

Species invasion in the marine fouling
communities of British Columbia:
factors that influence invasion
dynamics and how they may affect
Botrylloides violaceus

by

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Abstract

Species invasion has been recognized as a major threat to biodiversity. Knowledge of the factors that limit the establishment and spread of non-indigenous species (NIS), such as biotic resistance and unfavourable environmental conditions, are important to their effective management. To test the biotic resistance and environmental favourability hypotheses in the fouling communities of British Columbia (BC), 22 locations were compared using settlement tiles in a large-scale survey. Biotic resistance is believed to be stronger in more diverse communities, therefore NIS richness and abundance were compared to native species richness and environmental conditions to investigate their importance using generalized and linear mixed models. Invader taxonomic group may influence biotic resistance, and environmental tolerances vary by species, therefore factors that affected *Botrylloides violaceus* presence and abundance were investigated as a case study. The biotic resistance hypothesis was not supported for NIS richness or NIS abundance, but could not be fully discounted due to a trend toward a negative slope between native species richness and *B. violaceus* presence and abundance, and the absence of predator data. Environmental variables affected NIS: salinity had a positive influence on NIS richness, NIS abundance, and *B. violaceus* presence, and temperature had a positive effect on *B. violaceus* presence and abundance. Salinity had a positive impact on native species richness as well, supporting the environmental favourability hypothesis. This suggests that knowledge of relevant environmental conditions is more important for the management of invasive species than

the species richness of vulnerable communities.

Environmental conditions are not static, so species invasion must be considered in the context of climate change. To understand how climate change may influence species invasion, *B. violaceus* presence and abundance in BC were compared to a range of abiotic conditions. This comparison informed a GAMLSS model that used linear trends from historical shore station data to project potential abundance in BC forward 50 years. Overall, the abundance of *B. violaceus* in BC was projected to increase. A larger increase in *B. violaceus* abundance was forecast for locations where conditions increased into the range favourable for growth. If temperature and salinity become more favourable for *B. violaceus*, as projected, climate change could intensify the invasion.

Preface

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Chapter 1

Introduction

1.1 Species invasion in the northeast Pacific

Species invasion has been recognized as one of the main threats to global biodiversity, ranked among land-use change and climate change (Sala et al., 2000). Species invasion contributes to the homogenization of previously distinct ecosystems (Simberloff et al., 2013), and can alter habitat, food webs, and resource availability (Bock et al., 2011; Carver et al., 2006; Crooks, 2002; Epelbaum et al., 2009a; Wonham & Carlton, 2005). The availability of vectors for species introduction has increased due to the globalization of human societies, making it possible for species to invade locations that would not have been accessible by natural dispersal (Crooks, 2002; Ruiz et al., 1997; Wonham & Carlton, 2005). The modern era of human-mediated marine introductions to the northeast Pacific began with the influx of Europeans to North America in the 1500s (Wonham & Carlton, 2005), though marine introduced species were largely unnoticed until the late 1900s (Ruiz et al., 1997). In their new ranges, introduced species are referred to as non-indigenous, non-native, alien, or exotic (Mack et al., 2000). Introductions of marine species can occur through many vectors, such as intentional and accidental imports for aquaculture and fisheries, release of pets, and connections of water bodies via canals, but a substantial fraction of introductions appear to be mediated by shipping, either via ballast (water or sediment) or hull fouling, including sea chests (Coutts & Taylor, 2004; Minchin et al., 2009; Ruiz et al.,

1997; Wonham & Carlton, 2005).

Shellfish aquaculture, one of the main historical routes of transportation for non-indigenous species (NIS) to the northeastern Pacific, began with imports from the Atlantic coast in the late 1800s and from the western Pacific in the early 1900s (Quayle, 1988; Wonham & Carlton, 2005). Some NIS introductions were intentional for food cultivation, but hitchhikers associated with the target species were also unknowingly transported (Quayle, 1988; Wonham & Carlton, 2005). In the northeastern Pacific, aquaculture imports are responsible for 20 % of the introduced marine NIS while ballast water transport and hull fouling have contributed 13 % and 8 % respectively; these three routes are the most common pathways for marine introductions (Wonham & Carlton, 2005). More recently, hull fouling of recreational boats has been identified as an important vector (Clarke Murray et al., 2011; Davidson et al., 2010).

While there is consensus on the vectors of invasion, the number of NIS present is still uncertain. Wonham & Carlton (2005) documented 123 NIS have established in marine and estuarine waters of the Northeast Pacific (Cape Mendocino, California, USA, to Haida Gwaii, British Columbia, Canada), including 99 invertebrate species. However, a broad-scale survey using traps and settlement plates identified only 31 NIS on the west coast of the USA from San Diego, CA, to Kachemak Bay, AK (de Rivera et al., 2005). There is a great deal of difficulty in the detection of new species and identification of origin (Ruiz et al., 1997; Wonham & Carlton, 2005). Even if a new species can be identified, the lack of historical taxonomic information can prevent tracing its origin since study of marine invasions only began in earnest in the late 1970s, though new molecular techniques may help clarify historic patterns (Grosholz, 2002).

NIS can cause impacts through the introduction of novel parasites or pathogens to a region, increased competition for space or other resources with native species, direct

consumption of native species, genetic effects through hybridization or change in gene flow, and homogenization of ecosystems (Crooks, 2002). NIS may also be able to change food webs and disturbance regimes (Crooks, 2002). In marine ecosystems, an influx of non-indigenous filter-feeding species may also change the rate of water filtration, which could lead to an altered distribution of biomass and energy in marine food webs (Byrnes & Stachowicz, 2009). The physical structure of the habitat can also be altered by NIS (Crooks, 2002; Wonham & Carlton, 2005), with the potential to reduce available space for recruitment of native species (Bock et al., 2011; Carver et al., 2006; Epelbaum et al., 2009a).

In addition to ecological impacts, there are also financial consequences of many invasions. For example, the non-indigenous tunicates *Styela clava* and *Ciona intestinalis* have caused dramatic economic losses to mussel aquaculture in Prince Edward Island (Leblanc et al., 2007; LeGresley & Martin, 2008). Economic impacts associated with aquatic and terrestrial invasion in Canada are projected to be between \$13.3 to 34.5 billion/year (Colautti et al., 2006). The study of species invasions has the capability to help mitigate impacts by highlighting the areas of greatest potential risk through an understanding of the mechanisms influencing invasion patterns (Jeschke et al., 2012).

1.2 Where will species invade?

The likelihood of success and rate of species invasion are influenced by both biotic and abiotic factors such as competition, predation, resource availability, propagule pressure, and environmental conditions (Alpert et al., 2000; Simberloff, 2009). One hypothesis suggests that increased native diversity will reduce the establishment of NIS (Elton, 1958), called the biotic resistance hypothesis. Communities with greater diversity of native species may use resources with greater complementarity, or decrease the likelihood that the community

will be naive or susceptible to an invader (Kimbrow et al., 2013). However, only six of 11 marine empirical studies supported the biotic resistance hypothesis (Jeschke et al., 2012). Others have found that invasion risk increased with native species diversity (e.g. Davies et al., 2007; Dunstan & Johnson, 2004; Levine, 2000). This could be because the favourable conditions found in a location could benefit both NIS and native species; this hypothesis was termed the environmental favourability hypothesis (Davies et al., 2007; Levine, 2000). In the context of marine ecosystems, environmental conditions such as temperature and salinity often have a large influence on species distribution and abundance patterns, whether native or NIS (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008). Past studies have investigated whether biotic resistance can be detected in the invasion of marine fouling communities, but results have been mixed (Dunstan & Johnson, 2004; Grey, 2009; Stachowicz et al., 2002a, 1999). Thus, the first goal of this thesis was to investigate whether there was evidence in the pattern of species invasion in the marine fouling communities of British Columbia (BC) to support either the biotic resistance or the environmental favourability hypothesis.

While the current status of invasion in fouling communities is important, the abiotic conditions in which these communities exist will also be changing over time (Rosenzweig et al., 2007). This could change the distribution and abundance of NIS (Côté & Green, 2012; Dukes & Mooney, 1999; Hellmann et al., 2008; Hoegh-Guldberg & Bruno, 2010; Lambert & Lambert, 2003; Rahel & Olden, 2008; Sorte et al., 2013, 2010a,b; Stachowicz et al., 2002b; Walther et al., 2009; Zerebecki & Sorte, 2011). Climate change is expected to lead to warmer sea surface temperatures (Rosenzweig et al., 2007), and change patterns of precipitation, river discharge (Knowles & Cayan, 2004; Morrison et al., 2002), and evaporation rates (Scavia et al., 2002), which will alter the salinity of coastal BC waters. As temperature and salinity are important factors for the survival of marine species, it is

important to understand species invasion in the context of climate change. While altered abiotic conditions may limit NIS spread if temperature and salinity become less favourable, it is more likely that increasing temperature and salinity would relax natural abiotic barriers to NIS survival and proliferation (Cockrell & Sorte, 2013; Dukes & Mooney, 1999; Hellmann et al., 2008; Hoegh-Guldberg & Bruno, 2010; Rahel & Olden, 2008; Sorte et al., 2013, 2010b; Stachowicz et al., 2002b; Walther et al., 2009; Zerebecki & Sorte, 2011). Using *Botrylloides violaceus* Oka 1927 as a case study, the second goal of this thesis was to understand how climate change may influence the future distribution and abundance of NIS.

1.3 Structure of this thesis

To investigate the influence of native species richness and abiotic conditions on species invasion in BC, I focused on the fouling communities found in marinas and harbours. In Chapter 2, the biotic resistance and environmental favourability hypotheses were tested on non-indigenous species richness and abundance, with a specific investigation of these hypotheses in the invasion of *B. violaceus*. In Chapter 3, the abundance of *B. violaceus* was modelled in response to abiotic conditions. Then, using conditions expected as a result of climate change, the potential change in *B. violaceus* abundance was projected forward 50 years. Chapter 4 summarizes the research presented in the data chapters and puts it in the context of current knowledge, with a discussion of its limitations and future directions.

Chapter 2

Patterns of invasion in British Columbia marine fouling communities: Biotic resistance or environmental favourability?

2.1 Introduction

2.1.1 Determinants of invasion success:

Biotic resistance or environmental favourability?

Scientists have investigated and debated which factors influence where invasions will occur, and which species will successfully invade, for decades. One of the early hypotheses developed in invasion ecology was that systems with a more diverse set of native species would be able to resist the invasion of new species better than a system with fewer species, known as the biotic resistance hypothesis (Elton, 1958). Biotic resistance, exemplified by a negative relationship between native species diversity and non-indigenous species (NIS) diversity or abundance, was believed to be due to competitive exclusion at smaller spatial scales (Davies et al., 2007). Thus, sites with lower species diversity should be less resistant

to invasion, meaning that more NIS would be able to establish and spread, with evidence to support this view derived from multiple systems (Jeschke et al., 2012; Stachowicz et al., 2002a, 1999).

The relationship between native species diversity and NIS diversity is not always negative. A recent meta-analysis found that only 55 % of marine empirical studies supported the biotic resistance hypothesis (6 out of 11) (Jeschke et al., 2012). To explain the positive relationship that has been found between native species diversity and NIS diversity, an alternative hypothesis was developed based on the idea that conditions that are favourable to native species should also be favourable for NIS, termed the environmental favourability hypothesis (Davies et al., 2007; Levine, 2000). In the decades since the biotic resistance hypothesis was developed, debate has followed about whether native communities with higher native species diversity are more able to resist invasion or whether hospitable environments favour the establishment of both native and non-indigenous species. Low environmental stress and abundant resources should favour both native species and NIS (Davies et al., 2007). Thus, the mechanisms that increase native species diversity should also apply to NIS diversity. A positive relationship between NIS and native species diversity would support the environmental favourability hypothesis.

Environmental conditions that influence species richness, such as temperature and salinity, are often factors that have a large influence on species success or failure in marine environments (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008). Temperature and salinity can constrain the survival, reproduction and population growth of a species (Epelbaum et al., 2009a), and even affect recruitment timing of some NIS (Stachowicz et al., 2002a).

Survival and establishment of species can also be affected by the number of propagules that reach an area, also known as propagule pressure. A steady supply of propagules can

increase the chance that a whole introduced population could persist through a rescue effect (Simberloff, 2009). In addition, it could increase genetic variability and thus enhance the likelihood of survival in the conditions found in the introduced area (Simberloff, 2009). As such, high propagule pressure increases the chance of the successful establishment of a NIS (Clark & Johnston, 2009; von Holle & Simberloff, 2005). Vectors of propagules for aquatic species include hull-fouling, ballast water transfer, accidental imports for aquaculture or fisheries, release of pets, and connections of water bodies via canals (Minchin et al., 2009; Ruiz et al., 1997; Wonham & Carlton, 2005). Ports and harbours are often the first point of introduction for ship-mediated vectors of NIS (Dafforn et al., 2009) and can be a source of secondary spread of propagules to the surrounding area via hull fouling, especially of recreational boats (Clarke Murray et al., 2011; Davidson et al., 2010).

Biotic resistance and environmental favourability are not mutually exclusive (Cheng & Hovel, 2010; Fridley et al., 2007; Levine, 2000). The seemingly paradoxical finding of support for both hypotheses has been suggested to be scale dependent, likely due to different processes controlling the relationship at different spatial scales. Smaller scales are more likely to be influenced by biotic resistance due to competition, while at larger scales high native and non-indigenous diversity often correlate positively (Byers & Noonburg, 2003; Dunstan & Johnson, 2004; Shea & Chesson, 2002). This discrepancy at different scales has been found within multiple systems (Davies et al., 2005; Levine, 2000), but findings are not always consistent (e.g. Davies et al., 2007; Dunstan & Johnson, 2004; Grey, 2009; Stachowicz et al., 2002a). The relative importance of the two mechanisms may also vary in space, with one mechanism supplanting the other along a stress gradient (Cheng & Hovel, 2010).

2.1.2 *B. violaceus* and the fouling community: A case study

Taxonomic group of the invading species could affect the strength of biotic resistance from the native community (Kimbrow et al., 2013). In addition, the importance of environmental factors vary by species (Ojaveer et al., 2011). To investigate whether the native fouling communities were able to resist the invasion of a representative non-indigenous species in British Columbia (BC), *Botrylloides violaceus* was selected. The factors that affect this species were also compared to the factors that effect NIS as a group. On the east coast of the USA, Stachowicz et al. (1999) found that in fouling communities with higher species richness, there was decreased survival of *Botrylloides violaceus* recruits. Stachowicz et al. (2002a) subsequently noted that increased native diversity reduced open space and thus hindered NIS cover by more fully utilizing a limiting resource. On the west coast of the USA, Grey (2009) also found biotic resistance when she examined NIS cover relative to native species richness at local and regional scales in areas that included *B. violaceus*, though she did not find this trend at the community level.

Two environmental variables, temperature and salinity, have been found to be important factors for *B. violaceus* survival, growth and reproduction, thereby contributing to its spread (Dijkstra et al., 2008; Epelbaum et al., 2009a; Sorte et al., 2011). *B. violaceus* has broad temperature and salinity tolerances, so while there are no large-scale areas in British Columbia (BC) that are unfavourable to survival (Epelbaum et al., 2009a), some localized sites may be uninhabitable due to low salinity or temperature, or out of the range necessary for growth or reproduction. In addition, Stachowicz et al. (2002b) found that warmer winter temperatures led to earlier and greater recruitment of *B. violaceus* the following summer, though native species were not found to change recruitment timing with winter temperatures. In support of the environmental favourability hypothesis, Grey (2011) found that temperature and salinity were more influential in the success of *B. violaceus*

than species interactions.

Propagule pressure is also an important factor for *B. violaceus* introduction and spread as it is a common hull-fouling species. Adult colonies living on hulls may release tadpole larvae that would be able to colonize nearby dock surfaces (Clarke Murray et al., 2011). In addition, due to a low dislodgement velocity, whole or partial colonies may detach from the hull along boats' routes of travel (Clarke Murray et al., 2012). These colony fragments are able to reattach to new substrates as an efficient dispersal strategy (Bullard et al., 2007; Clarke Murray et al., 2012).

2.1.3 Research questions

Many attributes of the environment and ecology of BC marine waters may influence the diversity and distribution of NIS, but the relative importance of abiotic and biotic factors to invasion dynamics is not yet clear. Accordingly, the goal of this study was to answer the following questions:

1. Did biotic resistance or environmental favourability influence the patterns of invasion in the marine fouling communities of BC?
2. Was there evidence of biotic resistance against the invasion of *B. violaceus*?

To test whether the biotic resistance or environmental favourability hypothesis had greater influence in marine fouling communities, species richness and abundance were measured on controlled substrates across sites varying in environmental conditions. A set of mixed-effects models was constructed on the field data, where each model represented a hypothesis regarding the drivers of the observed pattern. These models were used to investigate the relative importance of biotic resistance and environmental favourability for NIS richness and NIS abundance, and also if the result for NIS was applicable to a specific species, where

B. violaceus was used as a case study. The drivers of native species richness and abundance were compared with the those of NIS patterns, to clarify whether marine species responded similarly to ecological pressures or if the origin of a species was a partitioning factor.

2.2 Methods

2.2.1 Field survey

This field survey utilized natural spatial variation in temperature, salinity and invasion level to explore the relationship between environmental conditions, community diversity and invasion success. Studies have shown that local diversity patterns of marine epifaunal communities are largely driven by regional patterns (Kimbrow et al., 2013; Witman et al., 2004). To account for this, I surveyed across three ecoregions in one biogeographic realm in British Columbia (Spalding et al., 2007). Species richness was not manipulated because the disrupted mortality rate could alter the mechanisms that influence invasion patterns (Dunstan & Johnson, 2004) .

Site descriptions

Twenty four sites were selected in three BC ecoregions: the north coast, the Salish Sea, and the west coast of Vancouver Island (Figure 2.1, GPS locations in Appendix A, Table A). Regions were selected to have a 3 °C difference in mean summer temperatures among them. Specific sites were selected to represent a range of salinities within regions. *In situ* loggers hung at one meter below sea level measured temperature and salinity every two hours for the duration of deployment to quantify the conditions experienced at each site. These data were checked against manual field measurements and inaccurate data were removed.

Two sites, Tofino and Gold River, had to be eliminated on the west coast of Vancouver

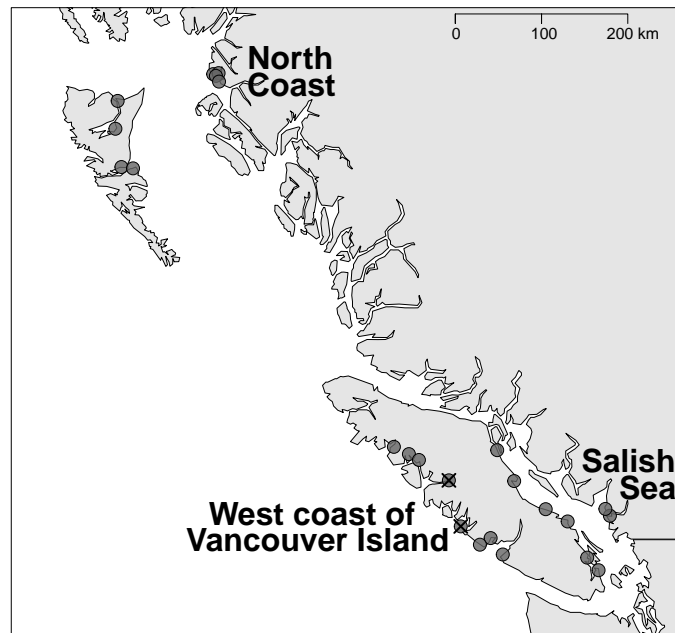


Figure 2.1: Map of field survey locations on the coast of British Columbia. Sites that were eliminated have been crossed out.

Island. Gold River had a maximum salinity of 0.76 ‰ and so was not saline enough to be suitable for a study on marine species. The temperature and salinity logger was lost at Tofino and a data substitution could not be found.

Sampling technique

At each site, ten 14.5 cm by 14.5 cm roughened PVC tiles were deployed face down at one meter below sea surface on a floating dock, spaced at least three meters apart. A brick was attached to the back of the tiles to keep them at the correct depth and orientation. Tiles were deployed between May 22 2011 and June 15 2011, and collected between September 23 2011 and October 10 2011. Only organisms that settled onto the downward-facing surface of the tile were evaluated, following the methods of Lindeyer & Gittenberger (2011). Tiles were preserved in 3 % formaldehyde and 0.5mm filtered seawater for transport back to the

lab for analysis.

Tile analysis

Tiles were transferred from 3 % formaldehyde into 40 % ethanol prior to analysis. Each tile was visually analyzed for percent cover using a 5 x 5 grid to aid with estimation following Dethier et al. (1993), then converted to square centimetres by multiplying by tile area. Percent cover was assessed in layers to ensure that species that are able to foul others were counted along with the ones upon which they grew. Only individuals over 0.5 mm were counted. Carlton (2007) and Lamb & Hanby (2005) were used to identify samples to the lowest taxonomic level possible. Species status was assigned as non-indigenous, native or cryptogenic according to literature consensus. A selection of difficult species identities and statuses were verified by Dr. James T. Carlton (*pers. comm.*). Some individuals could not be identified to a low enough taxonomic level for status assignment and so were excluded from further analyses.

2.2.2 Modelling approach

An information-theoretic approach was utilized to test the strength of evidence for a set of alternative hypotheses, each expressed as a model (Anderson et al., 2000). The response variables, NIS richness, NIS abundance, *B. violaceus* presence and *B. violaceus* abundance, were analyzed using a common set of models (Table 2.1). Temperature and salinity were selected to represent environmental favourability because they are two important drivers of the distribution of marine organisms (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008). Minimum temperature and salinity were given as the lowest 10th percentile rather than the absolute minimum to avoid over-emphasizing short, transient events.

Biotic resistance was evaluated through the slope of the relationship between the response variable (NIS richness or abundance, or *B. violaceus* presence or abundance) and native species richness. A negative slope between the response variable and native species richness would provide support for the biotic resistance hypothesis, while a positive slope would indicate environmental favourability. To test whether support of the biotic resistance and environmental favourability hypotheses could change between sites, models that allowed the slope for the richness term to vary by location were included. In the event that native species richness did influence the response variable, but the slope of the relationship changed between sites, the models where the slope was allowed to vary would be supported.

The distance in kilometres from the sampling location to the closest neighbouring docking facility, a measure of docking facility abundance in an area, served as a proxy for propagule pressure. For this study, it was assumed that higher boat traffic would occur where independent docking facilities were located in close proximity, as a greater number of boats would be required for multiple independent docking facilities to be financially feasible. As 65.7 % of boats surveyed in BC had fouled hulls, 25.7 % with NIS (Clarke Murray et al., 2011), docking facilities with more traffic and more boats would likely result in greater propagule pressure than areas with fewer boats. This proxy for propagule pressure will be referred to as “dock distance.” While propagule pressure is not technically a part of either the biotic resistance or the environmental favourability hypotheses, it was included to account for sites where the presence or abundance of species may be more heavily influenced by the availability of vectors to facilitate spread than the factors that affect establishment once the species is present.

The model set for native species was the same, but with native species richness replaced by NIS richness as an explanatory variable. If the same variables influenced native species and NIS, it would show additional support for the environmental favourability hy-

Table 2.1: Main set of models used to evaluate the evidence for the alternative hypotheses.

Model	Fixed effects	Hypotheses
int	Intercept only	Patterns explained by random effects and overall mean
TS	Temperature and salinity	Patterns explained by environmental factors
TSD	Temperature, salinity and dock distance	Patterns explained by environmental factors and propagule pressure
Sr	Native species richness	Patterns explained by biotic factors
SrVar	Native species richness	Patterns explained by biotic factors, but slope is allowed to vary by location
DSr	Dock distance and native species richness	Patterns explained by propagule pressure and biotic factors
DSrVar	Dock distance and native species richness	Patterns explained by propagule pressure and biotic factors, but slope of biotic influence is allowed to vary by location
TSDSr	Temperature, salinity, dock distance and native species richness	All variables are needed to explain the pattern found
TSDSrVar	Temperature, salinity, dock distance and native species richness	All variables are needed to explain the pattern found, and slope of biotic influence is allowed to vary by location

pothesis, as they responded as marine species rather than separately as native or NIS. All models included location nested within region as random effects to account for the spatial distribution of the sites in the observational survey.

The type of model employed varied with the response variable of interest. Linear mixed-models were fit on cube-root transformed abundances, while generalized linear mixed-models (GLMMs) were used to analyze the Poisson-distributed richness variables and binomial-distributed presence of *B. violaceus*. In order to meet model assumptions, *B. violaceus* was split into two model sets: a binomial GLMM for presence and absence, and a linear mixed-model on cube-root transformed abundance when *B. violaceus* was present.

All models were fit using maximum likelihood estimates (Bolker et al., 2009) and considered equivalent when within approximately two units of the lowest AIC_c (Burnham & Anderson, 2002). Each model in the top-ranked set was evaluated for spatial autocorrelation. After the top-ranked models were identified, the explanatory variable estimates and the amount of variability explained by the random effects were calculated by the modelling package. A normal approximation was used to calculate 95 % confidence intervals for the variable estimates. When the model with the lowest AIC_c value included a variable whose 95 % confidence interval overlapped zero, a subset of models was created without that variable and all of the models were compared with AIC_c to test the importance of that variable (Pinheiro & Bates, 2000). When the result of the AIC_c selection did not support one “best” model, multimodel inference was employed with the AIC_c equivalent models. Averaging the variable estimates over all of the candidate models may shrink the estimates to where they become unhelpful (Symonds & Moussalli, 2011); because the aim of this study was to relate the explanatory variables to the response variable, the variable estimates were instead preserved.

All analyses were conducted in R version 3.0.2 (www.R-project.org). The lme4 package (<http://lme4.r-forge.r-project.org/>) was used to fit the models, with AIC_c calculated according to Anderson et al. (2000), Symonds & Moussalli (2011), and R code adapted from (<http://glmm.wikidot.com/faq>). Akaike weights were calculated utilizing the qpcR package (<http://cran.r-project.org/web/packages/qpcR/index.html>). Following instructions in Fultz (2012), Moran’s I was calculated with the Ape package (<http://ape-package.ird.fr/>) to test for spatial autocorrelation.

2.3 Results

2.3.1 Field survey

A total of 51 sessile species were found in the fouling communities of BC, including 10 NIS, 16 native species, 24 uncategorized species, and one cryptogenic species (Appendix B, Table B). Richness varied across sites (Table 2.2).

Table 2.2: Species richness per type for each location. “Other” species richness includes cryptogenic species and those with uncertain identification. Average *B. violaceus* cover for each site is reported with standard error.

Region	Location	Native	Non-indigenous	Other	<i>B. violaceus</i> (cm ² \pm SE)	Number of tiles
North Coast	Digby Island	3	3	6	0	9
	Fairview	6	2	4	0	9
	Masset	1	2	4	6.17 \pm 1.81	10
	Port Clements	4	2	3	0	10
	Port Edward	3	2	3	0	8
	Queen Charlotte	4	2	9	18.34 \pm 7.67	9
	Rushbrook	7	3	2	0	10
	Sandspit	1	2	3	18.71 \pm 9.72	10
West coast of Vancouver Island	Bamfield	5	3	3	143.18 \pm 17.01	10
	Fair Harbour	1	1	2	0	9
	Gold River	1	0	1	0	10
	Tahsis	1	0	3	0	10
	Tofino	5	4	3	12.77 \pm 5.14	10
	Toquart Bay	3	3	1	82.63 \pm 32.70	10
	Ucluelet	6	4	7	37.00 \pm 11.56	10
	Zeballos	1	2	2	0	10
Salish Sea	Campbell River	5	3	3	0.07 \pm 0.05	10
	Comox Bay	2	2	1	0	10
	Eagle Harbour Yacht Club	3	0	1	0	10
	French Creek	3	4	5	0.42 \pm 0.42	10
	Maple Bay	5	4	5	14.72 \pm 5.67	10
	PBS	2	1	1	0	10
	Port Sidney	4	2	4	18.28 \pm 4.17	9
	Royal Vancouver Yacht Club	3	0	1	0	6

Averaged across site-level data loggers for the duration of tile deployment, the Salish Sea had a mean salinity (\pm standard error) of 20.71 ± 2.80 ‰, the west coast of Vancouver Island had a mean of 23.19 ± 1.56 ‰, and the north coast had a mean salinity of 25.92 ± 1.28 ‰. The Salish Sea had a mean temperature of 15.80 ± 0.69 °C, the west coast of Vancouver Island averaged 15.92 ± 0.53 °C, and the north coast had a mean temperature 12.96 ± 0.44 °C. However, salinity (Appendix C, Table C.1) and temperature (Appendix C, Table C.3) also varied from site to site within regions.

2.3.2 Factors that influenced NIS richness

There was substantial evidence that minimum salinity explained the variation in NIS richness across all sites (Table 2.3). There was some evidence for the models that included either temperature or dock distance, however these models had much lower weights, which suggested that the weight of the evidence was for minimum salinity alone (Burnham & Anderson, 2002). Minimum salinity was present in each of the top-ranked models, which emphasized its important role in the pattern of NIS richness in BC fouling communities. The 95 % confidence interval (CI) for the temperature variable estimate overlapped zero in the lowest AIC_c model, so the model comparison was re-run with the addition of models that lacked the temperature term (for the top-ranked models of the primary set, see Appendix D, Table D.1). Native species richness was not present in any of the models in the top-ranked set. None of the models had significant spatial autocorrelation, verified using Moran's I.

Table 2.3: Models for Poisson distribution of NIS richness within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC_c	Weight	Log-likelihood	Moran’s I (p value)
NISrichS	Minimum salinity	Region, location	534.96	0.457	-262.334	0.017 (0.062)
NISrichTS	Minimum temperature, minimum salinity	Region, location	536.44	0.218	-262.014	0.007 (0.285)
NISrichSD	Minimum salinity, dock distance	Region, location	537.08	0.159	-262.333	0.016 (0.064)

Minimum salinity had a positive influence on NIS richness, meaning that more NIS were found in areas with a higher minimum salinity 2.4). There was minimal support for the role of propagule pressure, measured through dock distance, as demonstrated through the low weight for the model that contained dock distance (Table 2.3) and that its confidence interval overlapped zero where present. There was additional variation in NIS richness among locations that was not captured by the fixed effects, but there was little of the unexplained variability accounted for by region (intercept random effects were much greater for location than for region). The explanatory variables were not strongly correlated (Appendix E, Table E.1).

Table 2.4: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for each of the top-ranked Poisson generalized linear mixed models of NIS richness.

<u>Model</u>	<u>Variable</u>	<u>Fixed effects estimate</u> Estimate (95 % CI)	<u>Random effects variance</u>	
			Location	Region
NISrichS	Intercept	-1.414 (-2.282, -0.546)	0.316	2.120E-12
	Minimum salinity	0.077 (0.038, 0.116)		
NISrichTS	Intercept	-0.451 (-2.907, 2.005)	0.304	8.876E-10
	Minimum temperature	-0.069 (-0.237, 0.099)		
	Minimum salinity	0.073 (0.034, 0.113)		
NISrichSD	Intercept	-1.409 (-2.291, -0.527)	0.316	2.441E-10
	Minimum salinity	0.077 (0.038, 0.116)		
	Dock distance	-0.002 (-0.080, 0.076)		

2.3.3 Factors that influenced NIS abundance

As with NIS richness, there was strong evidence that minimum salinity was the primary predictor of NIS abundance (Table 2.5). Native species richness was not present in the set of top-ranked models. The temperature term confidence interval overlapped zero in the lowest AIC_c model of the primary set, so a second model comparison was performed with

the inclusion of models where temperature was absent (for the top-ranked models of the primary set, see Appendix D, Table D.2). The models for NIS abundance were also free of significant spatial autocorrelation.

Table 2.5: Models for the cube root of NIS abundance within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC_c	Weight	Log-likelihood	Moran's I (p value)
NISabS	Minimum salinity	Region, location	662.28	0.466	-325.994	2.125E-04 (0.657)
NISabSD	Minimum salinity, dock distance	Region, location	664.28	0.172	-325.932	1.676E-04 (0.660)
NISabTS	Minimum temperature, minimum salinity	Region, location	664.37	0.164	-325.978	3.071E-04 (0.651)

The explanatory variables found to influence NIS abundance were very similar to those for NIS richness. Minimum salinity had a positive effect on NIS abundance, with NIS more abundant where the minimum salinity was more saline (Table 2.6). Location explained some of the variability for all three models, which indicates that there was between-site variability in NIS abundance that was not explained by the fixed effects. However, the region in which sites were located accounted for little to no variation in the models. Explanatory variables were not strongly correlated (Appendix E, Table E.2).

The residuals from the models for NIS abundance diverged from normality in the tails, but the analysis returned the same results with these outliers removed, so the result was considered robust.

Table 2.6: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for each of the top-ranked linear mixed models of cube root transformed NIS abundance.

<u>Model</u>	Variable	<u>Fixed effects estimate</u>	<u>Random effects variance</u>		
		Estimate (95 % CI)	Location	Region	Residual
NISabS	Intercept	0.2839 (-1.293, 1.861)	1.843	3.558E-10	0.973
	Minimum salinity	0.122 (0.047, 0.197)			
NISabSD	Intercept	0.340 (-1.264, 1.943)	1.832	0.000	0.973
	Minimum salinity	0.123 (0.048, 0.198)			
	Dock distance	-0.031 (-0.204, 0.142)			
NISabTS	Intercept	-0.173 (-5.513, 5.167)	1.840	0.000	0.973
	Minimum temperature	0.033 (-0.334, 0.400)			
	Minimum salinity	0.124 (0.046, 0.201)			

2.3.4 Factors that influenced *B. violaceus* presence

B. violaceus was present (defined as at least 0.1 cm² cover) on 26 out of 75 (34.7 %) tiles on the north coast, while it was present on 26 out of 59 (44.1 %) tiles on the west coast of Vancouver Island and 20 out of 75 (26.7 %) in the Salish Sea.

The evidence supported minimum salinity and minimum temperature as drivers of the variation in *B. violaceus* presence. The highest weighted model was comprised of minimum salinity and minimum temperature, which were also present in each model of the top-ranked set (Table 2.7). However, there was some evidence for dock distance and native species richness. None of the models had significant spatial autocorrelation.

Table 2.7: Models for binomial distribution of *B. violaceus* presence within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC_c	Weight	Log-likelihood	Moran’s I (<i>p</i> value)
aBvTS	Minimum temperature, minimum salinity	Region, location	106.74	0.495	-47.164	0.008 (0.258)
aBvTSDSr	Minimum temperature, minimum salinity, dock distance, native species richness	Region, location	107.60	0.322	-45.442	0.008 (0.248)
aBvTSD	Minimum temperature, minimum salinity, dock distance	Region, location	108.80	0.177	-47.122	0.008 (0.261)

There was strong evidence for minimum salinity and minimum temperature as predictors of *B. violaceus* presence. Minimum salinity and minimum temperature had positive effects on *B. violaceus* presence in each of the models, which indicated that higher minima corresponded with a higher likelihood of presence (Table 2.8). While there was some support for dock distance, the confidence interval for the parameter estimate overlapped zero in both models. Native species richness was present in the mid-weighted model, where it had a negative effect on *B. violaceus* presence, however the confidence interval overlapped zero. For each of the models, there was a fair amount of between-site variability that was not explained by the fixed effects.

As with NIS richness and abundance, salinity was important to the presence of *B. violaceus*. However, temperature impacted *B. violaceus* presence more than it did NIS richness or abundance.

Table 2.8: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for each of the top-ranked binomial generalized linear mixed models of *B. violaceus* presence.

<u>Model</u>	Variable	<u>Fixed effects estimate</u>	<u>Random effects variance</u>	
		Estimate (95 % CI)	Location	Region
aBvTS	Intercept	-40.496 (-62.088, -18.903)	5.449	0.000
	Minimum temperature	1.375 (0.366, 2.384)		
	Minimum salinity	0.924 (0.415, 1.433)		
aBvTSDSr	Intercept	-37.351 (-56.720, -17.982)	3.903	2.182E-10
	Minimum temperature	1.248 (0.354, 2.143)		
	Minimum salinity	0.947 (0.463, 1.431)		
	Dock distance	-0.059 (-0.411, 0.294)		
	Native species richness	-0.821 (-1.709, 0.068)		
aBvTSD	Intercept	-40.780 (-63.134, -18.427)	5.699	7.161E-09
	Minimum temperature	1.358 (0.314, 2.403)		
	Minimum salinity	0.937 (0.404, 1.471)		
	Dock distance	0.058 (-0.332, 0.449)		

Temperature and salinity constrained where *B. violaceus* was able to survive. In areas where either temperature or salinity were higher, the colonies were able to survive lower levels of the other factor. All regions in British Columbia had sites with and without *B. violaceus* (Figure 2.2).

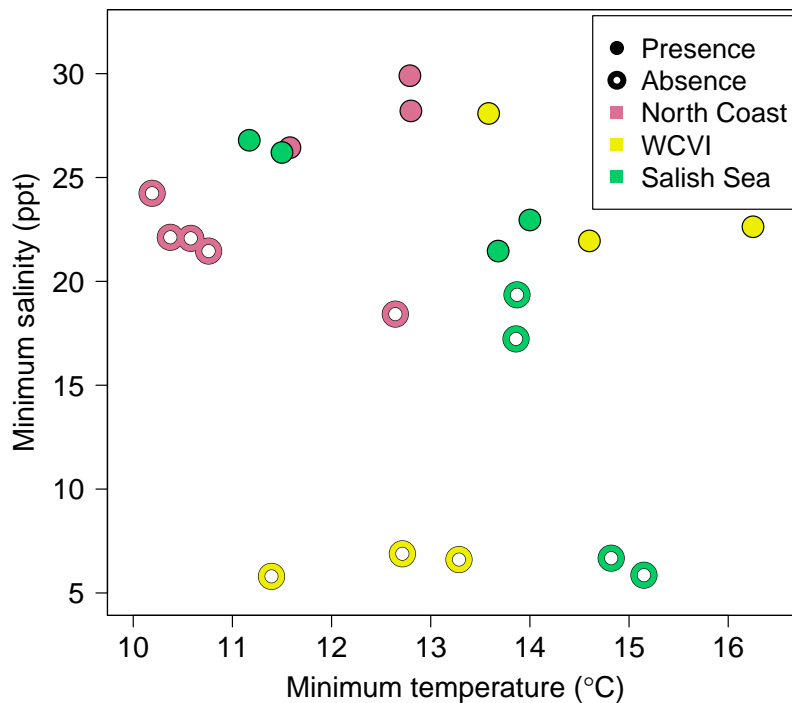


Figure 2.2: Presence and absence of *B. violaceus* by abiotic conditions, coloured by the three ecoregions.

2.3.5 Factors that influenced *B. violaceus* abundance

B. violaceus was present (at least 0.1 cm² cover) on only 72 out of the 209 tiles. Cover ranged from 0 to 100.92 cm² on the north coast, from 0 to 273.33 cm² on the west coast of Vancouver Island, and in the Salish Sea cover ranged from 0 to 52.56 cm². Assessed only on tiles where *B. violaceus* was present, the north coast had 15.92 ± 4.53 cm² *B. violaceus*

cover on average, while the west coast of Vancouver Island had $101.08 \pm 15.47 \text{ cm}^2$ cover, and the Salish Sea had $15.83 \pm 3.37 \text{ cm}^2$ cover.

Estimated only on tiles on which *B. violaceus* was present, two models were nearly tied for lowest AIC_c and highest weight for *B. violaceus* abundance (Table 2.9). The model with the lowest AIC_c did not contain any explanatory variables, and so was based on the overall mean and the random effects of region and location. Minimum temperature and salinity were present in the model that had a slightly lower weight, which was evidence that they may have influenced *B. violaceus* abundance. Native species richness was present in two models with lower weights, so there was some support for an effect. Moran's I verified that none of the models had significant spatial autocorrelation.

Table 2.9: Models for the cube root of *B. violaceus* abundance (only when present) within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC _c	Weight	Log-likelihood	Moran’s I (<i>p</i> value)
pBvint	Intercept	Region, location	241.96	0.272	-116.680	-0.006 (0.778)
pBvTS	Minimum temperature, minimum salinity	Region, location	242.30	0.229	-114.506	-0.012 (0.942)
pBvSr	Native species richness	Region, location	242.61	0.196	-115.850	-0.007 (0.811)
pBvTSD	Minimum temperature, minimum salinity, dock distance	Region, location	243.17	0.149	-113.709	-0.015 (0.963)
pBvDSr	Dock distance, native species richness	Region, location	244.30	0.084	-115.502	-0.006 (0.794)

There was evidence that *B. violaceus* abundance varied per site, but it was not clearly driven by any of the hypothesized factors, as indicated by the model based only on the overall mean and the random effects of region and location receiving the highest weight. Region accounted for approximately 2.3 times more of the unexplained variability than location in this model (Table 2.10), with a greater abundance of *B. violaceus* on the west coast of Vancouver Island (effect estimate of 1.160) than on the north coast or in the Salish Sea (effect estimates of -0.561 and -0.599, respectively).

The model that contained minimum salinity and temperature was weighted similarly to the intercept-only model, so there was evidence for their influence on *B. violaceus* abundance. Minimum salinity and temperature were present in two of the models, where temperature had a positive effect, but confidence intervals for salinity overlapped zero. There was some support for native species richness and dock distance as predictors of *B. violaceus* abundance, but the confidence intervals for the estimates of each overlapped zero. Region did not account for any of the variability when minimum salinity and temperature were present, but a fair amount when they were not. Though minimum temperature and minimum salinity were positively correlated, the rest of the explanatory variables were not strongly correlated (Appendix E, Table E.4).

Table 2.10: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for each of the top-ranked linear mixed models of cube root transformed *B. violaceus* abundance.

<u>Model</u>	Variable	<u>Fixed effects estimate</u>	<u>Random effects variance</u>		
		Estimate (95 % CI)	Location	Region	Residual
pBvint	Intercept	2.758 (1.639, 3.877)	0.350	0.811	1.197
pBvTS	Intercept	-3.839 (-13.855, 6.177)	0.411	0.000	1.196
	Minimum temperature	0.549 (0.140, 0.958)			
	Minimum salinity	-0.026 (-0.250, 0.197)			
pBvSr	Intercept	3.211 (1.875, 4.547)	0.316	0.883	1.172
	Native species richness	-0.211 (-0.528, 0.106)			
pBvTSD	Intercept	-4.126 (-13.646, 5.394)	0.350	0.000	1.186
	Minimum temperature	0.570 (0.181, 0.960)			
	Minimum salinity	-0.017 (-0.229, 0.195)			
	Dock distance	-0.076 (-0.191, 0.040)			
pBvDSr	Intercept	3.483 (2.043, 4.922)	0.301	0.803	1.167
	Dock distance	-0.264 (-0.602, 0.075)			
	Native species richness	-0.053 (-0.175, 0.070)			

2.3.6 Factors that influenced native species richness

There was strong evidence that minimum salinity and dock distance explained the distribution of native species richness in the fouling communities of BC (Table 2.11). NIS richness was present in a model with a low weight, which suggested that there may be some evidence of influence from biotic factors. The presence of dock distance in a mid-weight model provided evidence that propagule pressure may have affected native species richness.

Table 2.11: Models for Poisson distribution of native species richness within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC_c	Weight	Log-likelihood	Moran's I (p value)
natrichSD	Minimum salinity, dock distance	Region, location	606.58	0.452	-297.080	-0.019 (0.217)
natrichTSD	Minimum temperature, minimum salinity, dock distance	Region, location	608.18	0.203	-296.809	-0.020 (0.172)
natrichSDSr	Minimum salinity, dock distance, NIS richness	Region, location	608.34	0.187	-296.890	-0.019 (0.210)

Minimum salinity had a positive influence in each of the models for native species richness (Table 2.12), as it did for NIS richness. Both NIS and native species richness increased with more saline minimum salinity. Dock distance had a negative influence on native species richness. The closer the nearest neighbouring dock was to the sampling site, the higher the native species richness was at the sampling site. Though there was some evidence for the models that contained minimum temperature and NIS richness, the confidence intervals for each parameter estimate overlapped zero. The explanatory variables were not strongly correlated (Appendix E, Table E.5).

The models that were identified for native species richness were different from those that described NIS richness. The highest weighted model for native species richness included dock distance in addition to minimum salinity, whereas NIS richness was best determined by minimum salinity alone.

Table 2.12: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for the top-ranked Poisson generalized linear mixed models of native species richness.

<u>Model</u>	<u>Variable</u>	<u>Fixed effects estimate</u>	<u>Random effects variance</u>	
		Estimate (95 % CI)	Location	Region
natrichSD	Intercept	0.143 (-0.306, 0.591)	0.068	0.000
	Minimum salinity	0.034 (0.014, 0.054)		
	Dock distance	-0.071 (-0.118, -0.023)		
natrichTSD	Intercept	0.624 (-0.720, 1.969)	0.063	1.192E-07
	Minimum temperature	-0.035 (-0.128, 0.058)		
	Minimum salinity	0.032 (0.012, 0.053)		
	Dock distance	-0.067 (-0.115, -0.019)		
natrichSDSr	Intercept	0.131 (-0.313, 0.575)	0.064	3.063E-10
	Minimum salinity	0.032 (0.010, 0.053)		
	Dock distance	-0.070 (-0.117, -0.023)		
	NIS richness	0.043 (-0.091, 0.176)		

2.3.7 Factors that influenced native species abundance

The candidate model set for native species abundance differed from native species richness and NIS abundance (Table 2.13). The highest weighted model was comprised of only the overall mean and the random effect of region and location, which suggested that the drivers of the pattern of native species abundance were not among the hypothesized factors. There was some support for a role of NIS richness, both with and without allowing the slope between native species abundance and NIS richness to vary by location. In contrast, NIS abundance was mainly influenced by minimum salinity. None of the models had significant spatial autocorrelation, verified using Moran's I.

Table 2.13: Models for the cube root of native species abundance within approximately two units of the lowest AIC_c value. The “weight” column refers to the Akaike weight and “log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Model	Explanatory variables	Random effects	AIC_c	Weight	Log-likelihood	Moran’s I (p value)
natabint	Intercept	Region, location	519.11	0.394	-255.459	1.109E-04 (0.666)
natabSr	NIS richness	Region, location	519.98	0.256	-254.841	7.540E-05 (0.668)
natabSrVar	NIS richness	Region, location, slope of NIS richness varying by location	521.53	0.118	-251.312	-4.806E-04 (0.704)

Native species abundance varied among sites, but the variation was not clearly linked to any of the hypothesized drivers. For the model that contained only the overall mean and the random effects, the effect of location accounted for approximately 30 times more of the unexplained variability than region (Table 2.14). Though the effect of region was low, there was a slightly lower abundance of native species found on the west coast of Vancouver Island than average (effects estimate -0.147), about average found on the north coast (0.027), and a slightly higher abundance of native species than average in the Salish Sea (0.120).

There was some support for the role of NIS richness in the pattern of native species abundance, but the confidence interval for the parameter estimate in each model overlapped zero. Allowing the slope between native species abundance and NIS richness to vary with location explained only a slight amount of the variability in the model. The explanatory variables were not strongly correlated (Appendix E, Table E.6).

The residuals from the models for native species abundance diverged from normality in the tails, but the analysis returned the same results with these outliers removed, so the result was considered robust.

Table 2.14: Variable estimates for fixed effects with the 95 % confidence intervals and random effects variance for the top-ranked linear mixed models of cube root transformed native species abundance.

<u>Model</u>	<u>Fixed effects estimate</u>		<u>Random effects variance</u>			
	Variable	Estimate (95 % CI)	Location (intercept)	Location (NIS richness slope)	Region	Residual
natabint	Intercept	3.244 (2.602, 3.887)	1.848		0.063	0.457
natabSr	Intercept	3.376 (2.697, 4.056)	1.765		0.070	0.456
	NIS richness	-0.095 (-0.261, 0.071)				
natabSrVar	Intercept	3.244 (2.602, 3.887)	2.698	0.081	0.000	0.442
	NIS richness	-0.127 (-0.325, 0.071)				

2.4 Discussion

2.4.1 NIS and native species distribution patterns in the fouling community

Contrary to the biotic resistance hypothesis, native species richness did not have an effect on the species richness or abundance of NIS in this study. Instead, support was found for the environmental favourability hypothesis. As would be expected of marine species running up against physiological constraints, more species, both native and NIS, were found in areas of higher minimum salinity. NIS richness and abundance were both influenced mainly by minimum salinity.

One aspect of biotic resistance could not be investigated in this study: predation. Many of the predators in marine fouling communities are mobile species (Epelbaum et al., 2009b; Nydam & Stachowicz, 2007; Osman & Whitlatch, 2004; Simkanin et al., 2013), which this survey was not able to quantify. Predation by mobile species is capable of reducing the populations of some NIS (Epelbaum et al., 2009b; Nydam & Stachowicz, 2007; Osman & Whitlatch, 2004; Simkanin et al., 2013; but see Grey, 2010). While there was no evidence of biotic resistance from the native sessile communities in this study, the possibility of biotic resistance cannot be ruled out completely without examining the role of predation.

Other studies in marine fouling communities have found evidence of biotic resistance (e.g. Grey, 2009; Stachowicz et al., 2002a, 1999), though not all (Dunstan & Johnson, 2004). Aspects of methodology such as observational vs. manipulative studies, habitat type, the material used for settlement, and geographic location could have led to different results among studies. Artificial substrates may favour non-indigenous tunicates (Tyrrell & Byers, 2007), which could be one reason that the two methods in Grey (2009) produced different results. Biotic resistance was found in the manipulated fouling communities of

the Stachowicz et al. (1999) and Stachowicz et al. (2002a) studies. The communities in the Stachowicz et al. (2002a) field survey, Dunstan & Johnson (2004), Grey (2009), and this survey were not manipulated, but evidence of biotic resistance was mixed among these studies. Consistent with the findings of Levine (2000), methodology does appear to influence the probability of detecting biotic resistance, though the variability between studies is not fully explained by methodological differences. Another difference between these studies are their location. Freestone et al. (2013) and Kimbro et al. (2013) each found an influence of latitude on biotic resistance: higher latitude communities were less resistant to invasion than lower latitude communities. This pattern could be the result of increased predation pressure (Freestone et al., 2013) or greater species richness (Kimbrow et al., 2013) at lower latitudes. The studies described above that found biotic resistance all occurred at lower latitudes than this study.

Each of the aforementioned studies (i.e. Dunstan & Johnson, 2004; Grey, 2009; Stachowicz et al., 2002a, 1999) were conducted on established marine fouling communities, unlike the present study. The use of bare plates makes this study a conservative test of biotic resistance, because the native species competed to populate the new substrate at the same time as the NIS. However, harbours and marinas experience high levels of disturbance (Piola et al., 2009) and get cleaned, therefore free space can be present. As docking facilities are often first point of contact for ship-related invasions (Dafforn et al., 2009), bare plates can provide insight into invasion dynamics.

Contrary to what was found for NIS richness, native species richness was affected by the sampling location's proximity to other docking facilities (dock distance). This was unexpected as the assumption was that the source populations for native species would be the local area rather than fouling habitat. However, native species are also known to foul the hulls of recreational boats: 65.7 % of boats surveyed in BC had fouled hulls, while only

25.7 % had one or more NIS (Clarke Murray et al., 2011). Native species may be moved to new areas via hull fouling, which could increase the native species richness of the area. Potential habitat surrounding the sampling site was not surveyed in this study, so it is not known whether the species found on the docks were also found on the natural substrata. Even if the native species were present in the sampling areas prior to dock construction, the flow of new individuals from fouled hulls could provide benefits to these populations of native species that were similar to those that NIS may experience. Increased propagule pressure, which may be supplied by hull fouling, could increase genetic variability and thus the likelihood that beneficial traits would be present in the population (Simberloff, 2009). Steady propagule supply could also reduce the likelihood that a population could be eliminated due to stochastic events (Simberloff, 2009). Marinas and harbours have been documented to experience greater disturbance and changed environmental conditions relative to areas just outside of the facility (Rivero et al., 2013), which may alter the environment enough that it is just as novel to native species as it is to NIS. Thus, the adaptive advantage for native species could be lost (Byers, 2002), and the supply of new individuals to populations of native species could promote their persistence as it can for NIS.

None of the explanatory variables used in this study adequately described the pattern of native species abundance, as indicated by the model without explanatory variables receiving the highest weight. It is possible that the abiotic conditions were not limiting factors because the native species that were able to persist have had time to adapt to the local environments (Byers, 2002). The introduction of new species is very recent on the evolutionary time scale and native species may not have the ability to resist the novel source of competition, especially if disturbance has altered the habitat (Byers, 2002). However, rapid adaptation to new stressors cannot be completely ruled out (Strauss et al., 2006).

NIS richness may have had a minor effect on native species richness and abundance, demonstrated by the trend toward a positive slope for richness and a negative one for abundance. The weak evidence for a positive slope between native species and NIS richness emphasized that environmental favourability was more important than biotic interactions for species presence, which has been found for at least one NIS (*B. violaceus*) (Grey, 2011). The weak evidence for a negative slope between NIS richness and native species abundance could indicate that increased NIS richness reduced the availability of limiting resources for native species and thereby reduced their abundance, or that areas of high native species abundance were characterized by lower NIS richness. It would require experimentation to properly elucidate the mechanism behind this pattern. This study demonstrated that species origin was a factor in which variables affected species richness and abundance, as the explanatory variables that influenced native and non-indigenous species were not the same.

2.4.2 *B. violaceus* distribution pattern in the fouling community

Taxonomic group of the NIS may impact biotic resistance (Kimbrow et al., 2013) and the importance of environmental factors vary by species (Ojaveer et al., 2011). Therefore, this study compared the factors that influence NIS in general to one of an introduced species in BC marine fouling communities, *B. violaceus*. While there was no evidence of biotic resistance against NIS in general, there may have been a slight impact of native species richness on the presence and abundance of *B. violaceus*. The confidence interval for the native species richness estimate overlapped zero, but it trended toward a negative relationship, which could be evidence of either resistance of native communities or an impact of *B. violaceus* on native species. Reduced survivorship of *B. violaceus* recruits has been found in areas of higher native species richness previously, through manipulative experi-

ments in which the direction of the effect (i.e. whether native species affected the success of *B. violaceus* or *B. violaceus* impacted native species) could be determined (Simkanin et al., 2013; Stachowicz et al., 2002a, 1999). In light of these previous studies that found biotic resistance, it is possible that some of the communities in this observational study were able to resist *B. violaceus* invasion. The impact of native species richness was greater on the presence rather than the abundance of *B. violaceus*, which was contrary to other studies that found native species diversity having more influence on invasion success than invader establishment (Kimbrow et al., 2013; Levine et al., 2004). The inconsistent relationship between *B. violaceus* and native species richness could also be due to the interaction between biotic resistance and abiotic factors, because the strength of biotic resistance can depend on environmental conditions (Cheng & Hovel, 2010).

There is evidence that *B. violaceus* has been able to outcompete native species for space (Dijkstra et al., 2007; Rajbanshi & Pederson, 2007; Stachowicz et al., 2002b), which is the main limiting resource in marine fouling communities (Sellheim et al., 2010; Stachowicz et al., 2002a; Teo & Ryland, 1995). The studies that found competitive dominance of *B. violaceus* were conducted with different native species than were found in BC, so while these studies suggest that the role of competition in biotic resistance may be minor, it may not be the case in BC. However, predation may influence *B. violaceus* abundance in British Columbia. Osman & Whitlatch (2004) found that *B. violaceus* colonies over one week old were able to escape predation and dominate the community, though colonies could be significantly reduced or absent if exposed to predation before reaching that critical age. Survival of *B. violaceus* colonies, both adult and juvenile, was found to be higher in caged treatments that protected them from predators (Simkanin et al., 2013). The mossy chiton *Mopalia muscosa* was an effective predator of colonial tunicates, and reduced *B. violaceus* cover by 43 % (Nydam & Stachowicz, 2007). Epelbaum et al. (2009b) found

that red (*Strongylocentrotus franciscanus*) and green (*S. droebachiensis*) urchins, leather seastars (*Dermasterias imbricata*), and opalescent sea slugs (*Hermisenda crassicornis*) ate *B. violaceus* as well. However, these predators selected their regular prey over *B. violaceus* when given a choice (Epelbaum et al., 2009b) and Grey (2010) found that large predator exclusion did not affect the recruitment or abundance of *B. violaceus* in Washington, USA. Small numbers of *Hermisenda crassicornis* and juvenile seastars were found in this survey, but the sampling protocol was not optimized to quantify mobile species and so it was not possible to investigate predator interactions in this study.

Previous research found that abiotic conditions have more influence on the population growth of *B. violaceus* than direct species interactions (Grey, 2011), which supports the environmental favourability hypothesis. This may be why evidence of a relationship between *B. violaceus* (presence and abundance) and native species richness was not strong, while temperature and salinity acted positively on presence, and temperature acted positively on abundance. The impact of temperature and salinity on *B. violaceus* survival is consistent with past studies (Dijkstra et al., 2008; Epelbaum et al., 2009a; Sorte et al., 2011). Salinity and temperature may have had less of an effect on abundance than they did on presence because the abundance models were run strictly on tiles where *B. violaceus* was present. The analysis of *B. violaceus* abundance only where it was present, and the necessary filter of conditions that would represent, could be why the highest weighted model for abundance was based on the overall mean and the random effects of region and location alone, though temperature had a positive effect in lower ranked models. Increased temperature and salinity have been demonstrated to increase colony growth, but few of the sites in this survey had means in the ideal range of conditions for growth (above 26 ‰ and 15 °C) (Epelbaum et al., 2009a).

2.4.3 Conclusion

The biotic resistance hypothesis was not supported in terms of NIS richness or NIS abundance, but it cannot be fully ruled out for one key NIS due to the weak evidence for a negative slopes between native species richness and *B. violaceus* presence and abundance. However, because there was not strong evidence to support those negative relationships and because native species richness was not a factor for either NIS richness or abundance, there was no compelling evidence to support the biotic resistance hypothesis.

NIS richness and abundance were more affected by environmental variables. Salinity had a positive influence on NIS richness, NIS abundance, and *B. violaceus* presence, while temperature had a positive effect on *B. violaceus* presence and abundance. Salinity also had a positive influence on native species, which provided evidence to support the environmental favourability hypothesis. However, salinity and temperature are expected to be altered by climate change (Rosenzweig et al., 2007). Sea surface temperatures are expected to warm (Rosenzweig et al., 2007) and as patterns of precipitation, river discharge (Knowles & Cayan, 2004; Morrison et al., 2002), evaporation rates (Scavia et al., 2002) and currents are altered, salinity off of BC's coast will change. These changes will affect the species living in nearshore areas. It is possible that the altered abiotic conditions could result in the natural control of NIS spread if temperature and salinity become less favourable over time, but it is more likely that increasing temperature and salinity would relax the natural abiotic barriers to NIS survival and proliferation (Cockrell & Sorte, 2013; Dukes & Mooney, 1999; Hellmann et al., 2008; Hoegh-Guldberg & Bruno, 2010; Rahel & Olden, 2008; Sorte et al., 2013, 2010b; Stachowicz et al., 2002b; Walther et al., 2009; Zerebecki & Sorte, 2011). Climate change is not expected to slow anytime soon, so it is important to consider species invasion in this dynamic context (Ch. 3).

Chapter 3

Climate change and species invasion: using spatial variation in temperature and salinity to forecast potential changes in *Botrylloides violaceus* abundance in British Columbia

3.1 Introduction

3.1.1 The role of climate change in species invasion

Climate change is expected to alter temperature, precipitation, sea level, and frequency of extreme events (Harley et al., 2006; Rosenzweig et al., 2007). As a result, many important ecological properties, including temperature regimes, species' ranges and abundances, nutrient availability and the salinity profile of the ocean, are predicted to change (Harley et al., 2006; Hoegh-Guldberg & Bruno, 2010; Scavia et al., 2002). These changing condi-

tions could influence another important threat to ecosystems: species invasion (Cockrell & Sorte, 2013; Hellmann et al., 2008; Stachowicz et al., 2002a, 1999). Climate change is expected to alter vectors of species introduction and the effectiveness of control strategies, in addition to allowing new species to establish, and altering the distributions and impacts of already present NIS (Hellmann et al., 2008).

Two abiotic variables that substantially influence invader success or failure, and indeed the performance of all marine organisms, are temperature and salinity (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008). Climate change is expected to impact both temperature and salinity (Rosenzweig et al., 2007), therefore it is important to consider species invasions in the context of climate change because the relationship between them could have many consequences. It is possible that climate change could alter abiotic conditions from what is optimal for presently invading species, resulting in natural control of their spread. However, in light of past studies it is more likely that warming water temperature and altered salinity would release the natural abiotic barriers to non-indigenous species' survival and proliferation, and shift competitive interactions to favour invaders that are better adapted to the changing and new conditions (Côté & Green, 2012; Dukes & Mooney, 1999; Hellmann et al., 2008; Hoegh-Guldberg & Bruno, 2010; Rahel & Olden, 2008; Sorte et al., 2013, 2010a,b; Stachowicz et al., 2002b; Walther et al., 2009; Zerebecki & Sorte, 2011). Currently benign NIS may also begin to have negative impacts if conditions become more favourable in the future (Smith et al., 2012).

One of the most common non-indigenous tunicate species in the northeastern Pacific is *Botrylloides violaceus*. *B. violaceus* is a species of interest for both economic and ecological reasons. It is noted as a fouling concern for various shellfish and finfish growers whose aquaculture gear includes netting (Carver et al., 2006). Despite logistical issues created by this non-indigenous tunicate, there has not yet been evidence of impact on yield or survival

of industrially-grown mussels on the east coast of Canada (Carver et al., 2006; Cordell et al., 2012; Paetzold et al., 2012). The ecological concern is that *B. violaceus* has the ability to substantially alter hard substrata as it fouls structures as thin mats or irregular lobes (Bock et al., 2011; Carver et al., 2006; Epelbaum et al., 2009a), changing the texture of the substratum and reducing the amount of available space for recruitment. In addition to pre-emptive competition (Dijkstra et al., 2007; Stachowicz et al., 2002b), *B. violaceus* may monopolize space through interference competition by overgrowing species already present (Rajbanshi & Pederson, 2007). *B. violaceus* is expected to increase in invasiveness in many areas as water temperatures warm to a more favourable range for the species (Cockrell & Sorte, 2013; Stachowicz et al., 2002b). The potential for increased impacts as environmental conditions become more favourable makes it important to understand where this species is likely to proliferate.

3.1.2 Abiotic conditions in British Columbia and implications for *B. violaceus* invasions

Environmental conditions in British Columbia (BC) affect the distribution and abundance of *B. violaceus* (Epelbaum et al., 2009a). Based on the thermal tolerance of *B. violaceus* (Table 3.1), there are no large-scale regions that have uninhabitable temperatures year-round at present though conditions are below the optimal range in many locations (Epelbaum et al., 2009a). However, ocean surface temperatures could increase by 1.1 to 6.4 °C by the end of the century (Rosenzweig et al., 2007). The projected warming has the potential to elevate the temperature in more locations into the optimal growth range for *B. violaceus*, which may result in higher abundance in BC.

Table 3.1: Thermal tolerance for adult colonies of *B. violaceus*.

Study	Thermal tolerance	Temperatures tested	Sampling location	Conditions where samples collected
Epelbaum et al., 2009a	No survival below 0 °C (unpubl. data) Survivable range: ≤ 5 to ≥ 25 °C Growth range: 15 to ≥ 25 °C Optimal range: 20 to ≥ 25 °C	5, 10, 15, 20, 25 °C	British Columbia	Range at time of collection: 13 – 14 °C.
Sorte et al., 2011 (Northwest Atlantic)	LT ₅₀ 27.4 °C	Trials began at 17 °C and were elevated to 21, 25, 29, or 34 °C for a 24 hour period	Massachusetts	Mean summer sea surface temperature 2.4 °C higher than west coast site Annual range: 24.9 °C June - August, 2006 - 2010
Sorte et al., 2011 (Northeast Pacific)	LT ₅₀ 25.3 °C	Trials began at 17 °C and were elevated to 21, 25, 29, or 34 °C for a 24 hour period	California	Annual range: 12.4 °C June - August, 2006 - 2010

Changing patterns of precipitation, river discharge (Knowles & Cayan, 2004; Morrison et al., 2002), evaporation rates (Scavia et al., 2002) and currents will affect nearshore salinity in BC and the species living in these areas. *B. violaceus* cannot survive below 8 ‰ (Epelbaum et al., 2009a), so salinity can drop below the habitable range at sites where freshwater inputs are high relative to mixing and flushing times. Runoff from the Fraser River can lower the salinity in the summer to 8 ‰ in some areas of the Salish Sea, while the north coast is usually around 31‰, though will also vary locally with river runoff (Côté et al., 2012; Held & Harley, 2009). Low salinities at some areas in the Salish Sea have reduced the likelihood of invasion, while low temperatures in some areas of the north coast likely have limited invasion in spite of their higher (favourable) salinity Epelbaum et al. (2009a). This is consistent with the findings of Ch. 2. The wide range of temperature and salinity tolerances (Table 3.2), including the ability to survive short term exposure to salinities as low as 10 ‰ (Dijkstra et al., 2008), has enabled *B. violaceus* to survive in many introduced locations.

Table 3.2: Salinity tolerance for adult colonies of *B. violaceus*.

Study	Salinity tolerance	Salinity tested	Sampling location	Conditions where samples collected
Dijkstra et al., 2008	Survivable range: 15 to ≥ 30 psu	5, 10, 15, 20, 25, 30 psu	Gulf of Maine	Salinity during collection not given, but maintained at 30psu prior to experiments.
Epelbaum et al., 2009a	Survivable range: 20 to ≥ 38 ‰ Growth range: 26 to ≥ 38 ‰ Optimal range: 26 to ≥ 38 ‰	14, 20, 26, 32, 38 ‰	Strait of Georgia, BC	Salinity during collection not given. Unpublished data showed no survival below 8 ‰

Though the Strait of Georgia currently experiences reduced salinity in the summer (Harley et al., 2013) making it less suitable for *B. violaceus*, peak Fraser River outflow is expected to decrease with climate change (Morrison et al., 2002) with implications for the salinity regime in the Strait. This potential increase in minimum salinity will likely make the Strait of Georgia more invasible for species that are currently prevented from establishing due to hypo-osmotic stress. Furthermore, temperatures in the northeastern Pacific, while currently below optimum for *B. violaceus*, are expected to rise (Rosenzweig et al., 2007). Studies have shown that warmer temperatures (20 °C and warmer) favour *B. violaceus*, as it can grow and reach reproductive condition more quickly in warmer water (Epelbaum et al., 2009a). For this species, this could mean multiple reproductive events per summer (Epelbaum et al., 2009a), which, combined with earlier recruitment than native species (Stachowicz et al., 2002b), could result in this species quickly dominating available space.

3.1.3 Research question

Two methods for forecasting temporal processes that are otherwise unobservable include space-for-time substitutions and time-for-time predictions (Blois et al., 2013). Space-for-time substitutions for climate-driven changes utilize observed spatial relationships between abiotic conditions and a desired biotic metric to infer a future state of the ecological system (Blois et al., 2013). Time-for-time predictions use observed changes over time in one location to project future change for that same location (Blois et al., 2013). Time-for-time predictions may be more optimal as the dynamics unique to the location are accounted for, however space-for-time substitutions have been demonstrated to give reasonable predictions in models of community responses to climate change and do not require long-term monitoring data (Blois et al., 2013).

Docking facilities are recognized as focal points for invasion because they are often the first area of contact for ship-related vectors of potential invaders, therefore these areas can provide key information about how abiotic conditions affect species invasion (Dafforn et al., 2009). Temperature and salinity have demonstrated their ability to predict the distributions of both native and non-indigenous species, with increased predictive ability when geographic variables are added (Reusser & Lee II, 2008). Grey (2011) found that abiotic variables (specifically temperature and salinity) play a larger role in determining the success of *B. violaceus* invasions than species interactions, which was also found in Ch. 2. Thus, as biotic interactions are less relevant for *B. violaceus*, temperature and salinity should be able to approximate the future distribution, and potential abundance, of this species. This large-scale field study in harbours and marinas took advantage of the natural variation in salinity and temperature within BC, and between BC and California, to construct a space-for-time substitution model to answer the question: How might future changes in salinity and temperature due to climate change influence the abundance of *B. violaceus* in British Columbia?

3.2 Methods

3.2.1 Field survey

Site descriptions

In addition to the 24 sites in BC used for Ch. 2, eight sites in central California were selected to fit the model over a wider range of abiotic conditions (Figure 3.1, GPS locations in Appendix A, Table A.2 for California). Regions were selected to have a 4 °C range in mean summer temperatures among them from north to south. Sites were selected to represent a range of salinities within regions. *In situ* loggers measured temperature and salinity every

two hours for the duration of deployment for use in the model. These data were checked against manual field measurements and inaccurate data were removed. Missing salinity data for Loch Lomond and Moss Landing (California, USA) were substituted with buoy data measured near the sampling locations from the The Central and Northern California Ocean Observing System (<http://www.cencoos.org/>).

Four sites had to be eliminated, two on the west coast of Vancouver Island and two in California. Both California sites (Coyote Point and Pillar Point) were missing salinity logger data and one BC site (Tofino) did not have temperature or salinity logger data and substitutions could not be found. The second BC site (Gold River) had a maximum salinity of 0.76 ‰ and so was deemed unsuitable to include.

Sampling technique

For the sampling technique, please refer to Ch. 2, Section 2.2.1.

Tile analysis

Tiles were transferred from 3 % formaldehyde into 40 % ethanol prior to analysis. Each tile was visually analyzed for percent cover using a 5 x 5 grid to aid with estimation following Dethier et al. (1993). Percent cover was estimated in layers to ensure that species that are able to foul others are counted along with the ones upon which they grow. Only individuals over 0.5 mm were counted. Carlton (2007) was used to identify samples. *B. violaceus* cover was calculated as the sum of *B. violaceus* cover in all layers, divided by the total amount of cover for that tile in order to obtain the proportion of total cover occupied by *B. violaceus*. The proportion of cover that consisted of *B. violaceus*, averaged per site, was the response variable for the model.

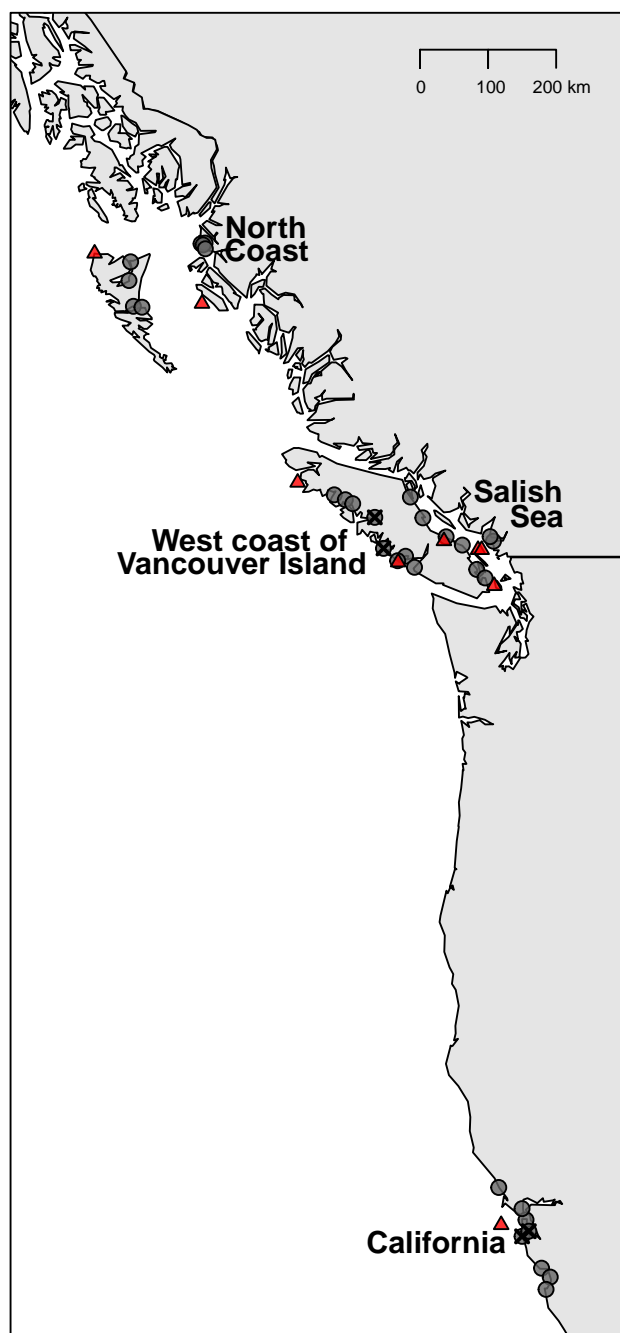


Figure 3.1: Map of field survey locations on the coasts of BC and California with eliminated sites crossed out. The red triangles mark approximate locations of the shore stations used to gather temperature and salinity trends.

3.2.2 Generalized additive model for location, scale and shape

Model selection

A zero-inflated beta distribution generalized additive model for location, scale and shape (GAMLSS) was created in an all-subset approach (Symonds & Moussalli, 2011) to describe the observed spatial relationships between abiotic conditions and *B. violaceus* abundance. Temperature and salinity affect the survival and growth of *B. violaceus* (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008), and therefore were included as possible explanatory variables in the models. Models were run with either the minimum or mean temperatures and salinities, as maximum values for temperature and salinity in BC are unlikely to be stressful for *B. violaceus*, even in the future. For the minima, the lowest 10th percentile was used rather than the absolute minimum to avoid over-emphasizing brief, transient events. The distance in kilometres from the sampling location to the closest neighbouring docking facility, a measure of docking facility abundance in an area, served as a proxy for propagule pressure. It was assumed for this study that higher boat traffic would occur where independent docking facilities were located in close proximity, as a greater number of boats would be required for multiple independent docking facilities to be financially feasible. Thus, as 25.7 % of boats surveyed in BC had hulls fouled with NIS (Clarke Murray et al., 2011), docking facilities with more traffic and more boats would likely result in greater propagule pressure than areas with fewer boats. Studies have shown that local diversity patterns in marine epifaunal communities are largely driven by regional patterns (Kimbrow et al., 2013; Witman et al., 2004). There were two options to account for spatial variation in the models: region, a categorical variable grouping locations by the ecoregion in which they occurred, and latitude. Only one spatial variable was used in parameters in which they were present to avoid over-fitting. Each continuous variable was run as a singular and quadratic term in separate models to account for possible quadratic

relationships in the data. AIC_c was used to select which terms were included in the final model.

Models were fit using the GAMLSS package (www.GAMLSS.org) in R version 3.0.2 (www.R-project.org). This method models both the mean of the statistical distribution that generates the observed values, as well as other parameters describing a user-defined shape for this distribution. In this case we chose a zero-inflated beta distribution. It is a unimodal distribution which resembles the normal under certain parameter values, but is only defined between 0 and 1, making it especially suitable to model percent cover data. An additional parameter, " ν ," describes the probability of obtaining zero percent cover. In accordance with the GAMLSS method, the sections of the model were fit sequentially with respect to the parameter hierarchy. First the mean percent cover per site when the species was present (μ) was fit using AIC_c for model comparison. The selected model from the μ fit was used to create the set of models for the parameter describing the probability of obtaining a value of zero (ν), also using the all-subset method to determine the variables to include in the ν parameter. Then, with the model selected from the ν fit as the base (which included the whole model: both μ and ν parameters), the parameter for scale (σ) was determined using the same method as the ν parameter. The model used as the base for each step was included with the all-subset model comparison to test whether the added parameter improved the overall fit. If the model with the highest Akaike weight was that used as the base (i.e. the model that did not include the parameter being fit in that step), then the parameter being fit was not included. The model with the highest weight was selected when multiple models were identified by the AIC_c comparison.

The probability of obtaining a zero was calculated as $\nu/(1+\nu)$. *B. violaceus* was considered absent at sites where the probability of obtaining a zero was estimated at 95 % or higher.

AIC_c was calculated according to Anderson et al. (2000) and Symonds & Moussalli (2011), with code adapted from (<http://glmm.wikidot.com/faq>), which was then updated to include the ν and σ parameters. Akaike weights were calculated using the qpcR package (<http://cran.r-project.org/web/packages/qpcR/index.html>). Spatial autocorrelation was calculated on the model residuals using Moran's I with the Ape package (<http://ape-package.ird.fr/> following instructions in (Fultz, 2012).

Temperature and salinity projections

Temporal trends for minimum and mean temperature and salinity during the warmest summer months (July to September, when tunicate growth and reproduction were maximal) from 1967 – 2011 were determined with data from the British Columbia Shore Station Oceanographic Program (BCSOP; <http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html>) . The shore stations used per region were Bonilla Island and Langara Point for the north coast, Amphitrite Point and Kains Island for the west coast of Vancouver Island, Chrome Island, Departure Bay, Entrance Island and Active Pass for the Salish Sea, and Farallon Islands for California (Figure 3.1).

Regional trends for BC were calculated on the shore stations within 100 km of any site within the region (without crossing land) with data from 1967 – 2011 and fewer than five years missing. Years with the summer months missing were not used to calculate the trend. Currently, sea surface temperatures in California are warmer than in BC. The relationships between the warm sea surface temperatures, salinity and *B. violaceus* abundance in California were used to inform the future values for *B. violaceus* in BC because sea surface temperatures are expected to increase with climate change (Rosenzweig et al., 2007). However, projections for the California sites were not calculated.

Temperature and salinity were projected 50 years into the future using the linear trend

of annual summer mean and minimum values, with the value used based on the variables selected in the model comparison. This trend was calculated for each shore station and averaged per region. The change from 2011 to 2061 was estimated per region and added to each site’s 2011 value from the logger data. Admittedly, the change is unlikely to be linear due to the non-linear increase in atmospheric CO₂ (Rosenzweig et al., 2007), decadal variability in sea surface temperature (Palmer et al., 2011), and the El Niño Southern Oscillation (Chung et al., 2013). However, a suitable model that was able to generate projections at a regional scale could not be found. Levitus et al. (2009) found that the linear trend accounted for 68 % of the variance in Pacific ocean heat content from 1969 – 2008, so while there is variation in the BCSOP data, projecting the observed trends using a linear regression should approximate the direction and magnitude of future environmental change.

3.3 Results

3.3.1 Field Survey

Nearshore temperature and salinity data were recorded by the *in situ* loggers to demonstrate the conditions the tiles had experienced at each site. Averaged across sites for the duration of tile deployment, the California region (averaged across all sites with standard error) had a mean salinity of 27.41 ± 2.05 ‰. The Salish Sea had a mean salinity of 20.71 ± 2.80 ‰, the west coast of Vancouver Island had a mean of 23.19 ± 1.56 ‰, and the north coast had a mean salinity of 25.92 ± 1.28 ‰. California had a mean temperature of 16.16 ± 0.82 °C, the Salish Sea had a mean of 15.80 ± 0.69 °C, the west coast of Vancouver Island averaged 15.92 ± 0.53 °C, and the north coast had a mean temperature 12.96 ± 0.44 °C. Salinity (Appendix C, Table C.1 for BC and Table C.2 for California)

and temperature (Table C.3 for BC and Table C.4 for California) also varied per site.

B. violaceus was found at three out of eight sites on the north coast, four of eight sites on the west coast of Vancouver Island (three of the six sites included in the analyses), four of eight sites in the Salish Sea, and seven of eight sites in California. The amount of *B. violaceus* cover ranged from 0 to 82.8 percent cover. The west coast of Vancouver Island had the greatest range within any of the regions, and had the two sites with overall highest cover (82.8 and 77.4 percent cover, Figure 3.2). The remaining site with *B. violaceus* present on the west coast of Vancouver Island had 26.7 percent cover. The three sites on the north coast with *B. violaceus* had 21.9, 8.5, and 3.2 percent cover. The four sites in the Salish Sea with *B. violaceus* had 15.9, 11.0, 2.6 and 0.3 percent cover. The seven sites in California that had *B. violaceus* ranged from 37.9 percent cover to 8.4 percent cover.

3.3.2 Generalized additive model for location, scale and shape

Model Selection

Fourteen models were within approximately two units of the lowest AIC_c value for the mean of the distribution for non-zero values (Table 3.3), and only one of the models displayed spatial autocorrelation. The model that included minimum temperature, dock distance and latitude (bolded) had the highest weight, and therefore was selected to move forward in the model fit.

The AIC_c comparisons for the ν and σ parameters each only identified single models. The ν parameter had the probability of obtaining a zero set by minimum salinity and region and was not spatially autocorrelated (Moran's I = -0.183, $p = 0.150$). The σ parameter was also not spatially autocorrelated (Moran's I = -0.115, $p = 0.443$), and was described by minimum temperature, minimum salinity and latitude.

Table 3.3: Models for the μ parameter of the GAMLSS model within approximately two units of the lowest AIC_c value.

Explanatory variables	AIC _c	Weight	Moran's I (<i>p</i> value)
Minimum temperature, dock distance, latitude	15.290	0.063	0.158 (0.056)
Mean temperature, dock distance, region	15.387	0.060	0.020 (0.568)
Minimum temperature, minimum salinity, dock distance, region	15.537	0.056	0.170 (0.032)
Minimum temperature, region	15.799	0.049	0.078 (0.256)
Minimum temperature, mean salinity, region	15.886	0.047	0.147 (0.069)
Minimum temperature, minimum salinity, region	16.122	0.042	0.149 (0.069)
Mean temperature, minimum salinity, dock distance, region	16.164	0.041	0.131 (0.092)
Minimum temperature, dock distance, region	16.370	0.037	0.069 (0.296)
Minimum temperature, mean salinity, dock distance, region	16.552	0.034	0.213 (0.012)
Mean temperature, region	16.598	0.033	0.108 (0.156)
Minimum temperature, minimum salinity (squared), dock distance, region	16.764	0.030	0.141 (0.074)
Mean temperature, mean salinity, dock distance, region	16.983	0.027	0.113 (0.136)
Mean temperature, mean salinity, region	17.451	0.021	0.129 (0.101)
Minimum temperature, dock distance (squared), latitude	17.705	0.019	0.104 (0.165)

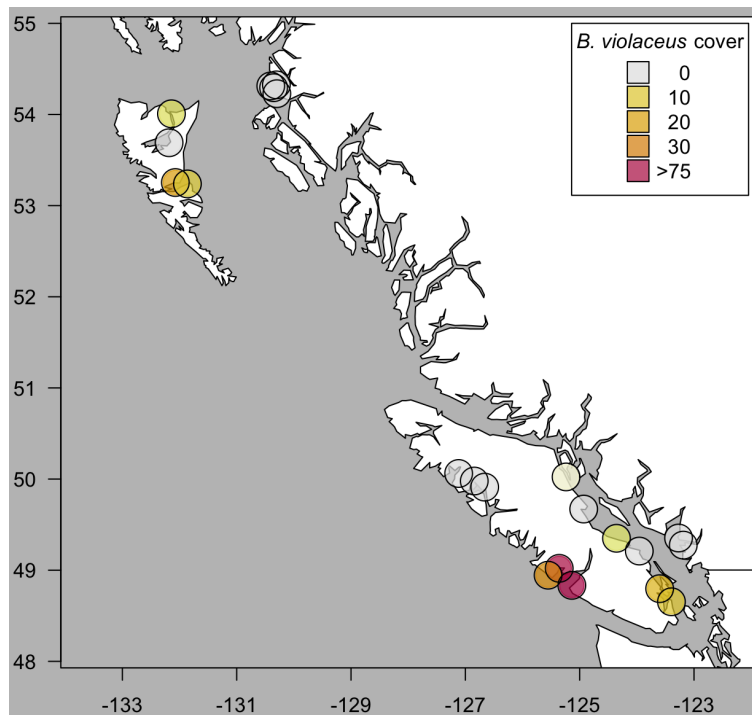


Figure 3.2: Distribution of *B. violaceus* in BC in 2011.

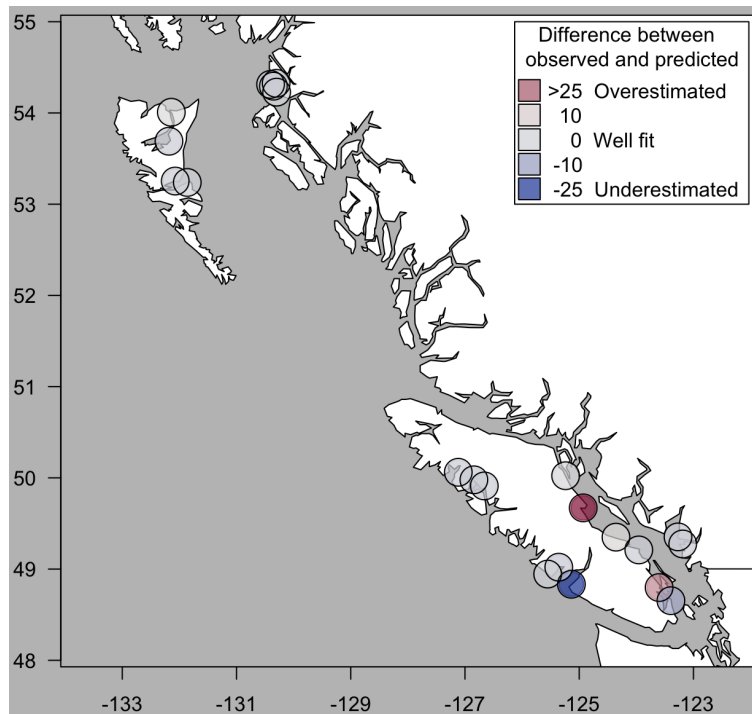


Figure 3.3: Map of the difference between model of current *B. violaceus* percent cover and observed data in BC.

In summary, the final model had the proportion of cover when the species is present based on minimum temperature, dock distance and latitude, the probability of obtaining a zero based on minimum salinity and region, and the scale of the data was based on minimum temperature, minimum salinity and latitude.

Model projection

Based on the trends of the summer BCSOP data, the north coast and the west coast of Vancouver Island were expected to warm by 0.25 °C and 0.41 °C in the next 50 years, respectively, while the Salish Sea was predicted to warm 2.09 °C. Salinity was predicted to decrease on the north coast by 0.28 ‰, but the west coast of Vancouver Island is projected to increase by 0.60 ‰, and the Salish Sea was projected to increase by 2.32 ‰. The projections varied between shore stations in each region and the range between the highest and lowest minima experienced per station between 1967–2011 was greater than the magnitude of the projected increase (Appendix ??app:LH, Table F.1 for temperature and Table F.2 for salinity).

Most of the model estimates for 2011 were near to the field value for *B. violaceus* abundance (Figure 3.3). Seventeen sites were modelled within five percent cover of the field value, with another two within eight percent cover. The site with the second greatest abundance of *B. violaceus* in the survey, Bamfield, was underestimated by 24.5 percent cover. The remaining two sites were overestimated by over 20 percent cover and were in the Salish Sea, Maple Bay (20.2) and Comox Bay (34.2). These two sites had habitable minimum temperatures, and Maple Bay had a minimum salinity in the survivable range while Comox Bay was just outside of it, and both were located within 1.3 km of other docking facilities. However *B. violaceus* was absent in Comox Bay and had a moderate abundance in Maple Bay (15.9 percent cover in the field). In California, five of six sites

were modelled within 10 percent cover of the field data. However, one California site where *B. violaceus* had high percent cover (37.9) was underestimated by 23.6 percent cover.

Increased *B. violaceus* cover was projected for BC over the next 50 years, in each region, though the amount varied between and within regions (Figure 3.4). The increase in *B. violaceus* on the north coast averaged 1.2 ± 0.6 percent cover and on the west coast of Vancouver Island the increase averaged 4.4 ± 2.1 percent cover. The greatest change was forecast for the Salish Sea, which averaged an increase of 32.2 ± 9.7 percent cover.

The projected increase of *B. violaceus* cover varied within regions (Figure 3.5), especially in the Salish Sea. Two sites were heavily dominated by the Fraser River outflow (specifically in the outer region of Burrard Inlet), which reduced the amount of *B. violaceus* cover. These two sites were accurately modelled as absent sites, and were not projected to have *B. violaceus* within the next 50 years. One other site was accurately modelled for current absence, however this site was expected to increase to 79.6 percent cover by 2061. As *B. violaceus* has previously been found at this site (Clarke Murray, 2012), presence of *B. violaceus* in the future would not be unexpected though the amount of increase for 2061 was surprisingly high. The final site where *B. violaceus* was not detected in the field was modelled at 34.2 percent cover with a large projected increase by 2061 (to 83.0 percent cover). The four sites where *B. violaceus* was detected were modelled at 3.0, 3.1, 10.4 and 36.1 percent cover for 2011, which increased to 22.4, 23.1, 52.2, and 84.1 percent cover, respectively.

The north coast did not vary as much and experienced relatively little increase. Four sites where *B. violaceus* was not detected were modelled accurately and were not expected to have *B. violaceus* by 2061. The remaining site where *B. violaceus* was not found had a slightly warmer temperature than the other sites without *B. violaceus*, though a lower salinity, and was estimated at 1.9 percent cover with a projected increase to 2.4. *B. vio-*

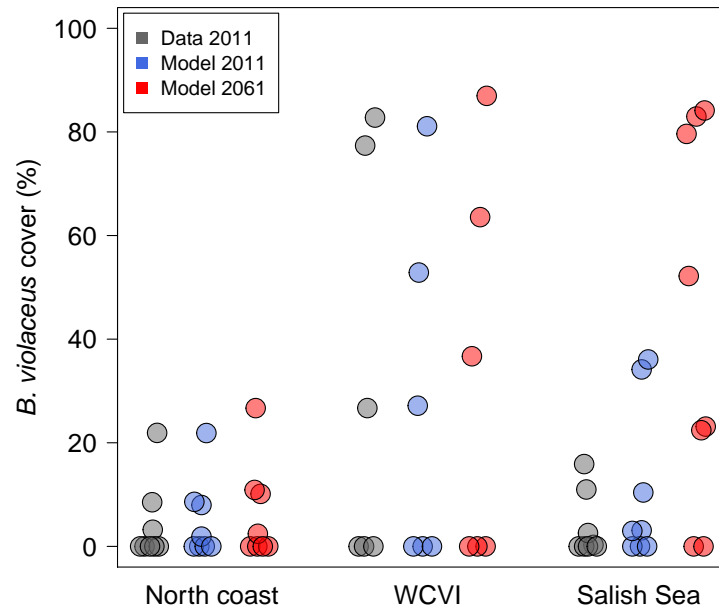


Figure 3.4: Field data for *B. violaceus* percent cover per region compared to model estimates for present and projected conditions.

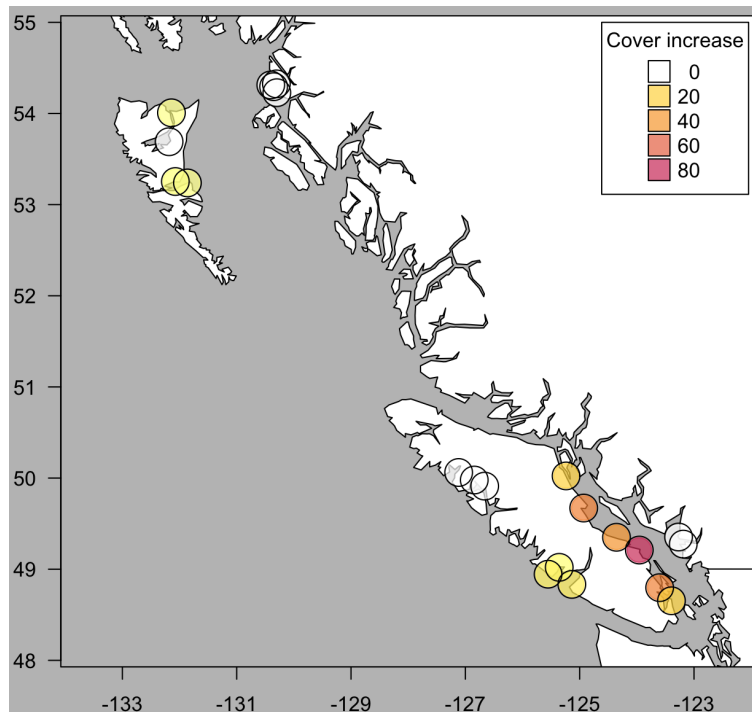


Figure 3.5: Projected increase of *B. violaceus* cover in BC. Warmer colours indicate a larger increase in percent cover.

laceus was found with low to moderate cover at three sites in the north coast, which were modelled at 8.0, 8.6 and 21.9 percent cover to 10.1, 10.9 and 26.7 percent cover.

The west coast of Vancouver Island had the two sites with the highest cover in the field survey, which were modelled at 52.9 and 81.1 percent cover for 2011, and these sites were projected to increase to 63.6 and 87.0 percent cover. The remaining site where *B. violaceus* was present in the field with 26.7 percent cover increased from a modelled 27.2 to 36.7 percent cover. *B. violaceus* was not detected in the field at three sites, possibly due to low minimum salinities, and were modelled with absence both for 2011 and in the projection.

3.4 Discussion

3.4.1 Potential change in *B. violaceus* abundance

Presence and abundance of *B. violaceus* was variable along the coast of BC, influenced at least in part by temperature and salinity. It follows that the expected increase in abundance over the next 50 years varied from site to site depending on current and projected values. On the north coast, where the increase in temperature was not sufficient to create conditions optimal for reproduction and growth of *B. violaceus* (see Tables 3.1 and 3.2 for survivable, growth, and optimal ranges of temperature and salinity), the current abundance and expected increase were low. However, all sites on the north coast with *B. violaceus* currently present were expected to see a slight increase in *B. violaceus* abundance as temperatures become more favourable for this species. While not all sites become more favourable, no sites become less favourable. On the west coast of Vancouver Island, the three sites that have conditions favourable for *B. violaceus* presently have high cover and are very close to optimal conditions. As the conditions at these sites were already highly favourable, *B. violaceus* has been able to exploit the habitat, therefore a low increase was

projected over the next 50 years. The three sites on the west coast of Vancouver Island where *B. violaceus* was not detected in the field or modelled for current conditions did not have *B. violaceus* in the projection as conditions did not improve enough to support survival. In the Salish Sea, some sites were expected to experience temperature and salinity increases that create conditions closer to the optimal range within the next 50 years. At these sites, there was a larger projected increase in abundance. The Salish Sea included the only site where *B. violaceus* was absent both in the field and in the model for current conditions, yet had *B. violaceus* present in the projection as conditions became favourable. The overall increase in *B. violaceus* was consistent with other studies, which projected increased abundance of this species with climate change (Sorte & White, 2013; Stachowicz et al., 2002b; but see Cockrell & Sorte, 2013).

All sites had at least some potential for *B. violaceus* introduction, since this work was conducted at active saltwater marinas and *B. violaceus* is a hull-fouling species, however *B. violaceus* was not detected at all of the sites. While this pattern did vary with abiotic conditions, the observed pattern of *B. violaceus* presence and abundance was not fully explained by temperature and salinity in the model. Proximity of the nearest neighbouring docking facility to the sampling location, which was used as a proxy for propagule pressure, explained some of the variability in the pattern. The more docking facilities in an area, indicated by shorter distances between them, the more boats that can be accommodated at one time. Docking facilities located in close proximity was likely only necessary in areas of higher boat traffic. Due to the increased boat traffic, there could be higher potential propagule pressure at those locations and a higher potential for *B. violaceus* establishment.

Not all of the sources of variability could be deciphered, but some of it was likely due to the amount of time that boats resided in each of the marinas (Clarke Murray et al., 2011), time since population establishment, or food supply, the increase of any of which would

increase *B. violaceus* abundance. The locations from which the boats arrived would also affect the amount of *B. violaceus*, because not all marinas are invaded (Clarke Murray et al., 2011). Another source of variability could be due to the frequency of dock cleaning, which could vary per site, and more frequent cleaning would likely reduce *B. violaceus* abundance. Other anthropogenic and environmental changes, such as acidification, increased human-mediated transport mechanisms, and development of the coast could change the rate of *B. violaceus* spread (Epelbaum et al., 2009a), and climate change is expected to modify human activity in ways that may increase the risk of invasion (Walther et al., 2009). Biotic interactions could also have been a source of variability. *B. violaceus* colonies under one week old were vulnerable to predation, where predation during that critical period could reduce or eliminate colonies (Osman & Whitlatch, 2004). Simkanin et al. (2013) found that both adult and juvenile colonies were more likely to survive when protected from predators. However, many predators selected their regular prey over *B. violaceus* when given a choice (Epelbaum et al., 2009b) and Grey (2010) found that large predator exclusion did not affect the recruitment or abundance of *B. violaceus*. *B. violaceus* has been found to be a dominant competitor for space in marine fouling communities (Dijkstra et al., 2007; Rajbanshi & Pederson, 2007; Stachowicz et al., 2002b), which is the main limiting resource (Sellheim et al., 2010; Stachowicz et al., 2002a; Teo & Ryland, 1995), so competition may not have a strong effect on *B. violaceus*. This was also found in Ch. 2.

As only temperature and salinity were allowed to vary in the model, if other factors change, the change in the abundance of *B. violaceus* could differ from the projection. Factors that could cause the future distribution and abundance of *B. violaceus* include competition, predation, resource availability, or vector-related factors such as boating traffic, marina size and number, or regulations against hull fouling. Nonetheless, previous studies have shown that temperature and salinity perform well in predicting species distributions

(Grey, 2011; Reusser & Lee II, 2008; though see Therriault & Herborg, 2008), lending some credence to the model projection of increased *B. violaceus* cover in BC.

3.4.2 Implications

The invasion and secondary spread of *B. violaceus* has been facilitated in part through its broad temperature and salinity tolerances (Epelbaum et al., 2009a), but what are the implications of this? Clarke Murray et al. (2011) found that 25.7 % of recreational boats in BC were fouled with NIS. In addition, *B. violaceus* was the third most commonly found NIS on boats and was the most consistently found NIS at surveyed marinas (Clarke Murray et al., 2011). BC has an estimated 400,000 boats with more visiting from the USA (Clarke Murray et al., 2011), providing ample opportunities for *B. violaceus* to spread. While ports and marinas are often the first location that NIS establish, NIS are able to spread to other areas through many human-mediated vectors, including hull fouling (Carlton, 1996; Floerl et al., 2009; Minchin et al., 2006; Wasson et al., 2001). Pristine areas and protected marine parks are popular spots to stop for recreational boaters, thus *B. violaceus* and other NIS could spread to undeveloped locations along the coast (Clarke Murray et al., 2011; Simkanin et al., 2012).

A greater distribution and increased abundance of *B. violaceus* could have consequences for both natural ecosystems and industry. Native communities could experience increased competition where *B. violaceus* is present. Pre-emptive competition may increase as adult ascidians such as *B. violaceus* can reduce the amount of space available for larval settlement of other species (Carver et al., 2006; Osman & Whitlatch, 1995; Zajac et al., 1989), which is an important limiting resource in marine fouling communities (Sellheim et al., 2010; Stachowicz et al., 2002a; Teo & Ryland, 1995). Interference competition may also increase because *B. violaceus* has been known to overgrow native species and can become competi-

tively dominant in subtidal benthic communities (Berman et al., 1992; Bock et al., 2011). Fouling organisms and algae were very vulnerable to *B. violaceus* overgrowth (Carver et al., 2006; Pederson et al., 2005), especially in terms of competition for space (Dijkstra et al., 2007; Rajbanshi & Pederson, 2007; Stachowicz et al., 2002b). The ability for *B. violaceus* to overgrow other species also makes them a concern for aquaculture (Bock et al., 2011; Carver et al., 2006; Epelbaum et al., 2009a). There is a risk that it could smother target species, reduce food availability, and make harvest difficult as tunicates coat aquaculture equipment (Bock et al., 2011; Carver et al., 2006). The fouling of aquaculture facilities may also increase local *B. violaceus* populations, as fragmented colonies created by high-pressure washing of contaminated equipment are viable if they resettle on suitable habitat (Bock et al., 2011; Paetzold & Davidson, 2010).

Climate change could exacerbate the competitive imbalance between *B. violaceus* and other species. As salinity and temperature along most of the coast of BC increase to ranges closer to what is optimal for *B. violaceus*, increased *B. violaceus* dominance, and the resulting changes to the substrate and available space, could result in reduced native diversity in the fouling community (Sellheim et al., 2010). Stachowicz et al. (2002b) found that warmer winter temperatures led to earlier and more abundant recruitment of *B. violaceus*, which means that climate change could favour its proliferation. *B. violaceus* would be able to establish before native species could arrive, thus dominating the limited available space. Further, native tunicate recruitment decreased with warmer winter temperatures (Stachowicz et al., 2002b). While the Stachowicz et al. (2002b) study was conducted in a different ocean basin and so does not directly apply to BC, it does highlight that there is a possibility that species may respond similarly here. That would mean that in addition to increased competition with *B. violaceus* as waters warm, climate change could directly affect the native assemblage of species in fouling communities, resulting in reduced native

species survival overall. Reduced native diversity could increase the likelihood of establishment of new non-indigenous species, leading to an invasion meltdown, adding further stress to native communities (Simberloff & Holle, 1999; Stachowicz et al., 2002b). While few of the surveyed sites in BC were currently dominated by *B. violaceus*, climate change could lead to an increase of sites with high *B. violaceus* cover.

3.4.3 Conclusion

This study provides predictions on province-wide trends in *B. violaceus* invasion, predicted on a small scale, and so sheds light on where it would be most important for managers to focus efforts to prevent introduction as conditions become more favourable. Increased temperature and salinity resulted in a projected increase of *B. violaceus* cover in BC over the next 50 years. Sites expected to undergo a large increase in temperature, or a salinity increase into a range in which *B. violaceus* can grow more quickly, were the most likely to experience increased abundance. If temperature and salinity become more favourable for *B. violaceus*, as the temporal trends in temperature and salinity project, climate change could make the invasion more widespread and severe.

Chapter 4

Conclusion

4.1 Summary of the results

Species invasion in coastal marine ecosystems can be harmful both ecologically and economically. Ecologically, non-indigenous species (NIS) can increase competition for limiting resources and alter habitat (Crooks, 2002; Dijkstra et al., 2007; Rajbanshi & Pederson, 2007; Stachowicz et al., 2002b). Economically, NIS can harm industry, such as the impact that invasive tunicates have had on mussel aquaculture in Prince Edward Island (Leblanc et al., 2007; LeGresley & Martin, 2008). The economic impacts associated with aquatic and terrestrial invasions are estimated to be between \$13.3 to 34.5 billion/year in Canada due to control costs, reduced yield, reduced land value, trade bans on exported goods, compensation paid to farmers, health care costs, and reduced tourism and tourism-related revenues (Colautti et al., 2006). Knowledge of the factors that influence invasion success are important to the effective management of NIS, and the study of species invasions can highlight areas of potential risk as the pattern of NIS distribution and abundance are better understood (Grey, 2011; Jeschke et al., 2012). Conditions will not remain constant, so it is necessary to consider species invasion in the context of climate change as the frequency of invasions is likely to increase (Hellmann et al., 2008). Accordingly, this thesis aimed to elucidate which factors had the greatest influence on NIS richness and abundance, and how the distribution and abundance of NIS may be altered by climate change.

In Ch. 2, the biotic resistance hypothesis was not supported in the fouling communities of British Columbia (BC), against NIS richness or abundance, which brings the proportion of marine studies that found evidence of biotic resistance (Jeschke et al., 2012) down to 50 % (6 of 12). The results are mixed even when focused specifically on marine fouling communities, and differences do not align between observational and manipulative studies (Dunstan & Johnson, 2004; Grey, 2009; Stachowicz et al., 2002a, 1999). However, latitude has been a factor in whether biotic resistance was found (Freestone et al., 2013; Kimbro et al., 2013), possibly due to increased predation pressure (Freestone et al., 2013) or greater species richness (Kimbrow et al., 2013) at lower latitudes. Lower latitude communities may be more resistant to invasion than higher latitude communities, and each of the studies that found biotic resistance in marine fouling communities occurred at a lower latitude than this study. Stachowicz et al. (1999) and Stachowicz et al. (2002a) conducted their studies at approximately 42.3 N, both finding resistance, while Grey (2009) studied at between 47.8 N and 48.6 N with mixed results, and Dunstan & Johnson (2004) did not find biotic resistance in their study at 42 S. Sites in this study were between 48.7 N and 54.3 N, which is higher than the studies included in the reviews of Freestone et al. (2013) and Kimbro et al. (2013).

Observed patterns of NIS richness and abundance were both affected primarily by minimum salinity. Salinity often has a large impact on whether species can survive, grow and reproduce in marine environments (Epelbaum et al., 2009a; Rahel & Olden, 2008; Reusser & Lee II, 2008), so this was not an unexpected result.

Minimum salinity was a factor in native species richness, as it was with NIS richness, which supports the environmental favourability hypothesis. However, contrary to what was found for NIS, native species richness was affected by both minimum salinity and proximity of the sampling location to other docking facilities. The main drivers of native

species abundance were not among the hypothesized factors, demonstrated by the support for the model based on the overall mean and the random effects of region and location, with location accounting for about 30 times more of the unexplained variability than region. It is possible that the abiotic conditions did not have a strong influence on native species abundance because the native species that were able to persist have had time to adapt to the local environments (Byers, 2002). As there were differences in the explanatory variables that influenced NIS and native species in terms of richness and abundance, this study demonstrated that species origin could be a factor in how marine species respond to ecological pressures.

The presence of *B. violaceus* was strongly influenced by minimum salinity and minimum temperature. However, there was weak evidence for reduced *B. violaceus* presence with higher native species richness, which may be evidence of a minor effect of biotic resistance against the presence of *B. violaceus*.

The model with the highest support for *B. violaceus* abundance was based on the overall mean and the random effects of region and location, with region explaining approximately 2.3 times more of the variability than location. However, there was evidence that temperature had a positive influence on *B. violaceus* abundance. Native species richness had a negative slope with *B. violaceus* abundance in separate models from minimum temperature, however the confidence intervals for the estimates overlapped zero so there was not strong evidence for the effect. The greater trend toward biotic resistance on the presence rather than the abundance of *B. violaceus* (more negative estimate with less overlap of positive values in the 95 % CI) was in contrast to previous studies that found that native species diversity had more influence on invasion success (population growth) than establishment (Kimbrow et al., 2013; Levine et al., 2004). The nature of the relationship between *B. violaceus* and native species richness could also be due to the interaction be-

tween biotic resistance and abiotic factors, as the strength of biotic resistance can depend on environmental conditions (Cheng & Hovel, 2010).

In Ch. 3, minimum temperature was projected to increase in all three regions of BC in the next 50 years, with the greatest increase in the Salish Sea. Minimum salinity was projected to decrease on the North coast, but expected to increase on the west coast of Vancouver Island and in the Salish Sea. Accordingly, *B. violaceus* abundance was projected to increase with the largest increases expected where future environmental conditions were closer to the optimal range for growth than they are now. All but one location where *B. violaceus* was not detected in 2011 were not projected to have presence in 2061. This is consistent with what would be expected based on the results for *B. violaceus* from Ch. 2, which found increased presence of *B. violaceus* with higher minimum temperature and minimum salinity, and greater *B. violaceus* abundance with higher minimum temperature. An expected increase of *B. violaceus* with climate change was also found in past studies of this species (Sorte & White, 2013; Stachowicz et al., 2002b; though see Cockrell & Sorte, 2013). Presence and abundance of *B. violaceus* was found to be variable along the coast of BC in the field survey. While the variability in abundance was conserved in the projection, the overall trend for the province was toward increased *B. violaceus* abundance by 2061.

The results of the model can be used to highlight which areas are most vulnerable to increased abundance of *B. violaceus*, and thus identify high risk areas for targeted NIS management (Grey, 2009). In addition, in light of the overlap between areas of invasion and aquaculture tenures (Epelbaum et al., 2009a) and the potential risks that *B. violaceus* poses to aquaculture (Bock et al., 2011; Carver et al., 2006; Epelbaum et al., 2009a), this information could also be useful to those who manage sea-based aquaculture ventures.

4.2 Limitations of the research

Ch. 2: Patterns of invasion in BC fouling communities

To determine which explanatory variables are responsible for the observed patterns for each of the response variables, experimental manipulations will be required. Such experiments will help determine the degree to which the relationships that were found based on observational evidence were, in fact, causal in the ways that were hypothesized.

Predators were not quantified in this study, as the sampling method was optimized only for sessile invertebrates. However, many marine fouling community predators are mobile species (Epelbaum et al., 2009b; Nydam & Stachowicz, 2007; Osman & Whitlatch, 2004; Simkanin et al., 2013), and past studies have shown that predation is capable of reducing the populations of some NIS (Epelbaum et al., 2009b; Nydam & Stachowicz, 2007; Osman & Whitlatch, 2004; Simkanin et al., 2013; but see Grey, 2010). Predation pressure cannot be assumed constant between locations as species richness and abundance varied per location (Table 2.2). Accordingly, biotic resistance cannot be dismissed as a possibility without examining the role of predation, though there was not evidence of resistance from the native sessile communities in this study.

Ch. 3: Climate change and species invasion

It is possible that the salinity and temperature from prior seasons were responsible for the presence and abundance of *B. violaceus* measured during the survey. For example, warmer winter temperatures may lead to earlier and greater recruitment of *B. violaceus* the following summer (Stachowicz et al., 2002b). Further, if the salinity remained below 10ppt for longer than two days, colonies could be eliminated (Dijkstra et al., 2008), which would then not be present in future seasons unless more propagules were introduced. Yet, the data collected for the abiotic conditions in the model were only from a single summer. This

model could be improved by monitoring the abiotic conditions and *B. violaceus* colonies over a longer time scale to include conditions for past growth and over-wintering seasons as this may affect the current distribution of *B. violaceus*.

An additional improvement would involve the method for projecting future climate conditions. The projections of temperature and salinity used in this thesis were based on linear trends from historical BCSOP data. Ideally, this would be done using climate models as climate is not likely to change linearly. However, a suitable model with regional, nearshore data on temperature and salinity is not yet available.

4.3 Future directions

To improve the model of present and future *B. violaceus* distribution and abundance, more aspects of environmental suitability and propagule pressure could be investigated. High amounts of suspended sediment can smother tunicates (Cohen et al., 1998) and water movement has a large influence on tunicate distribution (Lambert & Lambert, 2003), but these were not measured in this study. A more accurate measure of propagule pressure may increase the accuracy of the model. While boats did travel to the sampling sites, they might not have carried *B. violaceus*. Clarke Murray et al. (2011) detected *B. violaceus* on only 9.8 % of boats, so the proxy may have over-estimated the propagule pressure. Alternatively, there could be reproductive colonies of *B. violaceus* living on the docking facilities themselves, which would provide a steady supply of propagules to the tiles, but not be detected with the dock distance proxy and lead to an underestimate of propagule pressure. A more detailed understanding of the factors that contribute to the presence and abundance of *B. violaceus* at present could increase the predictive power of future models.

Unexpectedly, the distance between docking facilities was found to influence native species richness. To investigate whether this was a true result or simply an artefact of the

data, the natural areas proximal to the docks could be surveyed to compare the communities to those on the docks. The known range, geographically and in terms of abiotic tolerances, of the native species found on the docks should also be evaluated to test whether these species are expanding their range or simply taking advantage of a novel method of dispersal.

Though not discussed, some species observed during this study were able to survive close association with *B. violaceus* while other species did not. Research into why some species are more easily overgrown and smothered than others, and which species survive, could provide information on the ecological dynamics of the new communities that will be formed as *B. violaceus* invade BC. As most of the competition experiments with *B. violaceus* were conducted with different native species than are found in BC (Dijkstra et al., 2007; Rajbanshi & Pederson, 2007; Stachowicz et al., 2002b), it is worth repeating such experiments in BC to see if the results are consistent. This is especially important as our study and others (e.g. Sorte & White, 2013; Stachowicz et al., 2002b) have found that *B. violaceus* could become increasingly dominant with climate change.

4.4 Conclusion

In conclusion, the biotic resistance hypothesis was not supported for NIS richness or NIS abundance, but it cannot be fully ruled out due to the weak evidence for a negative slope between native species richness and *B. violaceus* presence and abundance, and the absence of predator data. However, because the confidence intervals for the native species richness parameter estimates for both *B. violaceus* presence and abundance overlapped zero, and because native species richness was not a factor for either NIS richness or abundance, there was no compelling evidence to support biotic resistance by native sessile species in the fouling communities of BC.

Environmental variables did have an effect on NIS. Salinity had a positive influence on

NIS richness, NIS abundance, and *B. violaceus* presence, as it did on native species richness, supporting the environmental favourability hypothesis. Temperature had a positive effect on *B. violaceus* presence and abundance. Some of the explanatory variables differed between NIS and native species in terms of richness or abundance, which suggested that species origin does affect how marine species respond to ecological pressures.

Salinity and temperature were projected to increase in BC over the next 50 years, and accordingly the cover of *B. violaceus* was also projected to increase. Projections occurred on a small scale, thus sites where temperature and salinity increased into a range in which *B. violaceus* could grow more quickly were the most likely to experience increased abundance. If temperature and salinity become more favourable for *B. violaceus*, as the temporal trends in temperature and salinity project, climate change could make the invasion more widespread and severe.

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Appendix A

Sampling site GPS locations

Table A.1: GPS locations for the BC sites in decimal degrees, with eliminated sites (Gold River and Tofino) included.

Region	Site	Latitude	Longitude
North Coast	Digby Island	54.3131	-130.4037
	Fairview	54.2936	-130.3541
	Masset	54.0077	-132.1413
	Port Clements	53.6901	-132.1823
	Port Edward	54.2281	-130.2976
	Queen Charlotte	53.2535	-132.0729
	Rushbrook	54.3248	-130.3056
	Sandspit	53.2383	-131.8616
West coast of Vancouver Island	Bamfield	48.8335	-125.1367
	Fair Harbour	50.0612	-127.1172
	Gold River	49.6791	-126.1169
	Tahsis	49.9115	-126.6617
	Tofino	49.1539	-125.9007
	Toquart Bay	49.0205	-125.3577
	Ucluelet	48.9452	-125.5526
	Zeballos	49.9785	-126.8439
Continued on next page			

Table A.1 – continued from previous page

Region	Site	Latitude	Longitude
Salish Sea	Campbell River	50.0235	-125.2382
	Comox Bay	49.6711	-124.9298
	Eagle Harbour Yacht Club	49.3531	-123.2705
	French Creek	49.3502	-124.3563
	Maple Bay	48.7977	-123.6013
	PBS	49.2101	-123.9569
	Port Sidney	48.6538	-123.3947
	Royal Vancouver Yacht Club	49.2753	-123.1882

Table A.2: GPS locations for the California sites in decimal degrees, with eliminated sites (Coyote Point and Pillar Point) included.

Region	Site	Latitude	Longitude
California	Bodega Bay	38.3300	-123.0577
	Coyote Point	37.5897	-122.3159
	Loch Lomond	37.9719	-122.4833
	Monterey	36.6043	-121.8909
	Moss Landing	36.8128	-121.7875
	Pillar Point	37.5024	-122.4822
	Santa Cruz	36.9632	-122.0018
	South Beach Harbor	37.7816	-122.3855

Appendix B

Species list for BC

Table B.1: Species list per region, with status is given for BC. When only one member of a taxon was present on a tile, but could not be identified further, it was designated “sp.” When more than one member of a taxon was present on a tile, and also could not be identified further, they were designated as “sp. A” and “sp. B” to differentiate between them. When an unidentified species was found repeatedly, it was given a code to keep it consistent among tiles, e.g. “Hydroid sp. 2,” “Porifera1V13,” and “stems.”

Taxon name	North Coast	Salish Sea	WCVI	Status
Phylum Annelida				
Serpulidae	x	x	x	Native
Serpulidae sp. A	x			Native
Serpulidae sp. B	x	x		Native
Phylum Arthropoda				
<i>Balanus crenatus</i>	x	x	x	Native
Cirripedia	x	x	x	Native
Phylum Bryozoa				
Anascina	x	x		Uncertain
Ascophora		x		Uncertain
<i>Bowerbankia</i> sp.		x	x	Uncertain
Bryozoan (encrusting hydroid)	x			Uncertain
<i>Bugula neritina</i>		x		Non-indigenous
<i>Bugula</i> sp.	x	x	x	Uncertain
<i>Bugula</i> sp. A	x		x	Uncertain
<i>Bugula</i> sp. B	x		x	Uncertain
<i>Cryptosula pallasiana</i>	x	x		Non-indigenous
Cyclostomatida	x			Uncertain

Continued on next page

Table B.1 – continued from previous page

Species name	North Coast	Salish Sea	WCVI	Status
<i>Dendrobeatia lichenoides</i>	x	x		Native
Encrusting bryozoan	x			Uncertain
<i>Membranipora</i> sp.	x	x	x	Native
<i>Schizoporella japonica</i>	x	x	x	Non-indigenous
<i>Schizoporella pseudoerrata</i>	x			Non-indigenous
<i>Schizoporella</i> sp.			x	Non-indigenous
<i>Tegella</i> sp.	x			Native
Phylum Chordata				
<i>Aplidium</i> sp.		x		Native
<i>Botrylloides violaceus</i>	x	x	x	Non-indigenous
<i>Botryllus schlosseri</i>	x	x	x	Non-indigenous
<i>Corella</i> sp.	x	x	x	Native
<i>Corella willmeriana</i>	x	x	x	Native
<i>Distaplia</i> sp.			x	Native
<i>Metandrocarpa</i> sp.	x			Uncertain
<i>Metandrocarpa taylori</i>			x	Native
Tunicate	x			Uncertain
Phylum Ciliophora				
Folliculinids			x	Native
Phylum Cnidaria				
Anemone	x	x	x	Uncertain
<i>Calycella syringa</i>			x	Native
<i>Ectopleura</i> sp.			x	Uncertain
Hydroid	x			Uncertain
Hydroid sp. 2	x			Uncertain
<i>Obelia dichotoma</i>	x	x	x	Non-indigenous
<i>Obelia longissima</i>	x	x		Non-indigenous
<i>Obelia</i> sp.	x	x		Non-indigenous
Segmented hydroid	x			Uncertain
Phylum Mollusca				

Continued on next page

Table B.1 – continued from previous page

Species name	North Coast	Salish Sea	WCVI	Status
Anomiidae	x			Uncertain
<i>Hiatella arctica</i>	x		x	Native
<i>Mytilus</i> sp.	x	x	x	Cryptogenic
Pectinidae			x	Uncertain
Phylum Porifera				
Porifera	x	x	x	Uncertain
Porifera1v13			x	Uncertain
Porifera1v3	x			Uncertain
Porifera2V3		x		Uncertain
Unknown phylum				
Fuzz			x	Uncertain
Stems	x			Uncertain

Appendix C

Abiotic conditions per site

Minima reported here are the lower 10th percentile, and the maxima used in the range are the upper 10th percentile, rather than the absolute values to avoid over-emphasizing brief, transient events. Means for each site are reported with standard errors.

Table C.1: Salinity (‰) for the summer of 2011 in BC.

Region	Site	Minimum	Mean (\pm SE)	Range
North Coast	Digby Island	21.46	24.24 (0.06)	5.66
	Fairview	22.12	24.62 (0.06)	4.37
	Masset	26.44	27.24 (0.004)	1.64
	Port Clements	18.43	19.35 (0.03)	1.70
	Port Edward	24.24	25.61 (0.04)	2.30
	Queen Charlotte	29.90	30.95 (0.02)	1.92
	Rushbrook	22.07	25.36 (0.06)	5.84
	Sandspit	28.21	29.96 (0.07)	5.65
West coast of Vancouver Island	Bamfield	21.95	25.60 (0.02)	5.96
	Fair Harbour	6.61	20.31 (0.21)	21.72
	Tahsis	5.80	20.67 (0.24)	22.87
	Toquart Bay	22.63	24.11 (0.04)	2.97
	Ucluelet	28.09	29.18 (0.04)	2.30
	Zeballos	6.89	19.25 (0.18)	18.77
Salish Sea	Campbell River	26.79	27.43 (0.02)	1.27
	Comox Bay	19.35	22.18 (0.07)	6.03
	Eagle Harbour	6.68	8.91 (0.07)	5.10
	Yacht Club			
	French Creek	21.46	24.73 (0.08)	7.05
	Maple Bay	22.96	24.13 (0.03)	2.98
	PBS	17.23	23.04 (0.12)	11.55
	Port Sidney	26.21	27.69 (0.04)	3.55
	Royal Vancouver	5.86	7.61 (0.07)	3.65
	Yacht Club			

Table C.2: Salinity (‰) for the summer of 2011 in California.

Region	Site	Minimum	Mean (\pm SE)	Range
California	Bodega Bay	22.00	27.89 (0.07)	10.21
	Loch Lomond	13.70	19.62 (0.04)	10.70
	Monterey	26.74	30.21 (0.04)	6.34
	Moss Landing	24.30	28.92 (0.03)	9.80
	Santa Cruz	33.43	33.88 (0.06)	1.53
	South Beach Harbor	19.07	24.00 (0.05)	8.23

Table C.3: Temperature ($^{\circ}\text{C}$) for the summer of 2011 in BC.

Region	Site	Minimum	Mean (\pm SE)	Range
North Coast	Digby Island	10.76	12.08 (0.03)	2.38
	Fairview	10.37	11.76 (0.03)	2.41
	Masset	11.58	13.06 (0.01)	2.75
	Port Clements	12.64	14.51 (0.04)	3.37
	Port Edward	10.19	11.61 (0.02)	2.37
	Queen Charlotte	12.79	14.36 (0.03)	2.80
	Rushbrook	10.58	12.01 (0.03)	2.47
	Sandspit	12.80	14.28 (0.03)	2.64
West coast of Vancouver Island	Bamfield	14.60	16.33 (0.04)	3.50
	Fair Harbour	13.29	16.03 (0.05)	5.26
	Tahsis	11.39	14.71 (0.06)	5.97
	Toquart Bay	16.25	18.23 (0.04)	4.10
	Ucluelet	13.58	14.88 (0.03)	2.56
	Zeballos	12.71	15.35 (0.05)	4.92
Salish Sea	Campbell River	11.17	12.56 (0.03)	2.92
	Comox Bay	13.87	16.70 (0.05)	5.42
	Eagle Harbour	14.82	17.00 (0.05)	4.41
	Yacht Club			
	French Creek	13.68	16.79 (0.06)	5.64
	Maple Bay	14.00	16.45 (0.05)	4.78
	PBS	13.86	16.93 (0.06)	5.52
	Port Sidney	11.50	12.78 (0.02)	2.48
	Royal Vancouver	15.15	17.16 (0.04)	4.12
	Yacht Club			

Table C.4: Temperature ($^{\circ}\text{C}$) for the summer of 2011 in California.

Region	Site	Minimum	Mean (\pm SE)	Range
California	Bodega Bay	12.94	14.44 (0.02)	2.85
	Loch Lomond	17.50	19.96 (0.04)	4.50
	Monterey	13.45	14.76 (0.02)	2.28
	Moss Landing	14.50	15.92 (0.03)	3.00
	Santa Cruz	13.88	15.41 (0.02)	2.52
	South Beach Harbor	14.49	16.49 (0.02)	3.13

Appendix D

Primary model results for sets with a dropped variable

Table D.1: Models for Poisson distribution of NIS richness within approximately two units of the lowest AIC_c value. “Log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Explanatory variables	Random effects	AIC _c	Log-likelihood	Moran’s I (<i>p</i> value)
Minimum temperature, minimum salinity	Region, location	536.44	-262.014	0.007 (0.285)
Minimum temperature, minimum salinity, dock distance	Region, location	538.56	-262.00	0.007 (0.283)

Table D.2: Models for the cube root of NIS abundance within approximately two units of the lowest AIC_c value. “Log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Explanatory variables	Random effects	AIC _c	Log-likelihood	Moran’s I (<i>p</i> value)
Minimum temperature, minimum salinity	Region, location	664.37	-325.978	3.071E-04 (0.651)
Minimum temperature, minimum salinity, dock distance	Region, location	666.35	-325.896	3.076E-04 (0.651)

Table D.3: The primary set of models for Poisson distribution of native species richness within approximately two units of the lowest AIC_c value. “Log-likelihood” refers to the natural log of the likelihood for the set of parameter values.

Explanatory variables	Random effects	AIC_c	Log-likelihood	Moran’s I (<i>p</i> value)
Minimum temperature, minimum salinity, dock distance	Region, location	608.18	-296.809	-0.020 (0.172)
Minimum temperature, minimum salinity, dock distance, NIS richness	Region, location	609.99	-296.636	-0.020 (0.197)

Appendix E

Correlations of fixed effects

E.1 NIS correlation tables

Correlations between fixed effects for the top-ranked models for NIS richness are found in Table E.1.

Table E.1: Correlation of fixed effects for NIS richness, in the order in which they were presented in Table 2.4.

Model	Fixed effects		
NISrichS		Intercept	
	Minimum salinity	-0.950	
NISrichTS		Intercept	Minimum salinity
	Minimum salinity	-0.514	
	Minimum temperature	-0.937	0.202
NISrichSD		Intercept	Minimum salinity
	Minimum salinity	-0.924	
	Dock distance	-0.182	-0.046

Correlations between fixed effects for the top-ranked models for NIS abundance are found in Table E.2.

Table E.2: Correlation of fixed effects for NIS abundance, in the order in which they were presented in Table 2.6.

Model		Fixed effects	
NISabS		Intercept	
	Minimum salinity	-0.929	
NISabSD		Intercept	Minimum salinity
	Minimum salinity	-0.892	
	Dock distance	-0.195	0.082
NISabTS		Intercept	Minimum salinity
	Minimum salinity	-0.518	
	Minimum temperature	-0.955	0.265

E.2 *B. violaceus* correlation tables

Correlations between fixed effects for the top-ranked models for *B. violaceus* presence are found in Table E.3.

Table E.3: Correlation of fixed effects for *B. violaceus* presence, in the order in which they were presented in Table 2.8.

Model		Fixed effects			
aBvTS		Intercept	Minimum salinity		
	Minimum salinity	-0.826			
	Minimum temperature	-0.842	0.399		
aBvTSDSr		Intercept	Minimum salinity	Minimum temperature	Native species richness
	Minimum salinity	-0.824			
	Minimum temperature	-0.828	0.393		
	Native species richness	0.135	-0.320	-0.092	
	Dock distance	-0.029	0.065	-0.147	0.261
aBvTSD		Intercept	Minimum salinity	Minimum temperature	
	Minimum salinity	-0.828			
	Minimum temperature	-0.826	0.376		
	Dock distance	-0.057	0.151	-0.135	

Correlations between fixed effects for the top-ranked models for *B. violaceus* abundance are found in Table E.4.

Table E.4: Correlation of fixed effects for *B. violaceus* abundance, in the order in which they were presented in Table 2.10.

Model		Fixed effects		
pBvint		Not applicable		
pBvTS		Intercept	Minimum salinity	
	Minimum salinity	-0.902		
	Minimum temperature	-0.890	0.611	
pBvSr		Intercept		
	Native species richness	-0.506		
pBvTSD		Intercept	Minimum salinity	Minimum temperature
	Minimum salinity	-0.903		
	Minimum temperature	-0.891	0.616	
	Dock distance	0.079	-0.100	-0.108
pBvDSr		Intercept	Native species richness	
	Native species richness	-0.596		
	Dock distance	-0.441	0.372	

E.3 Native species correlation tables

Correlations between fixed effects for the top-ranked models for native species richness are found in Table E.5.

Table E.5: Correlation of fixed effects for native species richness, in the order in which they were presented in Table 2.12.

Model		Fixed effects		
		Intercept	Minimum salinity	
natrichSD	Minimum salinity	-0.916		
	Dock distance	-0.188	-0.048	
		Intercept	Minimum salinity	Minimum temperature
natrichTSD	Minimum salinity	-0.540		
	Minimum temperature	-0.945	0.265	
	Dock distance	0.152	-0.104	-0.224
		Intercept	Minimum salinity	NIS richness
natrichSDSr	Minimum salinity	-0.809		
	Dock distance	-0.089	-0.385	
	NIS richness	-0.194	-0.074	0.082

Correlations between fixed effects for the top-ranked models for native species abundance are found in Table E.6.

Table E.6: Correlation of fixed effects for native species abundance, in the order in which they were presented in Table 2.14.

Model	Fixed effects	
natabint	Not applicable	
natabSr	Intercept	
	NIS richness	-0.344
natabSrVar	Intercept	
	NIS richness	-0.794

Appendix F

Variation in shore station trends from 1967–2011

Trends varied between shore stations used for the linear projections in Ch. 3 for both minimum temperature (Table F.1) and minimum salinity (Table F.2).

Table F.1: Linear trends in minimum temperature ($^{\circ}\text{C}$) between shore stations used for the projections from 2011 to 2061. The lowest and highest minima that occurred between 1967–2011 is reported with the year in which it occurred.

Region	Shore station	Linear projection	Lowest minimum (year)	Highest minimum (year)
North Coast	Langara Point	0.34	9.40 (1972)	12.11 (1981)
	Bonilla Island	0.16	9.70 (1985)	13.00 (1997)
West coast of Vancouver Island	Kains Island	0.56	10.61 (1970)	13.92 (1997)
	Amphitrite Point	0.27	11.08 (2001)	13.00 (1997)
Salish Sea	Chrome Island	2.49	10.83 (1972)	15.40 (1998)
	Departure Bay	0.78	11.13 (1972)	15.70 (1990)
	Entrance Island	2.27	11.21 (1972)	16.10 (1990)
	Active Pass	2.84	10.42 (1972)	15.21 (1990)

Table F.2: Linear trends in minimum salinity (‰) between shore stations used for the projections from 2011 to 2061. The lowest and highest minima that occurred between 1967–2011 is reported with the year in which it occurred.

Region	Shore station	Linear projection	Lowest minimum (year)	Highest minimum (year)
North Coast	Langara Point	-0.97	30.21 (2007)	32.00 (19.71)
	Bonilla Island	0.42	29.80 (2011)	31.60 (1989)
West coast of Vancouver Island	Kains Island	-0.04	29.40 (2003)	31.81 (1970)
	Amphitrite Point	1.24	27.72 (1976)	30.90 (1998)
Salish Sea	Chrome Island	1.47	21.80 (1977)	27.31 (1995)
	Departure Bay	0.82	15.91 (2011)	24.60 (2009)
	Entrance Island	3.00	15.34 (1976)	25.1 (1987 & 2009)
	Active Pass	3.99	12.08 (1974)	23.33 (1987)

