerant species grow on top of *W. subtorquata* that has settled on chemically protected hulls and are subsequently transported on surfaces unavailable to them without the assisting bryozoan (Floerl *et al.*, 2004). Mobile species, such as the caprellid amphipod *Caprella mutica,* also have been observed in hull fouling communities and may be transported on small boats if macrofouling species serve as refuge areas (Frey *et al.*, 2009).

Research on recreational boats has consistently revealed high variability in the degree of hull fouling present (James & Hayden, 2000; Floerl & Inglis, 2005; Ashton *et al.*, 2006). This pattern occurs despite large differences in sampling methods (Ashton *et al.*, 2006; Mineur *et al.*, 2008) and sometimes low sample sizes (Ashton *et al.*, 2006; Mineur *et al.*, 2008; Darbyson *et al.*, 2009b) but see (Floerl & Inglis, 2003, 2005 for exceptions). Studies of boat movements, as a proxy for the probability of spread, indicate a significant potential for recreational boaters to act as vectors in North America (MacIsaac *et al.*, 2004; Bossenbroek *et al.*, 2007; Darbyson *et al.*, 2009a,b), Australia (Floerl & Inglis, 2005) and New Zealand (James & Hayden, 2000; Floerl *et al.*, 2005). Previous research has equated NIS presence in hull fouling communities with transport of these species (Floerl & Inglis, 2005; Ashton *et al.*, 2006). However, stationary boats with high amounts of hull fouling would not pose a risk of NIS transport. Further, boats with little overall fouling but highly fouled niche areas could pose a greater risk than heavily fouled boats if travel frequency is high. Thus, to ascertain the level of risk posed by recreational boats, information on the amount and type of fouling and boat movements is required.

British Columbia's (BC) boating community is the largest in Canada, with an estimated 400,000 boats. In addition, the close proximity to Washington State and known connectivity to other US states on the coast make BC waters susceptible to primary international introductions. Further, southern harbours, such as the highly invaded San Francisco Bay (Cohen & Carlton, 1998), may act as source populations for secondary introductions to BC through stepping-stone invasions. Pleasure craft or other slower-moving hull fouling vectors (e.g. barges) are likely vectors for secondary invasions along the west coast of North America (Cohen *et al.*, 1998, 2005; Davidson *et al.*, 2006, 2008). Hub-and-spoke invasions of coastal marinas also may have occurred after primary introduction to centralized ports like the Port of Vancouver (Levings *et al.*, 2004). In BC, as elsewhere, pleasure craft is a popular travel mode to visit pristine areas and protected marine parks; places that could be particularly vulnerable to invasion and that are largely removed from traditional vectors such as commercial shipping or aquaculture. Several NIS, including ascidians, are common in BC marinas and often dominate fouling communities (C.C. Murray, unpublished data). Tolerance of these invasive species to varying environmental conditions suggests that much of BC's marine habitat could be at risk of invasion (Therriault & Herborg, 2008; Epelbaum *et al.*, 2009), but the role of specific vectors, including movements of BC boaters, has not yet been fully investigated (but see Herborg *et al.*, 2008 for an exception).

The goal of the current study is to investigate the recreational boating vector in a previously unstudied temperate, Northern hemisphere system with high boating activity and characterize the compliment of NIS being transported by recreational boating activities. To evaluate this vector, we pose three research questions: (1) Are NIS present in hull fouling communities of BC boats? (2) Are any of these NIS considered high-risk species with a history of invasion and impacts in other regions? and (3) Do fouled boats have travel or maintenance characteristics that make it likely they would transport hull fouling species?

METHODS

Dive survey

Hull fouling on recreational boats was surveyed using SCUBA at 24 marinas along the coast of BC (Fig. 1) in two

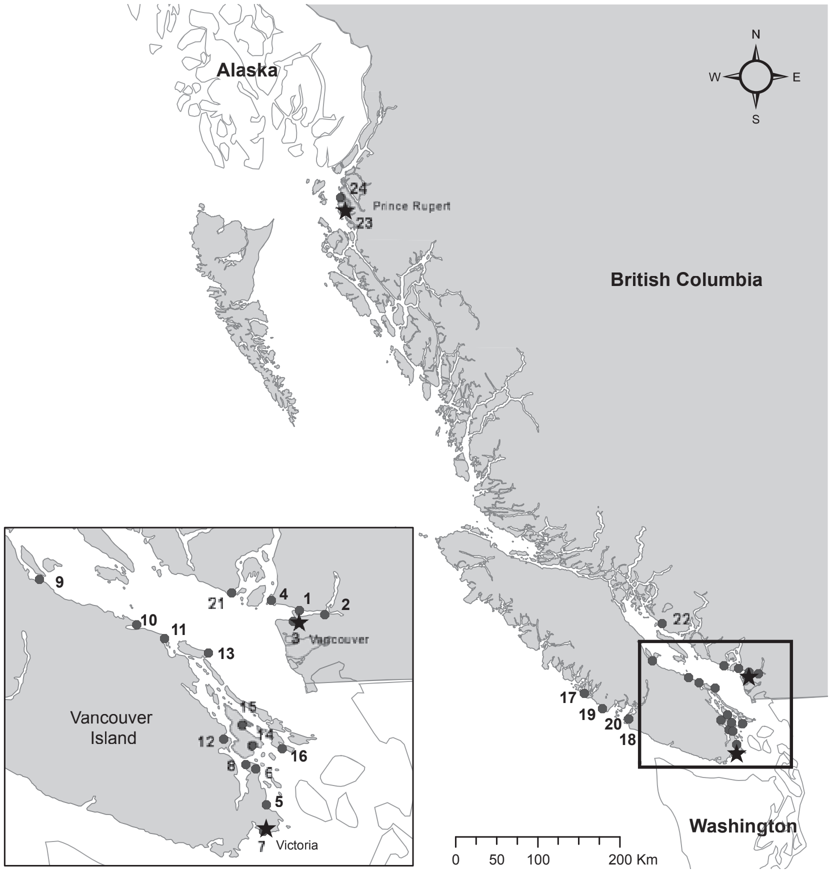

Figure 1 Map of British Columbia showing 24 marina study sites (black dots) sampled during the dive survey; stars mark major cities. Inset map shows close up of marinas sampled in Vancouver and on Southern Vancouver Island.

consecutive summers (2008–2009) with 10–30 boats examined and photographed at each marina. The first boat surveyed at each marina was selected randomly, but sequential boats along the dock were surveyed to reduce the risk to divers from boat traffic. A checklist was developed that included 12 species of known NIS in BC waters, and six species of potential invaders noted from elsewhere (Table 1). Species nomenclature was based on Carlton (2007) and references therein. For each boat, one diver searched the entire boat for known NIS and noted their presence on the checklist. The presence of general fouling taxa, such as barnacles, erect and encrusting bryozoans and macroalgae, also was recorded. The second diver photographed (minimum of 10 photos per boat) the submerged surfaces of each boat including six replicate randomly selected hull photos and one of each niche area (non-hull area) including the propeller, shaft, keel, vents and water intakes. The field of view was standardized using a fixed 30.5×30.5 cm quadrat attached to the camera. Samples of species with uncertain identifications were collected and identified in the laboratory. A subsample of all surveyed boats was subjected to image analysis ($N = 207$). Photographs were digitally overlaid with a 100-point grid to estimate per cent cover overall and functional group or species, where possible. Image analysis was performed using Image J (U.S. National Institutes of Health, Bethesda, MD, USA).

Boater questionnaire

Concurrent with the dive survey, a boater questionnaire was distributed during boating outreach events and left on each boat examined as part of the dive survey, with a prepaid return envelope provided. The questionnaire consisted of three sections, asking about the boat, its antifouling practices and its travel history (12 questions in total, see Appendix S1 in Supporting Information). Boaters were asked to report their travel history for the previous 12 months and check off places they had visited from a list of 104 BC destinations or list additional locations. They also were asked which trip types they undertook in the last 12 months: local or day trips (out and back to home marina in a single day), racing (trips made for the purpose of racing the boat), weekenders (trips of a few days duration visiting one or two different moorages), long trips (long haul travel to destinations further away, once there remain in a single moorage the entire time) and tours (long trips with multiple destinations along the way, staying in each moorage for only a few nights). Some respondents indicated ocean-crossing

Table 1 Non-indigenous species (NIS) actively searched for during dive survey, percentage of boats with NIS attached or entangled, and number of marinas where they were found on boats.

Species	Common name	% boats	No. of marinas
Mytilus spp.	Mussel	59.3	23
Styela clava	Clubbed tunicate	20.0	9
Botryllus schlosseri	Golden star tunicate	10.4	12
Botrylloides violaceus	Violet tunicate	9.8	15
Schizoporella japonica (=unicornis)	Horned bryozoan	9.0	13
Sargassum muticum	Japanese wireweed	7.5	10
Diplosoma listerianum	Colonial tunicate	3.1	6
Halichondria bowerbanki	Yellow sponge	1.6	8
Molgula manhattensis	Solitary tunicate	1.0	1
Didemnum vexillum	Colonial tunicate	0	0
Crassostrea gigas	Pacific oyster	0	0
Diadumene lineata	Orange-striped anemone	0	0
Musculista senhousia	Asian date mussel	0	0
*Clathria prolifera**	Red beard sponge	0	0
*Ciona intestinalis**	Vase tunicate	0	0
*Dreissena polymorpha**	Zebra mussel	0	0
*Caulerpa taxifolia**	Killer alga	0	0
*Undaria pinnatifida**	Kelp	0	0

*Species not known to occur in BC.

journeys (oceanic) in the other trip category, and these were added to the data analysis as a separate category. The questionnaire was approved by University of British Columbia's Behavioural Research Ethics Board (Approval #H08-00967).

Data analysis

Mean per cent cover of macrofouling for each boat was calculated by averaging per cent cover of replicate quadrat measurements. Given expected differences between niche and hull locations, quadrat photographs from these different areas were averaged separately to calculate hull only and niche only means. Per cent cover data were arcsine square root transformed to meet assumptions of normality and homogeneity of variance. Where transformation did not improve homogeneity, nonparametric analyses were performed. To assess the difference in fouling between hull and niche areas of the boat, Wilcoxon signed rank test was performed. To examine the variation in per cent cover between marinas, a Kruskal–Wallis test was used. Boater questionnaire variables were highly skewed, so nonparametric statistical analyses were performed. The relationship between age of antifouling paint and travel type was examined using Spearman's rank correlation. To examine whether fouled boats move, Spearman's rank correlation analyses were performed on per cent cover and age of antifouling paint (proxy for susceptibility to fouling colonization) and on the number of places visited in the last 12 months. All data analysis was performed using SPSS Version 10.0 (IBM Corporation, Somers, NY, USA).

RESULTS

Dive survey

In total, 491 boats were surveyed with 65.7% having macrofouling species attached to the hull and/or niche areas. Over a quarter of boats surveyed (25.7%) were fouled with one or more NIS. Non-indigenous *Mytilus galloprovincialis* and *Mytilus edulis* have hybridized with native *Mytilus trossulus* making them indistinguishable without the aid of genetic testing. Thus, all *Mytilus* are grouped together as *Mytilus* spp. in this study. The cryptogenic species complex, *Mytilus* spp., was present on 59.3% of boats surveyed, had the highest per cent cover per boat and was encountered on boats in 23 of 24 marinas.

Nine NIS were attached or entangled on the hull and niche areas of the boats surveyed. The *Mytilus* complex was encountered on almost 60% of the boats surveyed; however, we chose not to include *Mytilus* in further comparisons because of our inability to confirm the presence of invasive genotypes in this complex. The next most common NIS observed on surveyed boats was the solitary ascidian *Styela clava*, followed by the colonial ascidians *Botryllus schlosseri* and *Botrylloides violaceus* (Table 1). The NIS with the highest per cent cover per boat were *Schizoporella japonica* and *Diplosoma listerianum* (Fig. 2). The NIS found on boats at the most marinas surveyed were *B. violaceus* and *S. japonica* (Table 1). For all NIS, mean per cent cover was 0.583 (±0.138 SE). The invasive caprellid *C. mutica* was found incidentally in samples taken to the laboratory for identification of other species, but because it is not possible to identify this species underwater, it was not surveyed quantitatively. Five fouling species known to be present in BC were not detected in our surveys including the ascidians *Didemnum vexillum* and *Ciona savignyi*, the bivalves *Crassostrea gigas* and *Musculista senhousia*, and the cnidarian *Diadumene lineata*.

Across all marinas, boats surveyed had a mean per cent cover of 6.1 (±0.84 SE) macrofouling that ranged from 0% to

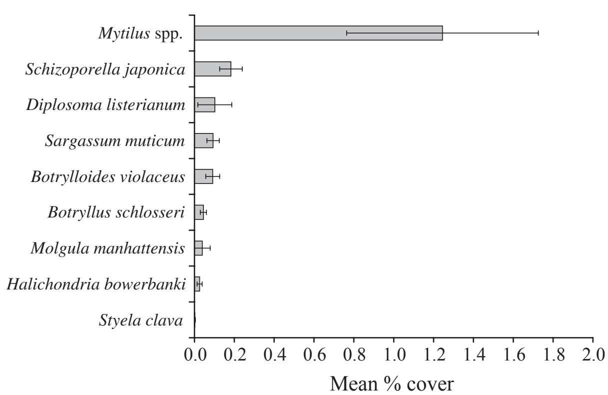

Figure 2 Mean per cent cover of cryptogenic and non-indigenous species encountered during the dive survey. Error bars depict standard error.

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79.78%. Seventy per cent of boats surveyed had < 5% macrofouling coverage, and niche areas (12.5%, ±1.34 SE) had significantly more macrofouling than hulls (1.2%, ±0.76 SE) (Wilcoxon Signed Ranks $Z = -9.882$, $P < 0.001$). Per cent cover of macrofouling differed significantly among marinas (Kruskall–Wallis $\chi^2 = 39.521$, d.f. = 22, $P = 0.012$). The three marinas with the highest average fouling were Gibson's Landing on the Sunshine Coast (#21), Rushbrooke Harbour in the North Coast (#23) and Burrard Yacht Club, Vancouver (#1) (Fig. 3). These also were the marinas with the highest variability in percentage cover. Three marinas, namely West Vancouver Yacht Club (#4), Institute of Ocean Sciences, Sidney (#8) and Poett Nook Bamfield (#20), had close to zero fouling (Fig. 3).

Boater questionnaire

In total, 616 completed questionnaires were returned, with 164 of these from boats sampled during the SCUBA survey. The majority of respondents were Canadian residents (93.3%) and most were from BC (90.6%). There were slightly more powerboat (51.8%) than sailboat (42.5%) respondents, and the average vessel length was 9.1 meters. Most respondents' home marinas were in southern BC and Washington State, reflecting a combination of population density and survey effort. Because survey effort was focused in marinas (rather than boat ramps), the majority of respondents had boats stored in water year-round (73.2%). Some respondents stored their boat in the water part of the year (9.3%), while the remainder trailered their boat between sites (13.8%).

Respondents had a high probability of utilizing antifouling practices. Most (80.5%) used antifouling paint and an even higher percentage used manual cleaning (83.3%). Manual cleaning often was used in combination with antifouling paint application (69.4%). Those boats reporting manual cleaning alone were those that trailered their boats overland and scrubbed their boats between uses. The age of antifouling paint ranged from 0 to 130 months, with a mean of 15.3 months. Maintenance typically was performed on dry land (52.8%), but cleaning also occurred in water (19.7%), in dry dock (12.8%) or on tidal grids (3.6%). One or more manual cleaning techniques were reported, including power washing (60.8%), scrubbing (50.2%), scraping (24.1%) and a range of other alternatives.

Respondents exhibited a range of travel behaviours. The most common was local or day trips, followed by weekend trips and tours (Fig. 4). The average amount of time boaters spent moored in marinas outside their home marina was 17.6 days, with a range from 0 to 330 days. Relatively few boats were never moored outside their home marina (*c.* 13%). Of 104 possible travel destinations in BC, boaters travelled to an average of 8.3 destinations. The maximum number of places reported visited was 86. Roughly one-fifth of respondents had travelled to the US in the past 12 months (20.9%); most had travelled to Washington State, whose marine waters are contiguous with those of BC.

Antifouling practices varied among trip types, with boaters reporting racing trips the most likely to employ antifouling paint (97.8%) and manual cleaning (86.0%). Boaters reporting local trips had a slightly lower probability of using antifouling paint (81.3%) but similar manual cleaning rates (86.0%). Boaters that travelled frequently had newer antifouling paint;

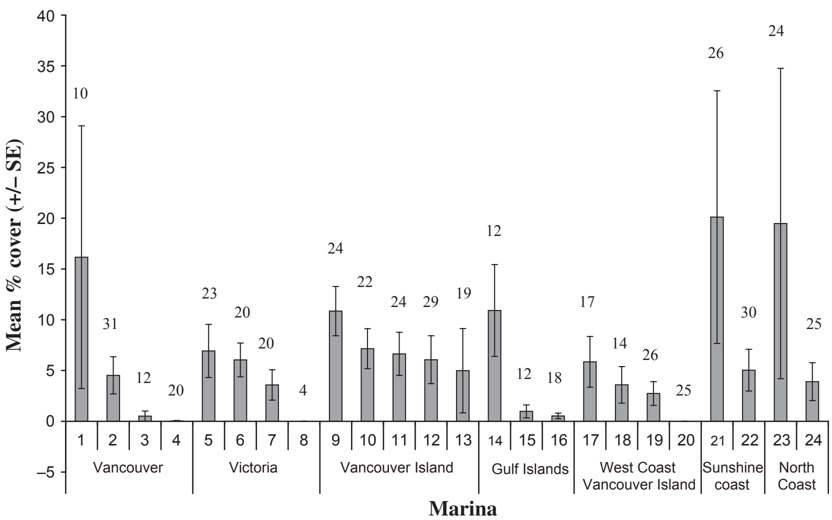

Figure 3 Per cent cover (± standard error) of macrofouling on boats surveyed by marina, grouped by region. Marina numbers correspond to locations on Fig. 1. Numbers above the bars represent the sample size for each marina. Marina codes: 1 – Burrard Yacht Club, 2 – Reed Point Marina, 3 – Royal Vancouver Yacht Club Jericho, 4 – West Vancouver Yacht Club, 5 – Royal Victoria Yacht Club, 6 – Sidney North Saanich, 7 – Victoria Causeway Marina, 8 – Institute of Ocean Sciences, 9 – Deep Bay Marina, 10 – Fairwinds Nanoose Bay, 11 – Nanaimo Yacht Club, 12 – Maple Bay Marina, 13 – Silva Bay Gabriola, 14 – Fulford Harbour Saltspring, 15 – Saltspring Marina, 16 – Poet's Cove Pender Island, 17 – Tofino Fisherman's Wharf, 18 – Hawkeye Bamfield, 19 – Ucluelet Hemlock Basin, 20 – Poett Nook Bamfield, 21 – Gibson's Landing Marina, 22 – Powell River Marina, 23 – Rushbrooke Harbour, 24 – Port Edward Harbour.

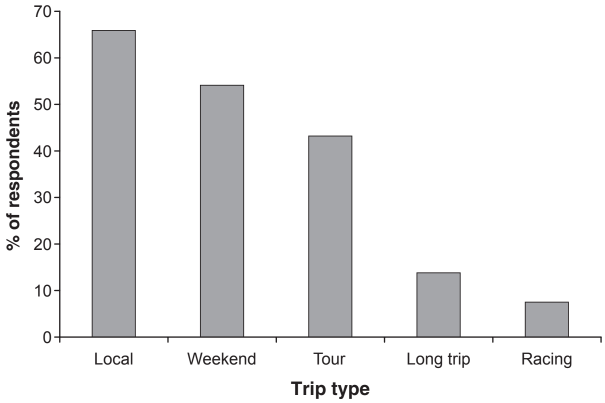

Figure 4 Percentage of respondents undertaking various trip types within the last 12 months.

there was a significant negative correlation between age of antifouling paint and number of places visited, though the relationship was weak (Spearman's rho = −0.124, $P = 0.006$, $r^2 = 0.014$).

Comparing dive-questionnaire results

There were 164 boats with both dive surveys and questionnaires. Heavily fouled boats were under-represented in the questionnaire results – only two boats with macrofouling greater than 40% returned questionnaires while the dive survey sampled 33 heavily fouled boats (6.8% of the sample population). As a result, two heavily fouled boats appear as statistical outliers (per cent cover > 2 standard deviations from the mean) and were removed from analyses (not included in regression) but are shown in Fig. 5 as they represent a valid segment of boaters. The influence of antifouling paint age on per cent macrofouling cover on boats surveyed varied by hull area (Fig. 5). Age of antifouling paint was most strongly related to per cent cover on the hull (Spearman's rho = 0.196, $P = 0.014$, $r^2 = 0.1345$). There was a weaker, yet significant, relationship with overall per cent cover (Spearman's rho = 0.258, $P = 0.001$, $r^2 = 0.0999$), and no significant relationship was observed between niche fouling and antifouling paint age (Fig. 5c).

To assess whether fouled boats were travelling, we examined the relationship between per cent cover and the number of places visited. In general, boats travelling to the most places had less fouling overall ($r^2 = 0.048$) and on the hull alone ($r^2 = 0.0471$), though the slopes were not significant. Fouling of niche areas had no relationship with travelling. For the subset of boats that were infected with NIS ($N = 44$), most visited < 10 places in the previous twelve months (63.7%), though a small fraction (11.4%) could be considered frequent travellers making > 20 trips per year. Two of the three marinas with highest fouling cover (Gibson's Landing and Rushbrooke Harbour) had older antifouling paint on average (24.8 and 17.2 months respectively) and low number of visits or voyages (4.0 and 3.6, respectively). Burrard Yacht Club was the

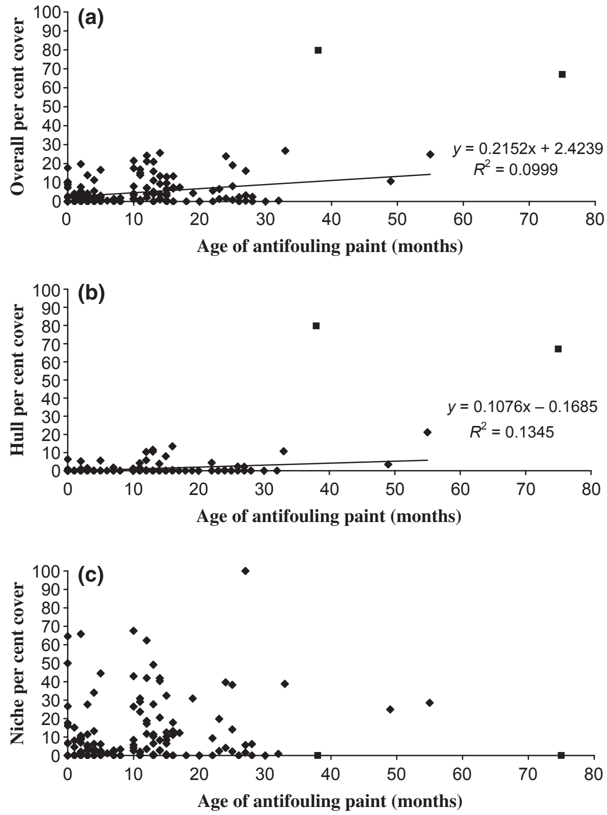

Figure 5 Relationship between age of antifouling paint (months) and (a) overall per cent cover, (b) hull per cent cover and (c) niche per cent cover. Diamonds represent individual boats; squares are statistical outlier points plotted but not part of fit line analyses.

exception; it had high fouling cover but low age of antifouling paint (4.0 months) and high number of visits (20.3). The marinas with lowest fouling cover had mixed maintenance and travel characteristics. West Vancouver Yacht Club had medium-aged antifouling paint (10.0 months) and a moderate number of visits in the previous 12 months (8.0). Poett Nook Bamfield had both low age of antifouling paint and low number of visits.

DISCUSSION

Are boats fouled with NIS?

The threat of invasive species transport by recreational boats in northern temperate marine waters appears to be high. Our results demonstrate that NIS are present in the hull fouling communities of BC's recreational boats and that prevalence can be high with over one-quarter of the boating community fouled by NIS. The incidence of NIS was much higher than previously observed in Atlantic Canada (Locke *et al.*, 2007; Darbyson *et al.*, 2009b), the Great Lakes region (Johnson *et al.*, 2001) or Europe (Mineur *et al.*, 2008). Two-thirds of surveyed boats had macrofouling present, suggesting that boats are both susceptible to colonization by fouling species and able to transport them between marinas. The proportion of boats examined with macrofouling present was much higher than previous studies in Scotland (59%) (Ashton *et al.*, 2006), Italy (40%) and New Zealand (14.5%) (reviewed in Minchin *et al.*, 2006), although all 70 boats examined in a northern Australian study were fouled (Floerl, 2002). Fouling levels observed as measured by per cent cover were similar to that of Australia and New Zealand (Floerl & Inglis, 2003, 2005). Although the magnitude of per cent cover might appear small, the actual introduction threat could be quite large. For illustrative purposes, if we consider the average boat size in the survey, a 9.1-m sailboat with wetted surface area of *c.* 84 m^2, 0.5 m^2 would be covered by NIS. Coupled with the high number of boats in BC, this indicates a level of propagule pressure similar to other regions where pleasure craft NIS introductions are believed to be high.

Macrofouling cover varied both by marina and region of the coast surveyed, and there was no relationship between fouling and environmental variables measured (temperature and salinity). The three marinas with boats having the highest per cent cover were in different regions of the coast, confirming the observed high variability in fouling occurs across regions. This variability can be attributed to either differences in boater behaviours or variation in the community composition and/or fouling rate between marinas. If this variation was a result of boater behaviours, we would expect that marinas with high fouling would have inactive boats (low number of visits) with older antifouling paint. This holds true in some marinas; both Gibson's Landing and Rushbrooke Harbour had boats with older antifouling paint (24.8 and 17.2 months, respectively) and low activity (4 and 3.6 visits in the previous year). In contrast, Burrard Yacht Club had boats with new antifouling paint and high activity, but contrary to expectations, this marina also had high fouling. Boats in Poett Nook in Bamfield had very low fouling and new antifouling paint but had low number of visits. This marina community was unique in that boaters trailered their boat overland to the marina and then stayed for the summer fishing season making only day trips out to local fishing grounds. Their boats were stored on land over the winter months and therefore had low fouling and NIS presence suggesting they represent a relatively low risk of NIS spread. West Vancouver Yacht Club had low fouling but mid-level activity levels and antifouling paint protection. The varying results suggest that boater behaviours are not the sole variables responsible for variability among marinas. Anecdotal information from boaters suggests that some marinas have higher fouling rates than others which could be the result of community composition or environmental variables such as temperature, salinity and water flow.

Non-indigenous species observed on surveyed boats included examples of high-risk invasive organisms. The ascidians *S. clava* and *B. violaceus* have caused severe impacts on shellfish aquaculture in eastern Canada (Locke *et al.*, 2007; Darbyson *et al.*, 2009a). Both species are native to the western North Pacific region. *Styela clava* was first reported from Newport Bay, California in 1933 (Abbott & Johnson, 1972), and its original introduction has been attributed to live oyster imports for the aquaculture industry (Cohen, 2005). It subsequently invaded Oregon and Washington, and the earliest report in British Columbia was from Nanaimo in 1994 (Lambert & Lambert, 1998). It remains unclear whether the BC introduction also resulted from live Pacific oyster importation or as a secondary stepping-stone introduction from southern populations. The first definitive west coast record of *B. violaceus* was in 1973 for San Francisco Bay (Cohen & Carlton, 1995), though it was likely introduced much earlier but went undetected because of its similarity to the native California species *Botrylloides diegensis*. The first BC report for *B. violaceus* was in 1993 in marinas on the southern coast of Vancouver Island (Lambert & Lambert, 1998), but again, this species could have been introduced much earlier.

Five of the nine NIS observed on boats in our study were ascidians. *Botryllus schlosseri* is native to the Mediterranean Sea (Berrill, 1950). It is common in BC marinas, but there have been no reports of negative impacts on shellfish aquaculture (Carver *et al.*, 2006). Similarly, *D. listerianum* is native to Europe and although it is a common fouling species in marinas in California, little is known of its possible vectors or impacts. The solitary ascidian *Molgula manhattensis* was only found in a single marina in Prince Rupert, a small fishing community in northern BC with a recently constructed container port and active cruise ship terminal. This species is native to the western North Atlantic, but the introduction vector is uncertain with hull fouling, oyster translocations and possibly ballast water having been suggested (Cohen & Carlton, 1995; Hewitt *et al.*, 2004). Non-indigenous ascidians were often observed together (both within marinas and on boats) suggesting that they are being transported by similar vectors or ascidians are facilitating transport and establishment of other ascidians. These hypotheses are not necessarily mutually exclusive. The invasive bryozoan *W. subtorquata* has chemical tolerances that allow it to settle early on copper-based antifouling paints, promoting its own transport as well as other species that settle on the bryozoan (Floerl *et al.*, 2004; Dafforn *et al.*, 2008), but it is unknown whether ascidians have similar chemical tolerances.

The well-known ascidian invader *D. vexillum* has been observed in BC marinas and harbours but was not detected fouling boats in the current study. This suggests that the vector of spread for this species in BC could be something other than recreational boating. However, additional research would be required to confirm *D. vexillum* is not able to utilize this vector. A species of *Didemnum* was observed fouling small boats in Ireland (Minchin & Sides, 2006), but the complex taxonomy of this genus makes it difficult to determine whether this is the same species. Previous studies have linked *D. vexillum* introductions to slow-moving barges (e.g. Bullard *et al.*, 2007), and this has been hypothesized as one of vectors for its introduction and spread in BC (Herborg *et al.*, 2008).

Hull fouling NIS observed were not always attached directly to boat surfaces; entanglement and refuge species also were sampled. Mineur *et al.* (2008) reported the marine alga *Sargassum muticum* often entangled on the propeller or propeller shaft; a finding supported by our study. This species originated in the western North Pacific and was likely first introduced with live oysters imported for aquaculture activities (Quayle, 1988). It is now widespread in BC (White & Shurin, 2007), and results of the current study suggest that its spread could be attributed to recreational boating. Plants could become entangled and transported to other locations, where dispersal occurs through fragmentation with propeller wash or maintenance activities. The caprellid amphipod, *C. mutica,* recently recorded from BC was collected incidentally in samples from hull fouling communities. This species is considered invasive, forming high densities and excluding native caprellid species (Ashton *et al.*, 2007). It is unknown whether this mobile species is transported on boats. However, it has also been sampled in commercial ships' sea chests (Frey *et al.*, 2009), and it potentially seeks refuge in niche areas or amongst more complex hull fouling communities during transport.

There is relatively little information about the vectors and possible impacts of *S. japonica* (=*unicornis*) and *Halichondria bowerbanki*. The encrusting bryozoan *S. japonica* was fairly common in hull fouling communities and represented the highest per cent cover per boat (after cryptogenic *Mytilus* spp.). This species is of Asian origin and believed to have been introduced with oyster products (Carlton, 1989). Its propensity for hull fouling lends to comparisons with the introduced bryozoan, *W. subtorquata*, and further study may reveal similar chemical tolerances for antifouling paint compounds. The sponge *H. bowerbanki* is native to the North Atlantic (Levings *et al.*, 2002), and its original vector of introduction also was attributed to oyster culture (Carlton, 1989). Although it was the most common sponge species observed on boats and within marinas, there is little information regarding possible commercial or ecosystem impacts.

Cryptogenic mussels (*Mytilus* species complex) were found on a majority of boats examined, even those travelling frequently and/or long distances. On travelling boats, small *Mytilus* were found mainly on unpainted (and thus unprotected) niche areas, such as the crevice between the motor mount and the hull. These results suggest that this region is at substantial risk for introduction of notorious mussel invaders, like quagga mussels (*D. rostriformis bugensis*) or zebra mussels (*D. polymorpha*) now confirmed in California and reported in Washington State (Whittier *et al.*, 2008).

As discussed earlier, five of the nine NIS species detected in this survey were likely introduced originally with the live oyster trade in the early 1900s. For the remaining species, we do not have enough evidence to hypothesize about their original vectors of introduction. The high occurrence of these species on small boats leads us to the general conclusion that fouling of recreational boats is likely the major vector responsible for their regional spread today. The temporal and spatial patterns of introduction in this temperate marine region are confounded by close proximity to infected harbours further south. Most invasions were noted first in southern BC, which is the most populated area and experiences higher propagule pressure. This area is both close to international shipping ports and historically experienced invasions via aquaculture introductions. Therefore, it is difficult to separate primary introductions direct from the western Pacific from secondary introductions from invaded southern harbours, but recent analyses are helping to clarify some of these patterns. For example, genetic studies have been used to examine the invasion patterns of two botryllid ascidians in Canada (Lejeusne *et al.*, 2011) and *B. schlosseri* in California (Stoner *et al.*, 2002).

Do fouled boats move?

It is important to distinguish between the presence of NIS on boats and the movement of these species. Previous studies have linked presence of NIS in hull fouling communities to transport, often without sufficient evidence that the species are actually carried to other destinations (Floerl & Inglis, 2005; Mineur *et al.*, 2008). A boat fouled with an invasive species may not necessarily move to other locations. In the current study, sedentary boats that had not moved in years had significant fouling, with often > 70% cover and usually more than one NIS present. Heavily fouled boats seen in the dive survey were underrepresented in questionnaire returns, as their owners probably do not use their boats often and thus would not find the questionnaires left for them. Although we cannot make predictions about the travel and maintenance patterns of heavily fouled boats based on available data, it is unlikely that they would be readily able to move any significant distance or even start their propellers if they have been neglected for a considerable period of time. Our results showed that travelling boats had lower fouling per cent cover (albeit with high variability). Furthermore, boats infected with one or more known NIS were reportedly travelling to as many as 45 locations (or 'destinations'). Although transoceanic boats were rare in the study, the few surveyed had small amounts of native barnacles attached in niche areas. This demonstrates that even travelling boats are both fouled and carry NIS and as a consequence may act as potential vectors for NIS introduction and spread.

The final stage in the invasion process, colonization and establishment in new marinas has not been quantified in the current study. Upon arrival, transported NIS may be sloughed from boats and dislodged fragments re-grow or individuals on the boats release gametes that successfully colonize the new habitat. Few studies address this part of the invasion process, but regardless, the widespread occurrence of NIS in BC means that it occurs with some frequency. Further research is required to examine the connectedness of invaded marinas in BC and pinpoint hot spots of boater movements and possible hubs in the invasion process. These hubs could then be targeted for directed monitoring and management activities.

Although per cent cover was relatively low on average, niche areas hosted a disproportionately greater amount of fouling, as much as 10 times the fouling cover observed on hull areas. Niche areas of commercial ships are susceptible to fouling because these areas often are overlooked or difficult to access during antifouling paint application (Coutts & Taylor, 2004), and the same seems to be true for recreational boats. For example, boaters indicated that sailboats rest on the keel during painting on land, and a single coat of antifouling paint is quickly applied to the keel as the boat is launched. Thus, the underside of the keel is inadequately protected, and this area was often found fouled during the survey (C. Murray pers. obs.). Piola & Johnston (2008) demonstrated that even small areas without antifouling protection can become heavily fouled. It appears that niche areas become vulnerable to colonization long before the rest of the vessel, and the lack of relationship between age of antifouling paint and niche per cent cover supports this conclusion. Other potential variables responsible for biofouling include other maintenance activities, boat activity patterns and voyage characteristics, in addition to numerous environmental variables. However, previous studies consistently have shown that age of antifouling paint is the most consistent predictor of level of fouling on small boats (Floerl *et al.*, 2005; Ashton *et al.*, 2006); a finding that appears to extend to temperate marine waters.

In addition to lack of antifouling paint, niche areas may experience reduced water velocities thereby promoting larval settlement and reducing dislodgement during voyages. Reduction in water velocity also may affect the performance of those antifouling paints that require water flow to release biocides. In contrast, niche areas that protrude into water flow may be exposed to higher levels of drag, wearing off antifouling paints faster than in other parts of the boat. Similar to dry docking support strips in large commercial ships (Coutts & Taylor, 2004), niche areas of recreational boats may represent the transport mechanism for long distance introductions of hull fouling invaders. Future studies should incorporate a random stratified survey design to capture the fouling of niche areas. This is because if fouling is present, even in small patches, it will occur in niche areas prior to hull surfaces. To decrease movement of NIS, information outreach should target boaters to encourage them to increase antifouling protection of niche areas. In addition, vector inspections should specifically target niche areas to increase chances of detecting hull fouling invasive species.

The habits of the marine boating community in BC showed high variability in both trip type and frequency. A high percentage of the boating community used antifouling paint in conjunction with manual cleaning to prevent fouling; however, two-thirds of the boats surveyed still had macrofouling species present. This suggests that current protection practices are insufficient to prevent the transport of NIS. Efforts to remove fouling from niche areas and more frequent renewal, or reapplication, of antifouling paint (within manufacturers' recommended limits) may reduce the fouling of boats in the BC community. Although boaters take steps to reduce fouling to improve fuel efficiency and speed (Minchin *et al.*, 2006), this goal aligns conveniently with the need to reduce colonization by fouling NIS. However, because niche areas are often overlooked, because they do not affect the boat performance, public outreach is needed to elevate boaters' awareness on the issue of NIS transport.

CONCLUSIONS

This study demonstrated that NIS are both present on recreational boats and, perhaps more importantly, travelling on boats in British Columbia suggesting the risk posed to other temperate marine ecosystems could be high. Within the boating community, we confirmed nine NIS, some of which are considered highly invasive, and many of these boats were visiting multiple marinas. Thus, the risk of spread of marine NIS in BC should be considered very high. Many of the NIS observed in hull fouling communities were likely introduced originally with live trade associated with Pacific oyster aquaculture. However, the current study provides evidence that the secondary spread of these species can likely be attributed to the recreational boating vector both in BC and in other regions as well. Fouling of niche areas is the most probable mechanism of introduction and spread as per cent cover was not related to travel frequency or antifouling paint age. Transport may not be restricted to short distances as non-indigenous ascidians *B. violaceus* and *M. manhattensis* were found in marinas as far north as Prince Rupert. Boats undertaking frequent or long distance travel still had fouling on niche areas suggesting this region is at continued risk of primary introductions via recreational boats. In contrast to other historically important vectors such as shipping and aquaculture, there are no management actions in place today aimed at limiting introduction and spread by the recreational boating vector. Boating activities are on the rise worldwide, both in terms of number of boats, number of marinas and connections between marinas, elevating the probability that NIS will be transported through this pathway into an increasing number of habitats, regions and possibly countries.

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SUPPORTING INFORMATION

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

Appendix S1 Complete boater questionnaire with questions and list of possible destinations.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Cathryn Clarke Murray's research focuses on the ecology of invasion and investigates the patterns and mechanisms underlying various stages of invasion and interaction with native diversity.

Evgeny Pakhomov's research focuses on topics ranging from species ecology, at the level from zooplankton to fish, to ecosystem structure as well as physical–biological and biochemical coupling.

Thomas Therriault's recent research has focused on characterizing and understanding the invasion dynamics of marine invaders with the goal of identifying high priority invaders and vectors that may require increased management efforts.

Author contributions: C.C.M., E.P. and T.W.T. conceived the ideas; C.C.M. collected the data; C.C.M. and T.W.T. analysed the data; and C.C.M., E.P. and T.W.T. led the writing.

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