

Research Article

Non-indigenous invertebrate species in the marine fouling communities of British Columbia, Canada

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Received: 19 May 2016 / Accepted: 30 August 2016 / Published online: 16 September 2016

Handling editor: John Mark Hanson

Abstract

Marine fouling communities on artificial structures are invasion hotspots for non-indigenous species (NIS). Yet, little is known about NIS in fouling communities of British Columbia (BC), Canada. To determine NIS identity and richness in BC fouling communities, we deployed settlement plates at 108 sites along the coast of BC between 2006 and 2012. Of the 295 invertebrate taxa identified to species, 20 were NIS while an additional 14 were cryptogenic, including several global invaders. This study documents the range expansion of tunicates *Botrylloides violaceus* Oka, 1927 and *Botryllus schlosseri* (Pallas, 1766), including the first known records on Haida Gwaii. NIS were detected within each of the six distinct geographic regions with the southern, more populated regions of BC (Straits of Georgia and Juan De Fuca) having the highest NIS richness and frequency of occurrence compared to the less populated northern regions. This study provides a contemporary baseline of invertebrate NIS identity and richness in fouling communities that will allow comparisons through time and a means to focus research and prioritize management efforts.

Key words: non-native species, introduced species, invasion, Northeast Pacific, West Coast, North America, biofouling

Introduction

Globally, there is growing concern regarding the ecological and economic impacts of non-indigenous species (NIS) (Pimentel et al. 2000; Grosholz 2002; Pimentel et al. 2005). Aquatic species are being transported from their native ranges to new areas, mediated by a variety of anthropogenic vectors such as aquaculture (Naylor et al. 2001), ballast water (Ruiz et al. 1997; Simkanin et al. 2009), and the fouling of ship hulls and sea-chests (Coutts and Dodgshun 2007; Drake and Lodge 2007). Further, secondary spread by additional vectors such as recreational boats is contributing to observed invasion patterns at regional scales (Clarke Murray et al. 2011;

Zabin et al. 2014). The artificial structures (e.g. docks and pilings) in close proximity to these vectors serve as invasion hotspots (Ruiz et al. 2009). Monitoring fouling communities on these structures can be valuable for detecting new introductions to an area, determining temporal and spatial invasion patterns, and informing management and policy decisions, including those that aim to mitigate the ecological and economic impacts of NIS.

In British Columbia (BC) Canada, little is known about NIS identity and richness in these fouling communities. There have been more than 120 non-indigenous and cryptogenic species documented in the marine and estuarine waters of BC (Levings et al. 2002; Gillespie 2007; Lu et al. 2007). However, to

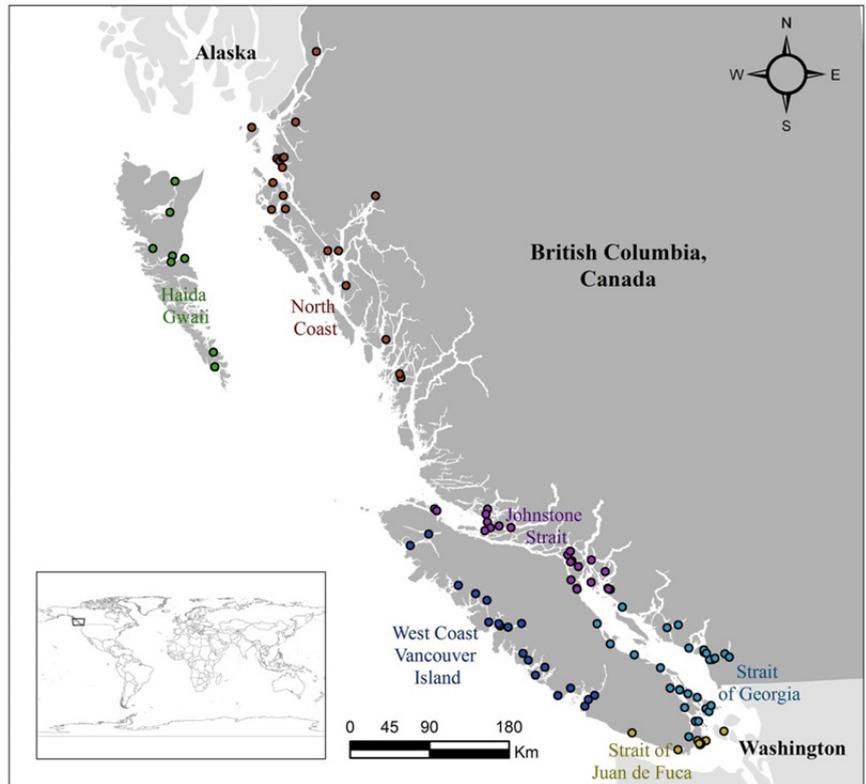


Figure 1. Site locations (circles) of fouling communities sampled along the coast of British Columbia, Canada between 2006 and 2012. The six regions of the coast sampled are the Strait of Juan de Fuca (n=10), Strait of Georgia (n=28), West Coast of Vancouver Island (n=20), Johnstone Strait (n=23), Haida Gwaii (n=8), and North Coast (n=19). For details see supplementary material Table S1.

date, these studies either have primarily focused on intertidal environments (Gillespie 2007) or have been geographically limited to areas such as ports (Richoux et al. 2006; Lu et al. 2007). There have been no comprehensive studies of fouling communities of the BC coast, including remote and seemingly pristine locations. This study aims to provide an inventory of invertebrate NIS identity and richness of fouling communities along the BC coast.

Methods

Study area

The BC coastline spans more than 27,000 km along a complex of inlets, straits, passes, sounds, and narrows. There are six geographic regions where differences in oceanographic and physical features can influence the community composition of invertebrate fouling communities (Thomson 1981; Zacharias and Roff 2001; Gillespie 2007). Between 2006 and 2012, we sampled 108 sites within all six regions of the province: Strait of Juan de Fuca, Strait of Georgia, West Coast of Vancouver Island, Johnstone Strait, Haida Gwaii, and the North Coast (Figure 1; supplementary material Table S1). Eight sites, primarily in the Strait of

Georgia, had settlement plates continuously immersed from the spring of 2006 through the spring of 2007, with sets retrieved every four months. In 2007 and 2011, settlement plates were deployed along the BC coast (at 81 and 24 sites, respectively) with the settlement plates installed in the spring or early summer and retrieved the subsequent fall. In addition, ports in Vancouver (4 sites; 2008–2012), Victoria (6 sites; 2009–2012) and Prince Rupert (1 site; 2011) were monitored with settlement plates installed in the spring or early summer and retrieved the subsequent fall. All plates installed in the spring or early summer and retrieved the subsequent fall typically had 3 to 6 months for species recruitment and community development.

Settlement structures

To characterize invertebrate fouling communities in BC, we deployed multiple settlement plates from floating structures that were located primarily in harbours and embayments. We used two settlement plate designs over the course of this study: 1) a plastic circular base (30 cm diameter), with four plastic, circular Petri dishes (9 cm diameter) attached to each base, or 2) a single polyvinyl chloride (PVC)

square plate (14.5 × 14.5 cm). Each circular design had two levels, with the first base suspended 15 cm below the surface and the second base 1 m below the first. Each PVC design had only one level that was suspended 1 m below the surface. In 2010, both plate designs were deployed together at six sites (n = 97) with no significant difference in species richness detected between the circular (mean = 12.49, SD = 7.25) and square plate (mean = 11.38, SD = 7.83) design (t-test, t = 0.70, df = 95, p = 0.49).

Sample processing

Upon collection, the fouling community on each settlement plate was immediately preserved in either formalin (10%) or ethanol (70%). In the laboratory, we sorted and identified all invertebrates larger than 1 mm to the lowest taxonomic level possible. Algae occasionally grew in low abundance, mainly on the edges and top of the plates, but were not identified due to inappropriate preservation and lack of available expertise. All invertebrate taxa were categorized as “NIS” (not native to the region), “cryptogenic” (unknown origin), “native” (native to the region) or “unknown” (including taxa identified to genus or higher, and those whose origin remains unclear). Identification and status were determined using taxonomic descriptions and keys and correspondence with global experts (see Acknowledgements). We listed taxa according to the World Register of Marine Species (WoRMS) nomenclatural system (WoRMS Editorial Board 2016).

Results

Within the sampled BC fouling communities, we identified 491 distinct invertebrate taxa: 295 to species, 100 to genus, and 96 to family or higher (supplementary material Table S1). Of the 295 invertebrate taxa identified to species, 20 were characterized as NIS (6.8%) and 14 as cryptogenic (4.7%) species (Table 1).

NIS

We detected NIS at 74 sites (68.5%) and within each of the geographic regions of the province (Table 1, Figure 2). The Straits of Juan de Fuca and Georgia had the highest proportion of sites with NIS (90.0% and 89.3%, respectively) and the highest NIS richness (11 and 19, respectively). The North Coast had the lowest proportion of sites with NIS (36.8%) as well as the lowest NIS richness (2).

The most widespread NIS were: *Schizoporella japonica* Ortmann, 1890; *Caprella mutica* Schurin,

1935; *Botrylloides violaceus* Oka, 1927; and *Botryllus schlosseri* (Pallas, 1766) (Table 1). Both *S. japonica* and *C. mutica* were present in all geographic regions, and were found at 42 (38.9%) and 34 (31.5%) sites, respectively. *B. violaceus* and *B. schlosseri* were present in all geographic regions except the NC, and were found at 36 (33.3%) and 24 (22.2%) sites, respectively.

Cryptogenic species

We detected cryptogenic species at 80 sites (74.1%) and within each of the geographic regions of the province (Table 1, Figure 3). Haida Gwaii had the highest proportion of sites with cryptogenic species (87.5%), though this represents a wide distribution by a low number (n = 3) of cryptogenic species. The West Coast of Vancouver Island had the lowest (60.0%) proportion of sites with cryptogenic species.

The most common cryptogenic species were: *Celleporella hyalina* (Linnaeus, 1767); *Obelia dichotoma* (Linnaeus, 1758); *Alcyonidium polyoum* (Hassall, 1841); and *Amathia gracili* (Leidy, 1855) (Table 1). Both *C. hyalina* and *O. dichotoma* were present in all geographic regions, and were found at 54 (50.0%) and 49 (45.4%) sites, respectively. In addition, *A. polyoum*, and *A. gracilis* were present in all geographic regions except for Haida Gwaii, and were present at 35 (32.4%) and 28 (25.9%) sites, respectively. It is important to note that *C. hyalina*, *A. polyoum*, and *A. gracilis* may each represent a species complex in the Northeast Pacific (Carlton 2007). Future study may help resolve taxonomic uncertainties and determine geographic origin.

Discussion

NIS and cryptogenic species were present in all geographic regions of the province. This wide-spread distribution represents the long-term accumulation of NIS within BC, including both initial introduction events and secondary spread. Several well-known vectors of introduction are currently, or were historically, operating in BC waters. Aquaculture has been suggested as one of the greatest vectors for the introduction of NIS worldwide (Wasson et al. 2001; Ruesink et al. 2005). Commercial imports of live oyster seed and adults to the Pacific coast of North America began as early as the 1880s (specifically 1903 in BC; Quayle 1988) and continued unregulated until the 1930s, bringing intentional and accidental introductions to the coast (Levings et al. 2002; Wonham and Carlton 2005). BC has a long history of commercial shipping, and there are several major ports (and a myriad of smaller ones) currently in

Table 1. The 20 non-indigenous and 14 cryptogenic species found in fouling communities along the BC coast. Invasion statuses were assigned according to Carlton 2007 or by personal communication with Carlton. Single quotations around a name indicate it may represent a species complex in the Northeast Pacific. The geographic region(s) and number of sites at which each was recorded is listed for each species. SFJ=Strait of Juan de Fuca, SG=Strait of Georgia, WCVI=West Coast of Vancouver Island, JS=Johnstone Strait, HG=Haida Gwaii, NC=North Coast.

Phylum	Species	Invasion Status	Geographic Region(s)	Number of sites	
Cnidaria	<i>Obelia dichotoma</i> (Linnaeus, 1758)	Cryptogenic	SFJ, SG, WCVI, JS, HG, NC	49	
	<i>Phialella fragilis</i> (Uchida, 1938)	Cryptogenic	SFJ	3	
Arthropoda	<i>Amphibalanus improvisus</i> (Darwin, 1854)	Non-indigenous	SG	1	
	<i>Amphioe valida</i> Smith, 1873	Non-indigenous	SG	4	
	<i>Caprella drepanochir</i> Mayer, 1890	Non-indigenous	SFJ, SG	4	
	<i>Caprella mutica</i> Schurin, 1935	Non-indigenous	SFJ, SG, WCVI, JS, HG, NC	34	
	<i>Caprella penantis</i> Leach, 1814	Cryptogenic	SFJ	1	
	<i>Incisocallope derzhavini</i> (Gurjanova, 1938)	Non-indigenous	SFJ, SG	3	
	<i>Leptochelia 'savignyi'</i> (Krøyer, 1842)	Cryptogenic	SFJ	1	
	<i>Melita nitida</i> Smith, 1873	Non-indigenous	SG	3	
	<i>Monocorophium acherusicum</i> (Costa, 1853)	Non-indigenous	SFJ, SG	8	
	<i>Monocorophium insidiosum</i> (Crawford, 1937)	Non-indigenous	SFJ, SG	6	
	<i>Podocerus 'cristatus'</i> Thomson, 1879	Cryptogenic	WCVI	1	
Platyhelminthes	<i>Koinostylochus ostreophagus</i> (Hyman, 1955)	Non-indigenous	SG	1	
Annelida	<i>Capitella 'capitata'</i> (Fabricius, 1780)	Cryptogenic	SFJ, SG, WCVI, JS, NC	7	
	<i>Eulalia viridis</i> (Linnaeus, 1767)	Non-indigenous	SG	2	
	<i>Eumida sanguinea</i> (Ørsted, 1843)	Non-indigenous	SG	2	
	<i>Parougia caeca</i> (Webster & Benedict, 1884)	Non-indigenous	JS	1	
	<i>Polydora cornuta</i> Bosc, 1802	Non-indigenous	SFJ, SG, JS	6	
	<i>Polydora limicola</i> Annenkova, 1934	Cryptogenic	SG	1	
	<i>Polydora websteri</i> Hartman in Loosanoff & Engle, 1943	Cryptogenic	SFJ, SG, JS, NC	8	
	<i>Scolecopsis (Parascolelepis) tridentata</i> (Southern, 1914)	Cryptogenic	SG	1	
	Bryozoa	<i>Alcyonidium 'polyoum'</i> (Hassall, 1841)	Cryptogenic	SFJ, SG, WCVI, JS, NC	35
		<i>Amathia 'gracilis'</i> (Leidy, 1855)	Cryptogenic	SFJ, SG, WCVI, JS, NC	28
<i>Bugula 'neritina'</i> (Linnaeus, 1758)		Cryptogenic	SG	2	
<i>Celleporella 'hyalina'</i> (Linnaeus, 1767)		Cryptogenic	SFJ, SG, WCVI, JS, HG, NC	54	
<i>Cryptosula 'pallasiana'</i> (Moll, 1803)		Cryptogenic	SFJ, SG, HG, NC	14	
<i>Membranipora membranacea</i> (Linnaeus, 1767)		Non-indigenous	SFJ, SG, JS, HG	14	
<i>Schizoporella japonica</i> Ortmann, 1890		Non-indigenous	SFJ, SG, WCVI, JS, HG, NC	42	
Entoprocta	<i>Barentsia benedeni</i> (Foettinger, 1887)	Non-indigenous	SG, JS	2	
Chordata	<i>Botrylloides violaceus</i> Oka, 1927	Non-indigenous	SFJ, SG, WCVI, JS, HG	36	
	<i>Botryllus schlosseri</i> (Pallas, 1766)	Non-indigenous	SFJ, SG, WCVI, JS, HG	24	
	<i>Molgula manhattensis</i> (De Kay, 1843)	Non-indigenous	SFJ, SG	3	
	<i>Styela clava</i> Herdman, 1881	Non-indigenous	SG, JS	9	

operation. Thus, ballast water (Levings et al. 2004; Lo et al. 2012), hull fouling (Sylvester et al. 2011), and sea chests (Frey et al. 2014) have been documented vectors in the province. Additionally, the recreational boating community has been identified as a significant vector for secondary spread of NIS in BC (Clarke Murray et al. 2011), including many of the fouling species identified here. The attribution of NIS to a single vector is problematic, creating so-called polyvectic species (Carlton and Ruiz 2005),

and many of the NIS documented here may have arrived to BC by more than one of these vectors (Ruiz et al. 2011; Clarke Murray et al. 2014). This study provides a current snapshot of the long-term accumulation and the spatial distribution of NIS in the fouling communities of BC and can inform future research and management efforts.

The spatial patterns of NIS in fouling communities of BC indicates the southern, more populated regions of BC are more invaded than those of the northern,

Figure 2. The number of NIS detected and the percent of fouling sites with NIS for each geographic region. SJF=Strait of Juan de Fuca (n=10), SG=Strait of Georgia (n=28), WCVI=West Coast of Vancouver Island (n=20), JS=Johnstone Strait (n=23), HG=Haida Gwaii (n=8), NC=North Coast (n=19).

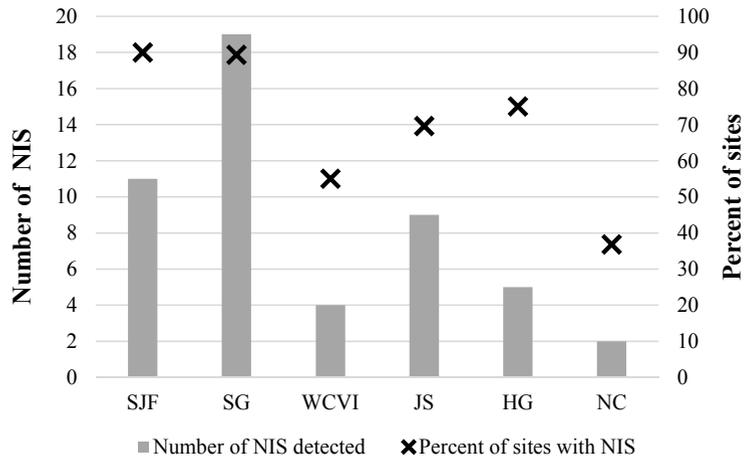
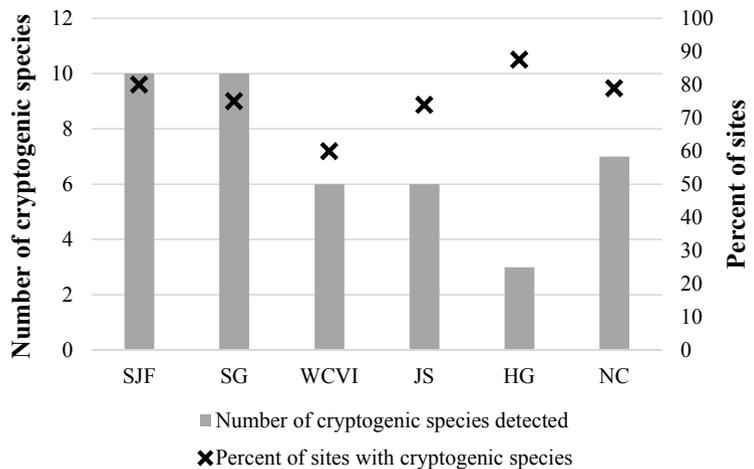


Figure 3. The number of cryptogenic species detected and the percent of fouling sites with cryptogenic species for each geographic region. SJF=Strait of Juan de Fuca (n=10), SG=Strait of Georgia (n=28), WCVI=West Coast of Vancouver Island (n=20), JS=Johnstone Strait (n=23), HG=Haida Gwaii (n=8), NC=North Coast (n=19).



less populated regions. The Straits of Juan de Fuca and Georgia had both the highest number and the percent of sites with NIS detected. These are the two regions with the greatest human population density, by dissemination area, for the BC coast (Statistics Canada 2007). This relationship between NIS richness and human activity has been found in similar spatial studies of plant and fish fauna (Vilà and Pujadas 2001; Dark 2004; Leprieur et al. 2008) and is likely related to the associated disturbance of natural ecosystems combined with high levels of propagule pressure (Leprieur et al. 2008). It will be important to consider this spatial pattern in future vector management, in order to prevent the spread of many of these NIS to less invaded areas. However, NIS distributions and richness in BC are determined by a combination of abiotic, biotic, and anthropogenic factors (Clarke Murray et al. 2014) that warrant

further investigation to monitor, predict, and manage the future introduction and subsequent spread of species in BC.

Monitoring fouling communities for future introductions and subsequent spread of NIS is a recommended practice as this study supports the previous findings that marine fouling communities of artificial structures are invasion hotspots for NIS (Ruiz et al. 2009). NIS (20) and cryptogenic (14) invertebrate species richness in the fouling communities of BC was higher than recent similar studies conducted in BC seagrass habitats (NIS = 11 and cryptogenic = 8; Mach 2012) and intertidal habitats (both hard and soft substrate) of several BC ports (NIS = 18; Choi 2011). Gillespie (2007) reported more NIS invertebrates (29) in the intertidal environment in a study that summarized all reported species introductions to date, in both hard and soft substrate

environments. In our study of BC, NIS invertebrate richness was similar to fouling community studies conducted in Oregon (25, Chapman et al. 2010) but much higher than those conducted in Alaska (4, Ruiz et al. 2006). In contrast, NIS richness was slightly lower than a similar study carried out in Puget Sound, Washington (35; Cohen et al. 1998) and much lower than studies in California (e.g. 66; Cohen et al. 2005), both areas that have large, active ports and are known hotspots for invasion (Mills et al. 1999; Foss et al. 2007). With the globalization of marine waterways (Galil et al. 2007), it is important to monitor the fouling communities in the ports of BC as they are becoming increasingly connected by shipping activities both to these highly invaded southern ports of the Pacific coast and other international ports. This is especially relevant for BC ports with plans for increased shipping activities and new trade routes, particularly Prince Rupert and Kitimat, as they are located in the relatively less invaded North Coast.

We identified a number of well-known species with global invasion histories as part of the current study. The ascidian species *Styela clava* Herdman, 1881, *B. violaceus*, and *B. schlosseri* have a history of invasion, often resulting in measurable impacts in other parts of Canada and the world (e.g. Lambert 2007; Arsenault et al. 2009; Arens et al. 2011; Zhan et al. 2015). This study documents the range expansion of *B. violaceus* and *B. schlosseri* with the first known records on Haida Gwaii (first in 2007 and again in 2011). The range expansion of the invasive caprellid amphipod *C. mutica* into BC waters was detected as part of the current surveys and detailed in Frey et al. (2009). *Schizoporella japonica*, which was first introduced to California as early as 1938 (Powell 1970), and has been found in fouling communities from Morro Bay, California to Prince William Sound, Alaska (summarized in Ryland et al. 2014), was found to be widely distributed along the BC coast. Given the presence of these known global invaders, and the fact that NIS invertebrates were found at 74 sites (68.5%), we suggest that future study is needed to examine which of these species are able to transfer from these artificial structures to colonize local natural environments (*sensu* Simkanin et al. 2012).

This study provides a direct comparison of NIS richness in fouling communities across the geographic regions of BC, using similar methods. However, our results may underestimate total NIS richness if rare species have been under sampled or if cryptogenic and unresolved species actually represent NIS yet to be recognized. Species richness documented from fouling panels may not fully capture diversity in

fouling communities due to the passive nature of this sampling device, the substrate and orientation of the plates, and the complex pre- and post-settlement processes that occur prior to sampling (e.g. Connell 1961; Stoner 1990; Epelbaum et al. 2009). For example, we did not detect the invasive colonial ascidian *Didemnum vexillum* (Kott, 2002) on any of the settlement plates, despite its known presence in some of the marinas at deeper depths, fouling the benthos (Gartner, unpublished data). The results of this study are best included in a larger, long-term monitoring program which would include a diversity of sampling methods (e.g. subtidal dive surveys, sediment grabs and intertidal surveys). In addition, both difficulty in identification and uncertainty of taxonomic invasion status remain an issue for the region. As an example, the bryozoan *Membranipora membranacea* (Linnaeus, 1767) is currently listed as an introduced species, but there is some major taxonomic revision underway for this group. The sponge *Halichondria* sp. likely includes the introduced, bay-dwelling *Halichondria (Halichondria) bowerbanki* Burton, 1930; however, specimens in this genus were not identified to species level in the current study given the difficulty of taxonomic identifications (i.e., requiring accurate measurement of spicules). This study provides a baseline against which future study may help resolve taxonomic uncertainties and geographic origins.

This study was the first to document NIS in fouling communities throughout the entire BC coast. Historical introductions and currently operating vectors make the introduction and spread of NIS difficult to control. However, the NIS baseline data presented here, including NIS identity and richness, will allow future comparisons over time and provide a basis to inform research, management, and policy efforts.

Acknowledgements

Special thanks to the ports, marinas, and aquaculture facilities for granting access to collections sites. Research guidance and support was provided by Verena Tunnicliffe (University of Victoria), Evgeny Pakhomov (University of British Columbia), Christopher Harley (University of British Columbia), and Glen Jamieson (Fisheries and Oceans Canada). Field and lab assistance was provided by: Canadian Coast Guard, Francis Choi, Theraesa Coyle, Trampus Goodman, Lucie Hannah, Jacob Hupman, Greg Murray, Lindsay Orr, John Sherrin, Xoco Shinbrot, Angela Stevenson, and Jessica Yu. Species identification and invasion status information were provided by Biologica Environmental Services Ltd., James Carlton, David Denning, Will Duguid, Gretchen Lambert, Linda McCann, Sandra Millen, and Henry Reisinger. Research funding was received from Fisheries and Oceans Canada, the Second Canadian Aquatic Invasive Species Network (CAISN II) and the Bioinformatics Research and Interdisciplinary Training Experience; CCM was supported in part by a National Science and Engineering Research Council postgraduate scholarship.

References

- Arens CJ, Paetzold SC, Ramsay A, Davidson J (2011) Pressurized seawater as an antifouling treatment against the colonial tunicates *Botrylloides violaceus* and *Botryllus schlosseri* in mussel aquaculture. *Aquatic Invasions* 6: 465–476, <http://dx.doi.org/10.3391/ai.2011.6.4.12>
- Arsenault G, Davidson J, Ramsay A (2009) Temporal and spatial development of an infestation of *Styela clava* on mussel farms in Malpeque Bay, Prince Edward Island, Canada. *Aquatic Invasions* 4: 189–194, <http://dx.doi.org/10.3391/ai.2009.4.1.19>
- Carlton JT (2007) The Light & Smith Manual: intertidal invertebrates from central California to Oregon. University of California Press, Ltd, London, England, xvii+1001 pp
- Carlton JT, Ruiz GM (2005) Chapter 3: Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA (ed), *Invasive Alien Species: A New Synthesis*, 63: 36
- Chapman JW, Therriault T, Harris L, Breitenstein R (2010) The 2010 PICES Rapid Assessment Survey of shallow water nonindigenous, native and cryptogenic marine species of central Oregon, 48 pp
- Choi FMP (2011) Assessing intertidal marine non-indigenous species in Canadian ports. MSc Thesis, University of British Columbia, Vancouver, BC, xii+118 pp
- Clarke Murray C, Pakhomov EA, Therriault TW (2011) Recreational boating: a large unregulated vector transporting marine invasive species. *Diversity and Distributions* 16: 1161–1172, <http://dx.doi.org/10.1111/j.1472-4642.2011.00798.x>
- Clarke Murray C, Gartner H, Gregr EJ, Chan C, Pakhomov E, Therriault TW (2014) Spatial distribution of marine invasive species: environmental, demographic and vector drivers. *Diversity and Distributions* 20: 824–836, <http://dx.doi.org/10.1111/ddi.12215>
- Cohen A, Mills C, Berry H, Wonham M, Bingham B, Bookheim B, Carlton J, Chapman J, Cordell J, Harris L, Klinger T, Kohn A, Lambert C, Lambert G, Li K, Secord D, Toft J (1998) A rapid assessment survey of non-indigenous species in the shallow waters of Puget Sound. Washington State Department of Natural Resources United States Fish and Wildlife Service, 37 pp
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2005) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7: 995–1002, <http://dx.doi.org/10.1017/S0025315406014354>
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723, <http://dx.doi.org/10.2307/1933500>
- Coutts ADM, Dodgshun TJ (2007) The nature and extent of organisms in vessel sea-chests: A protected mechanism for marine bioinvasions. *Marine Pollution Bulletin* 54: 875–866, <http://dx.doi.org/10.1016/j.marpolbul.2007.03.011>
- Dark SJ (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Diversity and Distributions* 10: 1–9, <http://dx.doi.org/10.1111/j.1472-4642.2004.00054.x>
- Drake JM, Lodge DM (2007) Hull fouling is a risk factor for intercontinental species exchange in aquatic ecosystems. *Aquatic Invasions* 2: 121–131, <http://dx.doi.org/10.3391/ai.2007.2.2.7>
- Epelbaum A, Herborg LM, Therriault TW, Pearce CM (2009) Temperature and salinity effects on growth, survival, reproduction, and potential distribution of two non-indigenous botryllid ascidians in British Columbia. *Journal of Experimental Marine Biology and Ecology* 369: 43–52, <http://dx.doi.org/10.1016/j.jembe.2008.10.028>
- Foss SF, Ode PR, Sowby M, Ashe M (2007) Non-indigenous aquatic organisms in the coastal water of California. *California Fish and Game* 3(3): 111–129
- Frey MA, Gartner HN, Clarke Murray C, Therriault TW (2009) First confirmed records of the non-native amphipod *Caprella mutica* (Schurin 1935) along the coast of British Columbia, Canada, and the potential for secondary spread via hull fouling. *Aquatic Invasions* 4: 495–499, <http://dx.doi.org/10.3391/ai.2009.4.3.10>
- Frey MA, Simard N, Robichaud DD, Martin JL, Therriault TW (2014) Fouling around: vessel sea chests as a vector for the introduction and spread of aquatic invasive species. *Management of Biological Invasions* 5: 21–30, <http://dx.doi.org/10.3391/mbi.2014.5.1.02>
- Galil BS, Nehring S, Panov V (2007) Waterways as invasion highways—Impact of climate change and globalization. In: Nentwig W (ed), *Biological Invasions*, Springer Berlin Heidelberg (Ecological Studies), pp 59–74, http://dx.doi.org/10.1007/978-3-540-36920-2_5
- Gillespie GE (2007) Distribution of non-indigenous intertidal species on the Pacific Coast of Canada. *Nippon Suisan Gakkaishi* 73: 1133–1137, <http://dx.doi.org/10.2331/suisan.73.1133>
- Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27, [http://dx.doi.org/10.1016/S0169-5347\(01\)02358-8](http://dx.doi.org/10.1016/S0169-5347(01)02358-8)
- Lambert G (2007) Invasive sea squirts: A growing global problem. *Journal of Experimental Marine Biology and Ecology* 342: 3–4, <http://dx.doi.org/10.1016/j.jembe.2006.10.009>
- Leprieux F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish Invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology* 6: 404–410, <http://dx.doi.org/10.1371/journal.pbio.0060028>
- Levings CD, Cordell JR, Ong S, Piercey GE (2004) The origin and identity of invertebrate organisms being transported to Canada's Pacific coast by ballast water. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1–11, <http://dx.doi.org/10.1139/f03-135>
- Levings C, Kieser D, Jamieson GS, Dudas S (2002) Marine and estuarine alien species in the Strait of Georgia, British Columbia. In: Claudi R, Nantel P, Muckle-Jeffs E (eds), *Alien Invaders in Canada's Waters, Wetlands, and Forests*. Natural Resources Canada, Canadian Forest Service, Science Branch, Ottawa, pp 111–131
- Lo VB, Levings CD, Chan KMA (2012) Quantifying potential propagule pressure of aquatic invasive species from the commercial shipping industry in Canada. *Marine Pollution Bulletin* 64: 295–302, <http://dx.doi.org/10.1016/j.marpolbul.2011.11.016>
- Lu L, Levings CD, Piercey GE (2007) Preliminary investigation of aquatic invasive species of marine and estuarine microbenthic invertebrates on floating structures in five British Columbia Harbours. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2814, 34 pp
- Mach ME (2012) Research on marine coastal impacts to promote ecosystem-based management: non-native species in northeast Pacific estuaries. PhD Thesis, University of British Columbia, Vancouver, BC, xvi+189 pp
- Mills C, Cohen A, Berry H, Wonham M, Bingham B, Bookheim B, Carlton J, Chapman J, Cordell J, Harris L, Klinger T, Kohn A, Lambert C, Lambert G, Li K, Secord D, Toft J (1999) The 1998 Puget Sound expedition: A shallow-water rapid assessment survey for non-indigenous species, with comparisons to San Francisco Bay. In: Pederson J (ed), *Marine Bioinvasions: Proceedings of a conference January 24–27, 1999*, MIT, Cambridge, pp 130–138
- Naylor RL, Williams SL, Stron DR (2001) Aquaculture—a gateway for exotic species. *Science* 294(5547): 1655–1656, <http://dx.doi.org/10.1126/science.1064875>
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50(1): 53–65, [http://dx.doi.org/10.1641/0006-3568\(2000\)050\[0053:EAEECON\]2.CO;2](http://dx.doi.org/10.1641/0006-3568(2000)050[0053:EAEECON]2.CO;2)
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 50(1): 53–65, <http://dx.doi.org/10.1016/j.ecolecon.2004.10.002>

- Powell N (1970) *Schizoporella unicornis*—an alien bryozoan introduced into the Strait of Georgia. *Journal of the Fisheries Research Board of Canada* 27(10): 1847–1853, <http://dx.doi.org/10.1139/f70-201>
- Quayle DB (1988) Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences 218, vi+241 pp
- Richoux NB, Levings CD, Lu L, Piercey GE (2006) Survey of indigenous, nonindigenous and cryptogenic benthic invertebrates in Burrard Inlet, Vancouver, British Columbia. Canadian Draft Report of Fisheries and Aquatic Sciences 1183, 20 pp
- Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics* 36: 643–689, <http://dx.doi.org/10.1146/annurev.ecolsys.36.102003.152638>
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37: 621–632, <http://dx.doi.org/10.1093/icb/37.6.621>
- Ruiz GM, Huber T, Larson K, McCann L, Steves B, Fofonoff P, Hines AH (2006) Biological invasions in Alaska's coastal marine ecosystems: establishing a baseline. Final report submitted to Prince William Sound Regional Citizens' Advisory Council and United States Fish & Wildlife Service, 112 pp
- Ruiz GM, Fofonoff PW, Steves B, Foss SF, Shiba SN (2011) Marine invasion history and vector analysis of California: a hotspot for western North America. *Diversity and Distributions* 17: 362–373, <http://dx.doi.org/10.1111/j.1472-4642.2011.00742.x>
- Ruiz GM, Freestone AL, Fofonoff PW, Simkanin C (2009) Habitat distribution and heterogeneity in marine invasion dynamics: The importance of hard substrate and artificial structure. In: Wahl M (ed), *Marine Hard Bottom Communities*. Springer Berlin Heidelberg (Ecological Studies), pp 321–332, http://dx.doi.org/10.1007/b76710_23
- Ryland JS, Holt R, Loxton J, Spencer Jones ME, Porter JS (2014) First occurrence of the non-native bryozoan *Schizoporella japonica* Ortmann (1890) in Western Europe. *Zootaxa* 3780(3): 481–502, <http://dx.doi.org/10.11646/zootaxa.3780.3.3>
- Simkanin C, Davidson I, Falkner M, Sytsma, Ruiz G (2009) Intra-coastal ballast water flux and the potential for secondary spread of non-native species on the US West Coast. *Marine Pollution Bulletin* 58: 366–374, <http://dx.doi.org/10.1016/j.marpolbul.2008.10.013>
- Simkanin C, Davidson IC, Dower JF, Jamieson G, Therriault TW (2012) Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. *Marine Ecology* 33: 499–511, <http://dx.doi.org/10.1111/j.1439-0485.2012.00516.x>
- Statistics Canada (2007) Canada population density, 2006 by dissemination area (DA) (map). “Thematic Maps”. “2006 Census”. Cencus. <http://www.statcan.gc.ca/pub/91-003-x/2007001/figures/4129885-eng.htm>
- Stoner DS (1990) Recruitment of a Tropical Colonial Ascidian: Relative Importance of Pre-Settlement vs. Post-Settlement Processes. *Ecology* 71: 1682–1690, <http://dx.doi.org/10.2307/1937577>
- Sylvester F, Kalaci O, Leung B, Lacoursière-Roussel A, Clarke Murray C, Choi FM, Bravo MA, Therriault TW, MacIsaac HJ (2011) Hull fouling as an invasion vector: can simple models explain a complex problem? *Journal of Applied Ecology* 48: 415–423, <http://dx.doi.org/10.1111/j.1365-2664.2011.01957.x>
- Thomson RE (1981) Oceanography of the British Columbia coast. Canadian Special Publication of Fisheries and Aquatic Science 56, 291 pp
- Vilà M, Pugadas J (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biological Conservation* 100: 397–401, [http://dx.doi.org/10.1016/S0006-3207\(01\)00047-7](http://dx.doi.org/10.1016/S0006-3207(01)00047-7)
- Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* 102: 143–153, [http://dx.doi.org/10.1016/S0006-3207\(01\)00098-2](http://dx.doi.org/10.1016/S0006-3207(01)00098-2)
- Wonham MJ, Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biological Invasions* 7: 369–392, <http://dx.doi.org/10.1007/s10530-004-2581-7>
- WoRMS Editorial Board (2016) World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ (accessed 2016-08-22), <http://dx.doi.org/10.14284/170>
- Zabin CJ, Ashton GV, Brown CW, Davidson IC, Sytsma MD, Ruiz GM (2014) Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors. *Management of Biological Invasions* 5: 97–112, <http://dx.doi.org/10.3391/mbi.2014.5.2.03>
- Zacharias MA, Roff JC (2001) Explanations of patterns of intertidal diversity at regional scales. *Journal of Biogeography* 28: 471–483, <http://dx.doi.org/10.1046/j.1365-2699.2001.00559.x>
- Zhan A, Briski E, Bock DG, Ghabooli S, MacIsaac HJ (2015) Ascidiaceans as models for studying invasion success. *Marine Biology* 162: 0, <http://dx.doi.org/10.1007/s00227-015-2734-5>

Supplementary material

The following supplementary material is available for this article:

Table S1. Non-indigenous (NIS), cryptogenic (C), native (N), and unknown (U) taxa identified at each deployment site in the fouling communities of the six geographic regions of the BC coast. The six geographic regions are: Strait of Juan de Fuca (SJF), Strait of Georgia (SG), West Coast of Vancouver Island (WCVI), Johnstone Strait (JS), Haida Gwaii (HG), North Coast (NC).

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