# The context-dependent spread and impacts of invasive marine crabs

by

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# Abstract

Following the establishment of a non-native species, there is often speculation about the potential impacts to the native ecosystem. While these early predictions may be necessary for management, they are often based on a general understanding of invasion ecology rather than context-specific research. The unique nature of each introduction event means these generalizations are prone to over- or under-estimating invasive species impacts. This thesis predicts the impacts of invasive marine true crabs (infraorder Brachyura), with a focus on the invasive European green crab (*Carcinus maenas*), using both general 'rules of thumb' and context-specific research. In Chapter 2, I conduct a meta-analysis to demonstrate that while native and invasive crabs typically have a similar overall impact on prey species, some combinations of prey type and experimental design can favour invasive crabs. In Chapter 3, I examine the geographical variability of green crab impacts worldwide. Using green crabs collected from invasive (South Africa and Canada) and native (Northern Ireland) populations, I conduct a comparative functional response experiment to show how the foraging behaviour of an invasive species varies among regions. In Chapter 4, I use an enclosure experiment to determine how the impact of green crabs on eelgrass (*Zostera marina*) ecosystems changes with crab density, and conclude that there is the potential for extensive loss of habitat-forming eelgrass in the presence of high densities of green crabs. In Chapter 5, I explore the issue of site-level variability in the abundance, and therefore potential impact, of green crabs on the west coast of Vancouver Island, British Columbia. I develop a species distribution model to identify small-scale biotic and abiotic predictors of 'hyper-abundant' populations of green crab. The thesis as a whole explores the generalizations often used to predict invasive impacts and prioritize impact mitigation efforts. I find that, for green crabs, generalizations that rely on the origin or specific invasion history of an invasive species are prone to over-estimating impact. However, measures of density or abundance, paired with an understanding of context-specific behaviours, are more likely to produce reliable impact predictions for these invasive species.

**Keywords**: aquatic invasive species; behavioural ecology, ecological impact; ecosystem engineering; marine crustaceans; risk assessment

# Dedication

To my mom, for teaching me to be fearless and for sea turtles.

To my dad, for the happy memories and sea shanties.

To my brother, for always standing beside me on the shore.

To my sister, for her love of nudibranchs and all things marine.

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I have never really been able to believe my luck that my co-supervisors, neither of whom I knew before I showed up at SFU, turned out to be patient, kind, funny, and passionate people, in addition to being world-class scientists. Isabelle and Tom have shepherded me through times of both joy and sadness and all while shaping me into an actual, real scientist. While I am a much better writer now than I was six years ago, I cannot adequately express in writing my gratitude to you both for taking a chance and giving me this opportunity.

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This thesis is dedicated to my parents, who believed I could do anything even when my Kindergarten teacher did not, and my siblings. My mom sent her nerdy 17-year-old daughter to Costa Rica to count sea turtles and I never looked back. My dad inspired me to keep learning always, and this PhD is very much dedicated to his memory. I am blessed with the best siblings in the world. My brother was a good kid, but he is an amazing adult. I cannot imagine the last six years without Cole right there beside me. I am grateful for my little sister every day because she inspires and challenges me, and also makes me laugh harder than anyone. Our shared love of the ocean makes me so happy. All the things Cole, Kate, and I have gone through together are woven into this thesis. Finally, thanks to Bits, Mouse, Pixel and Gizmo for being the best floofs ever.

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# Chapter 1.

# Introduction

> *Nothing happens in contradiction to nature, only in contradiction to what we know of it.*
>
> *Special Agent Dana Scully (X-Files)*

The introduction of non-native species into new areas by humans, whether intentional or not, has been occurring globally for centuries. In some cases, these introductions have led to devastating negative consequences for native ecosystems, including loss of habitat, biodiversity, and ecosystem services (Clavero & Garcia-Berthou 2005, Gallardo et al. 2016). However, not all introduced species successfully establish, and even fewer go on to have detectable impacts on recipient ecosystems (Zenni & Nuñez 2013). These variable outcomes for introduced species is a result of context-dependency.

For an introduced species to establish and spread, it must first be able to tolerate the new physical environment. The species must then successfully negotiate interspecific interactions with a foreign biological community, without the benefit of several thousand years of coevolution with the prey, predators, competitors, and diseases native to the ecosystem (Lockwood et al. 2007). As such, every species introduction could be considered a unique event that creates a new ecosystem. This makes studying and predicting invasive species impacts a challenge and means that the management of invasive species typically relies on either context-specific *post-hoc* explanations or *a priori* generalizations, based on observations of invasions elsewhere (Thomsen et al. 2011). While the former has the benefit of providing information specific to the invaded system, it often arrives too late to be used proactively by management. For example, it took over a decade for researchers to connect collapsing populations of bald eagles (*Haliaeetus leucocephalus*) in northwestern Montana to the introduction of opossum shrimp (*Mysis relicta*) into Flathead Lake. By the time the complex trophic dynamics involved were fully understood, bald eagle numbers had decreased by more than 90% in the area (Spencer et al. 1991). One of the contributing factors to this lag in understanding was that opossum shrimp were assumed to be harmless, based on over 100 similar introductions in similar lakes throughout North America (Spencer et al. 1991). This demonstrates how using generalizations to direct invasive species management may sometimes lead to delayed or inappropriate management actions. To improve invasive species management, there is a need to better understand context-dependency itself and identify both the specific and general properties of invaded systems that are reliable predictors of invasive species impacts (Thomsen et al. 2011).

One of the explanations for invasive species impacts that is often treated as a general property of invaded systems is that invasive consumers will have a greater impact on prey populations than native consumers (Salo et al. 2007). This comes from the prey-naïveté hypothesis which posits that the lack of co-evolution between invasive consumers and native prey puts prey at a disadvantage due to a lack of specifically evolved anti-predator behaviours or defenses (Sih et al. 2010). A classic example of the impact of prey-naïveté is the loss of several endemic bird species after the introduction of the brown tree snake (*Boiga irregularis*) on Guam, an island without native predatory mammals or reptiles (Wiles et al. 1995). The prey-naïveté hypothesis has generated a large body of literature, in part to determine how often and under what circumstances we can expect invasive consumers to have the advantage over native prey (Sih et al. 2010). One way to quantitatively test the universality of prey-naïveté is to use meta-analyses, which converts a large amount of context-specific ecological research into a single common analytical currency – the effect size (Stewart 2010). By comparing effect sizes generated from the scientific literature on invasive species interactions, it is possible to ground-truth some of the common generalizations relied upon to make management decisions.

The identity of the invasive species is another general property often invoked when predicting invader impact (Thomsen et al. 2011). It is reasonable to assume that a species known to be a high-impact invader in one region will behave similarly in other regions. The water hyacinth (*Eichhornia crassipes*) is one such example; once established, this plant has consistently serious impacts for native ecosystems worldwide (Villamagna & Murphy 2010). However, the impacts of most invasive species are spatially variable among regions. While the cause of this variability may lie in regional differences in either the abiotic environment or the native biotic community, the genetic differences between founding populations of the invasive species or the expression of different phenotypic responses to regional conditions can also contribute to the observed impact variability (Melbourne et al. 2007, Kumschick et al. 2015). The only way to isolate genetic, behavioural, or morphological differences among populations of an invasive species is to conduct research on widespread populations in a standardized way. Genetic analyses of globally distributed invasive species are being used with increasing frequency for this reason (Cristescu 2015). Comparative functional response analysis (CFRA) is another tool used to compare the behaviour of geographically different populations of invasive species. CFRA quantifies and standardizes consumptive behaviours so that it is possible to determine whether there is true behavioural variability among different populations of an invasive species, regardless of the context-specific properties of an ecosystem (Dick et al. 2014).

No property of an invaded system is more widely used to predict impact than invader abundance. Impact prediction tools in the invasion ecology literature regularly include a measure of abundance (e.g., the Parker-Lonsdale equation (Parker et al. 1999), the Invader Relative Impact Potential equation (Dick et al. 2017), the TEAS risk assessment method (Leung et al. 2012)). This is because impact severity is expected to increase, linearly or non-linearly, with invader population size (Parker et al. 1999, Byers et al. 2002, Dick et al. 2017). This relationship can be applied at any scale, including locally, as sites with a higher abundance of the invader are more likely to be affected than sites with a lower abundance. By quantifying density-impact relationships between invasive and native species at local scales, it is possible to both predict those impacts as the species grows in population size and to set threshold densities below which an invasive species should be maintained to minimize impact. For example, knowing that damage caused by invasive rabbits (*Oryctolagus cuniculus*) on native vegetation in Australia scales exponentially with rabbit density, it is advisable to suppress rabbit populations to less than 0.5 rabbits ha$^{-1}$ (Mutze et al. 2016).

Using system-specific research, such as density-impact relationships, to successfully mitigate invasive species impacts requires managers to know where and how many individuals of an invasive species are present within a region. This too will be context-dependent, as variation in abiotic and biotic properties among sites will cause species to be distributed unevenly across a heterogenous landscape (Epanchin-Niell et al. 2012). Because collecting relative abundance measures for a species at every site, even over a small portion of an invaded range, is beyond the scope of most management programs, alternative means of predicting site-level abundance are needed. One such approach that is increasing in utility is species distribution modelling (SDM), which can be used to understand how species abundance varies across a landscape, based on the availability of relevant abiotic and biotic characteristics (e.g. food sources, predators, access to cover, anthropogenic features) (Guisan & Thuiller 2005). For invasive species in particular, this method can provide surprising insights about what drives their abundance (and possibly impact). In France, SDM identified a strong association between ornamental, non-native trees in an urban environment and the highly invasive ring-necked parakeet (*Psittacula krameri*) (Le Louarn et al. 2018). This relationship had been previously underestimated because earlier studies in London, England found parakeet abundance was best predicted by access to bird feeders (Le Louarn et al. 2018). This highlights how the uniqueness of every invaded system makes creating useful generalizations difficult.

This thesis aims to look at the reliability of shared properties, of both invasive species and recipient ecosystems, for predicting and thus informing management for invasive species. I hope to identify which of these properties may mislead managers into over or under-estimating the impacts of an invader, and which are useful, general properties of high-impact invasions. While context-dependency is the common theme throughout this thesis, each chapter uses a different analytical approach to dissect context-dependent spread, impact, and potential management of invasive marine crabs (infraorder Brachyura) worldwide. As a group, marine crabs are common invasive species but, like most invasive marine invertebrates, are not well-researched (Carlton et al. 2011). In Chapter 2, I use meta-analyses to determine if invasive crabs universally have a greater impact on native species abundance than native crabs. While there was no universal difference, the type of interaction (i.e., direct or indirect), the prey species, and experimental design can all influence the predatory impacts of invasive crab species compared to native ones. In Chapter 3, I investigate why the globally invasive European green crab (*Carcinus maenas*) can be a significant, wide-spread invader in some regions and a relatively inconsequential one in others. I used CFRA to compare the predatory behaviour of European green crabs collected from four populations from around the world representing both native and invaded locations. Chapter 4 then looks at how the impacts of invasive green crab in British Columbia, Canada scale with density. I was particularly interested in impacts in native eelgrass (*Zostera marina*) ecosystems, given the importance of eelgrass as biogenic habitat and its susceptibility to disturbance. In Chapter 5, I use SDM to identify the site-level biotic and abiotic characteristics that affect green crab abundance along the coast of British Columbia. This investigation into the context-specific drivers of abundance at the site level will help inform management efforts for this species within British Columbia. In the last chapter, I reflect on the overall reliability of generalizations for predicting impacts and advising management, especially for new and emerging invasive species, given the ubiquity of context-dependence.

# Chapter 2.

# Contrasting ecological impacts of native and non-native marine crabs: a global meta-analysis[1]

## Abstract

Concern about the impacts of invasive species on invaded communities is often linked to the expectation that invasive consumers will be more effective at using resources than native ones. Many invasive marine crabs (infraorder Brachyura) are regarded as particularly capable consumers; however, native crabs can also exert significant influence on community structure. We used marine crabs as a focal group to test whether non-native consumers have greater impacts on native prey populations than native ones by conducting a systematic review and meta-analysis of 834 crab foraging experiments. In addition to the effect of crab origin (non-native or native) on prey abundance, we examined the effects of interaction type (direct or indirect), prey type, and experimental design. Overall, direct consumption by non-native crabs did not reduce prey abundance more than predation by native crabs, although the magnitude of reductions in prey abundance varied with prey type and experimental design. Indirect interactions with crabs (i.e., through trophic cascades with crabs as the initiators) generally increased the abundance of native species. The direct and indirect impacts of non-native crabs were significantly greater than those of native crabs on primary producers and in simplified experiments with low species diversity. Thus, detecting differences between native and non-native crabs may be heavily influenced by experimental design. Importantly, we found few studies that considered direct interactions (competitive or predatory) between native and non-native crabs. These interactions should be a focus of future research because they could greatly alter consumption rates and overall prey mortality in the wild.

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[1] A version of this chapter appears as Howard, BR, Therriault, TW, & Côté IM 2017. Contrasting ecological impacts of native and non-native marine crabs: a global meta-analysis. Marine Ecology Progress Series 577: 93-103.

# Introduction

Invasions by non-native species are a leading cause of population declines and biodiversity loss worldwide (Sala et al. 2000, Clavero et al. 2009, Butchart et al. 2010). Impacts can occur due to changes in species interactions, including competition (Kenward & Holm 1993, Shochat et al. 2010, Martin et al. 2010), parasitism (Daszak et al. 2000), and disease (Prenter et al. 2004), with the direct and indirect trophic effects of invasive consumers probably the best-studied mechanism for these declines (Lockwood et al. 2007). For example, the introduction of the brown tree snake (*Boiga irregularis*) to the island of Guam, which previously lacked any predatory mammals or reptiles, resulted in massive population declines of the island's avifauna due to predation by this novel predator species (Rodda et al. 1992, Wiles et al. 1995). Similar case studies, including the invasion by Indo-Pacific lionfish (*Pterois volitans*) in the Caribbean (Green et al. 2012) and feral cats (*Felis silvestris catus*) in New Zealand (Dowding & Murphy 2001), reinforce the popular narrative of the "voracious invasive" (Salo et al. 2007).

However, non-native consumers are not universally detrimental to native prey biodiversity. Some non-native consumers have negligible or undetectable effects on native prey populations (Parker et al. 1999). For instance, the predatory impacts of invasive cane toads (*Rhinella marinus*) in Australia have been largely imperceptible, despite the species' formidable reputation as a predator (Shine 2010). Invasive rats (*Rattus* spp.) can have highly variable impacts on seabird colonies depending on the life history traits of the prey species (Jones et al. 2008). In other cases, non-native species may have minimal impact if they behave similarly to native ecological equivalents (Greenlees et al. 2006, Lepori et al. 2012).

Two of the most prominent mechanisms underpinning the observed variability in impacts of invasive consumers are naïveté by both prey and predators and species distinctiveness (Ricciardi & Atkinson 2004, Lockwood et al. 2007, Sih et al. 2010). Native prey might not recognize non-native consumers as being dangerous (i.e., prey naïveté), but conversely non-native consumers might not perceive native prey as being edible (i.e., predator naïveté), because of a lack of co-evolutionary history (Sih et al. 2010). Both native prey and non-native consumers might therefore exhibit inappropriate avoidance/escape and attack behaviours, respectively, during encounters, leading to variable impacts. In addition, the extent to which naïveté influences the impact of non-native predators on native prey will often be mediated by distinctiveness, which describes how novel an introduced species is in a recipient ecosystem (Ricciardi & Atkinson 2004). Typically, the more distinctive an introduced consumer is, either taxonomically or functionally, from native consumers, the greater its impacts (Ricciardi & Atkinson 2004, Thomsen et al. 2014). The variability in impacts of invasive consumers on prey abundance and/or biodiversity makes predicting the effects of new and emerging invasive species a significant challenge (Parker et al. 1999, Byers et al. 2002, Leung et al. 2012).

One group of invasive consumers of growing concern is marine crabs (infraorder Brachyura; Breen and Metaxas 2012). International shipping has been a vector for crab invasions since the 1800s (Carlton & Cohen 2003). A survey of publicly accessible invasive species databases and select publications shows that the frequency of new introductions and detections of non-native marine crabs continues unabated (Fig. 2.1; Table A.1), creating a need for a better understanding of their potential impacts (Grosholz & Ruiz 1996, Breen & Metaxas 2012). Non-native crabs can have significant negative direct and indirect effects on native populations. For example, the globally invasive European green crab (*Carcinus maenas*) is recognized as an effective shellfish predator and has been implicated in large declines of some shellfish populations (Glude 1955, Welch 1968, Grosholz et al. 2000). Similarly, the Asian shore crab (*Hemigrapsus sanguineus*) both preys upon and competes with native crab species (e.g., fiddler crab, *Uca pugilator,* and flatback mud crab, *Eurypanopeus depressus*) along the east coast of the United States and has been implicated in large declines in native crab abundance (Jensen et al. 2002, Kraemer et al. 2007, Peterson et al. 2014, Griffen & Riley 2015). While the indirect effects of non-native species, including marine crabs, are not as well studied (White et al. 2006), there is some evidence for trophic cascades. For example, the European green crab can indirectly reduce mortality of sessile invertebrates (i.e., barnacles and mussels) and primary producers (i.e., cordgrass *Spartina alterniflora*) through direct consumption of intermediate consumers (Trussell et al. 2003, 2006, Griffen & Byers 2009, Bertness & Coverdale 2013).

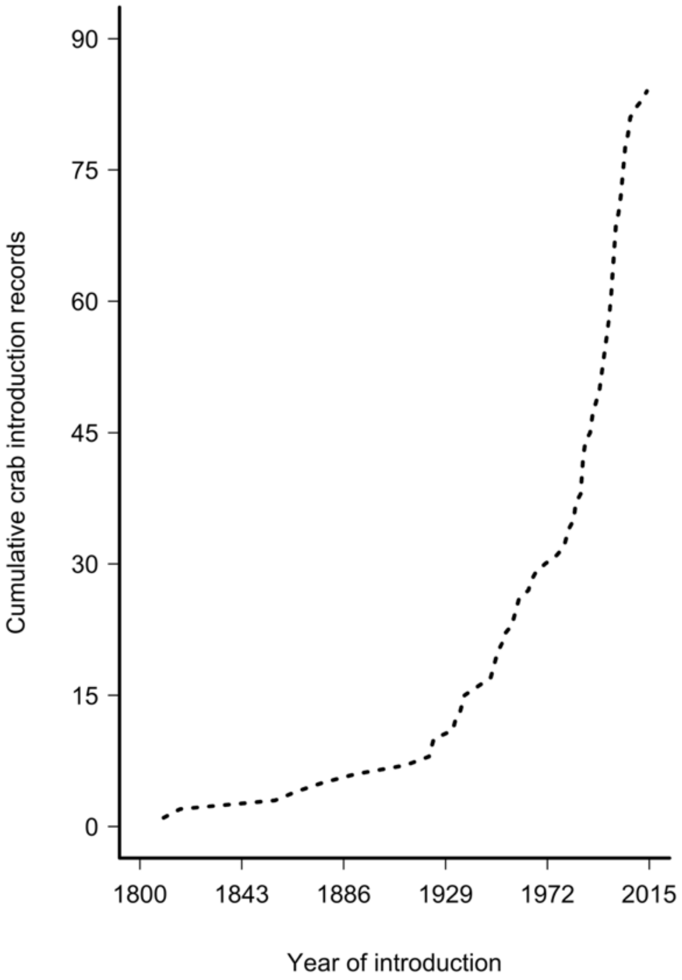

**Figure 2.1 Cumulative number of newly recorded introductions of marine and euryhaline crab species worldwide.**
Data from national (Australia, New Zealand, USA, South Africa, United Kingdom), regional (Europe), and international (IUCN/SSC Invasive Species Specialist Group) online databases for invasive species monitoring as well as select publications (see Table A.1 for details).

While studies support the general notion that non-native crabs can negatively impact prey populations, they do not address how these effects compare to those of native crabs. Recent meta-analyses have found that invasive consumers tend to have a greater negative impact on prey abundance than native consumers (Salo et al. 2007, Paolucci et al. 2013). However, the majority of studies in these meta-analyses were derived from terrestrial and freshwater ecosystems (100% in Salo et al., 2007; 85% in Paolucci et al. 2013), where the impact of predators on their prey is usually less marked than in marine systems, especially intertidal areas (Sih et al. 1985). Marine crabs in particular are known to play important roles in structuring intertidal and near-shore marine communities (Boudreau & Worm 2012). For example, within its native range, European green crab can significantly reduce bivalve abundance and has a strong effect on temporal variation in these populations (Richards et al. 1999). Similarly, on the east coast of the United States, the native blue crab (*Callinectes sapidus*) is considered a keystone predator, having population-level effects on native mud crabs (*Panopeus herbstii*), oyster (*Crassostrea virginica*), and cordgrass through both direct and indirect trophic interactions (Silliman & Bertness 2002, Grabowski et al. 2008, Hill & Weissburg 2013). Thus, native crabs might have both direct and indirect ecological effects that are as large as (or larger than) those of non-native crabs, despite the general expectation that non-native species will have larger impacts.

To estimate the relative ecological impacts of native and non-native crabs, we conducted a systematic review and meta-analysis of the substantial experimental literature on crab foraging. We asked three main questions. First, do crabs have different effects on the abundance (as a proxy for survival) of species with which they interact directly (i.e., prey) and indirectly (i.e., via potential trophic cascades)? We expected that prey abundance would decrease in direct interactions and increase in indirect interactions with predatory crabs. Second, do native and non-native crabs differ in their effects on the abundance of species with which they interact? If the narrative of the ‘voracious invasive’ holds, then non-native crabs should have larger negative effects on their prey than native crabs (Salo et al. 2007), but it is not clear whether this difference will reverberate across multiple trophic levels (i.e., in indirect interactions) (White et al. 2006). Third, are certain prey types more susceptible to predation by non-native than native crabs? Assuming no difference among prey in capacity to recognize non-native predators, we predicted that prey, especially those with limited escape abilities, might be more vulnerable to non-native crab predation (e.g., Sih et al. 2010, Grason & Buhle 2016).

# Materials and methods

## Literature search, selection criteria, and data extraction

We searched the ecological literature for experiments quantifying the direct and indirect impacts of crabs on their prey. Two online databases, the Web of Science (WOS; ‘all years’ ending December 2016) and the Aquatic Sciences and Fisheries Abstracts

(ASFA; ‘all years’ ending December 2016), were searched using keyword combinations of crab* + predat* (to capture predation, predatory, predator) + compet* (to capture competition, competitor, competitive) + marine. In addition, we looked at relevant cited literature from the papers we found. A total of 5,429 abstracts were returned. After removing duplicates, conference proceedings, and irrelevant search results, the remainder (556 abstracts) were systematically reviewed (Fig. A.1, Table A.2).

To be included in our meta-analysis, each study was required to meet the following criteria. (1) The focal crab species was a true crab (infraorder Brachyura) in its adult form and was a near-shore or intertidal species. (2) The study examined the interspecific effect of crab presence (i.e., studies of cannibalism were excluded). (3) Crab presence had a potential direct or indirect effect on the survival of another species through consumption (i.e., parasitic interactions were excluded). (4) Crab presence was manipulated (either directly or using spatial/temporal gradients) so there was a ‘no-crab’ control. (5) The response of the species affected by crabs was measured in terms of abundance (e.g., density, biomass, percent cover) either removed or remaining by the end of the experiment (prey abundance at the start of experiments was always assumed or shown to be equal across treatments). Finally, (6) the study reported the required data to calculate an effect size for each species affected by crabs.

We considered each responding species’ abundance reported in a study as an individual experiment (see section on non-independence below). For each experiment the mean abundance of responding species, standard deviation, and sample size for both with- and without-crab treatment groups were recorded. When the data required were only available from figures, we used the program GraphClick v 3.0.2 to extract values for the parameters needed. When standard errors or confidence intervals were provided, we converted them to standard deviations.

We recorded as potential moderators of the ecological effect of crabs whether the crab species was native or non-native, whether the interaction was direct or indirect, the functional group of the responding species, and details about the experimental design (Table A.3). Responding species were categorized into one of five functional groups based on habitat and mobility: (1) primary producers, including seaweeds, seagrasses, and phytoplankton; (2) sessile invertebrates, including mussels, oysters, barnacles, and encrusting epifauna; (3) mobile epifauna, including other decapods, gastropods, scallops, and echinoderms; (4) mobile infauna, including clams, marine worms, and infaunal crustaceans (amphipods and isopods); and (5) vertebrates, which was limited to birds and fish (Table A.3). Because experimental design can strongly affect the results of a study (Fernandes et al. 1999), we categorized designs based on similarity to natural conditions. The five categories ranged from ‘natural experiments’, which used spatial or temporal variation in crab presence to measure effects on responding species abundance in the field, to increasingly precisely manipulated laboratory experiments where a crab predator interacted with a single responding species (Table A.3).

Two additional factors could be important in determining the impacts of non-native species. First, time since arrival in a new area has been proposed as a predictor of the potential impacts of marine invaders (Rossong et al. 2012, Byers et al. 2015). Unfortunately, there was insufficient information on the timing of marine crab introductions at the precise locations at which experiments were conducted to consider this variable in our analyses. Second, body size is an important determinant of both predatory and competitive interactions in crabs (Boudreau et al. 2013, Hill & Weissburg 2013, Tina et al. 2015). To address whether there was a bias towards larger non-native marine crabs than native ones we compiled information on average crab carapace width (mm) for every species in the dataset from a variety of sources (Table A.4) and compared mean sizes of native and non-native species with a Mann-Whitney test.

## Data analysis

We generated individual effect sizes for each comparison using the standardized mean difference (i.e., Hedge’s *g*) of the responding species’ abundance at the end of an experiment, weighted by the inverse of the variance for each. Hedge’s *g* was calculated as the mean difference in abundance at the end of an experiment between treatments without and with crab, divided by the pooled standard deviation across groups (Viechtbauer 2010). This metric is preferable to ratios when means can have values of zero (Hedges et al. 1999), which was the case here. Abundance at the end of each experiment was reported either as number remaining or number consumed. If crabs have an effect on a responding species, the former measure would yield a positive value, while the latter would yield a negative one. For consistency and to make the results more intuitive, we reversed the sign of the effect size for experiments reporting remaining abundance so that across all studies, negative values denoted a decline in responding species abundance in the presence of crabs. For all mean effect sizes, we calculated 95% confidence intervals (CI). Mean effect sizes are considered to be significant when the CI does not overlap zero.

The direct and indirect interactions of crabs with responding species are expected to have opposite effects on species abundance, i.e. decreasing the abundance of prey consumed, and increasing the abundance of species released from interactions with those prey. We first tested the effect of interaction type (fixed factor: direct or indirect) on Hedge's *g* using a mixed-effects model, with the source publication (study ID) included as a random effect to control for multiple experiments from individual studies. Because the results supported our expectation (see Results), we considered direct and indirect interactions separately for all subsequent analyses, including testing for publication bias (see below). We conducted all analyses in R, using the rma() function within the *metafor* package to generate models (R Development Core Team 2008, Viechtbauer 2010).

We conducted a two-step analysis (e.g., Magrach et al. 2014; Stein et al. 2014; Gallardo et al. 2016). We first ran a set of single-moderator mixed-effect models to estimate how the effect of crab presence on Hedge's *g* varied with (1) crab origin (fixed factor: native or non-native), (2) responding species functional group (fixed factor: five categories described above), and (3) experimental design (fixed factor: five categories, Table A.3). Source publication (study ID) was included as a random effect. Then we used a new set of mixed-effects models to assess the difference between native and non-native crabs specifically by examining interactions between crab origin and, separately, prey functional group and experimental design (with study ID included as a random effect in all cases). For all models we estimated residual heterogeneity using the restricted maximum-likelihood estimator $\tau^2$ and used $Q_E$ to test for significance. To determine if there were significant differences between the levels of the categorical moderators, we used Cochran's Q-test ($Q_M$) with the 'mods' argument in *metafor* to ignore the intercept (Viechtbauer 2010). To determine whether the effect of native and non-native crabs differed in the interaction models we used Wald-type chi-squared tests (Viechtbauer 2010).

## Testing for non-independence and publication bias

A common problem with meta-analyses is non-independence. In our study, non-independence arose from three main sources, which we tried to minimize. First, in some studies, the same control group was used as the baseline for multiple experimental treatments. On average, there were 1.9 (+/- 2.3) experiments per control treatment in our dataset. In such cases, we used only the lowest and highest density treatments (and their shared control) to ensure that the minimum and maximum impacts were captured and disregarded all intermediate treatments (Romero et al. 2015). Second, in longitudinal studies, abundance was reported as a time-series. In these instances, we used only the last point of the series (Romero et al. 2015). Third, studies often contributed more than one experiment to the dataset. Studies in our dataset contributed an average of 6.1 (+/- 7.5) experiments. The first and third sources of non-independence were largely attributed to a few large enclosure studies that examined the response of multiple species to crab presence and did not use fully factorial experimental designs. We therefore cross-validated our data using a leave-one-out approach to see if any individual experiments or entire studies significantly influenced the overall effect size of direct and (separately) indirect interactions. To do so, we systematically removed each study and each individual experiment from the direct and indirect datasets and recalculated the overall effect size of the random-effects model. An influential experiment or study should change the overall effect size significantly when left out.

Another problem with meta-analyses is the disproportionate publication of significant results leading to overestimates of the overall effect size. Publication is expected to be biased against smaller studies, which are more likely to find non-significant results (Borenstein et al. 2009). We tested for potential publication bias in the direct and indirect interactions datasets separately. We first examined funnel plot asymmetry, which suggested a dearth of non-significant, small studies in both datasets (Fig. A.2). Instead of using a trim-and-fill method (Duval & Tweedie 2000), which can be unduly influenced by one or two anomalous experiments (Borenstein et al. 2009), we ran cumulative meta-analyses where studies were added sequentially from most to least precise, based on variance (Fig. A.3). As variance typically increases as studies become smaller (i.e., less within-study replication), variance can be used to identify the threshold at which small studies start to influence the overall effect size (Borenstein et al. 2009). These thresholds were estimated visually to be at variance values of 0.73 for studies of direct effects of crabs, and 1.02 for studies of indirect effects. Studies with variances smaller than these thresholds (n = 394, or 61% of the complete dataset, for direct effects; n = 148, or 79% of the complete dataset, for indirect effects) were then retained in “large-studies-only” datasets, and all analyses were repeated on these restricted datasets (Borenstein et al. 2009). Given that the results from analyses of the full and “large-studies-only” datasets were similar (Table A.5), and that Rosenthal’s fail-safe numbers (direct: 321,152; indirect: 20,412) were large relative to sample sizes for the full datasets, we present the results from the full datasets here. However, we caution the reader that if the funnel plot asymmetries are due to bias, the effect sizes we report might be slightly inflated.

Finally, because studies of European green crab contributed more than one-third (38%) of experiments on non-native crabs, we repeated the analyses omitting this species. There were few differences in results between the restricted and full datasets, which we attribute mainly to increased variance owing to smaller sample sizes (Table A.6).

# Results

## Overview

A total of 137 papers, published between 1977 and December 2016, met all selection criteria, contributing 834 individual estimates of the effect of non-native (35%) and native (65%) crabs on the survival of responding species (Table A.2). The most commonly studied crab species was the European green crab (38%). It was also the only species to have experiments conducted in both its native and non-native range. The most commonly studied prey types were sessile invertebrates (32%) and infauna (29%). All experimental designs were well represented (between 18% – 31%), with the exception of natural field experiments (3%). Experiments originated from all continents except Asia and Antarctica. However, northern temperate latitudes (> 23° N) (88%) and North America (65%) had the greatest representation in the dataset. The majority of experiments tested the direct (consumptive) effect of crabs (78%).

There was no significant difference in mean carapace width between native (mean ± 1 SD: 60.5 mm ± 49.7 mm) and non-native crab species in the database (34.4 mm ± 21.3 mm; Mann-Whitney test, U = 132.0, n = 55, p = 0.37).

Direct (n = 647) and indirect (n = 187) interactions between crabs and responding species had significantly different effects on the abundance of responding species ($Q_M$ = 176.72, df = 1, $p < 0.01$). As expected, direct interactions (i.e., consumption by crabs) had a significant, negative effect on prey abundance ($g$ = -1.06, 95% CI = -1.25 to -0.88, $p < 0.01$) while indirect interactions had a significant, positive effect ($g$ = 0.34, 95% CI = 0.11 to 0.58, $p < 0.01$).

The sequential omission of two large enclosure studies reporting direct interactions changed the magnitude of the overall effect size [without Griffin et al. (2008): $g$ = -1.26, 95% CI = -1.45 to -1.07; without Fernandes et al. (1999): $g$ = -1.25, 95% CI = -1.44 to -1.06], but the confidence intervals in both cases still encompassed the overall effect size of the complete dataset. The same was observed for two large studies of indirect interactions [without Tyrrell et al. (2006): $g$ = 0.77, 95% CI = 0.40 to 1.15; without Matassa and Trussell (2011): $g$ = 0.67, 95% CI = 0.34 to 1.00]. However, because the direction and statistical significance of the models were not changed in either case, we chose to leave these studies in the datasets for further analyses.

## Direct interactions

Overall, non-native crabs did not significantly reduce the abundance of responding species any more than native ones ($Q_M$ = 0.25, df = 1, p = 0.61; Fig. 2.2). Prey abundance was significantly reduced by crabs in all experiments, with the strongest effects occurring in laboratory-based experiments (i.e., mesocosms and single-species predation experiments) ($Q_M$ = 46.96, df = 4, $p < 0.01$; Fig. 2.2). Mesocosm experiments were the only design type where native and non-native crab had significantly different effects, where non-native crabs reduced prey abundance more than native crabs (Table 2.1).

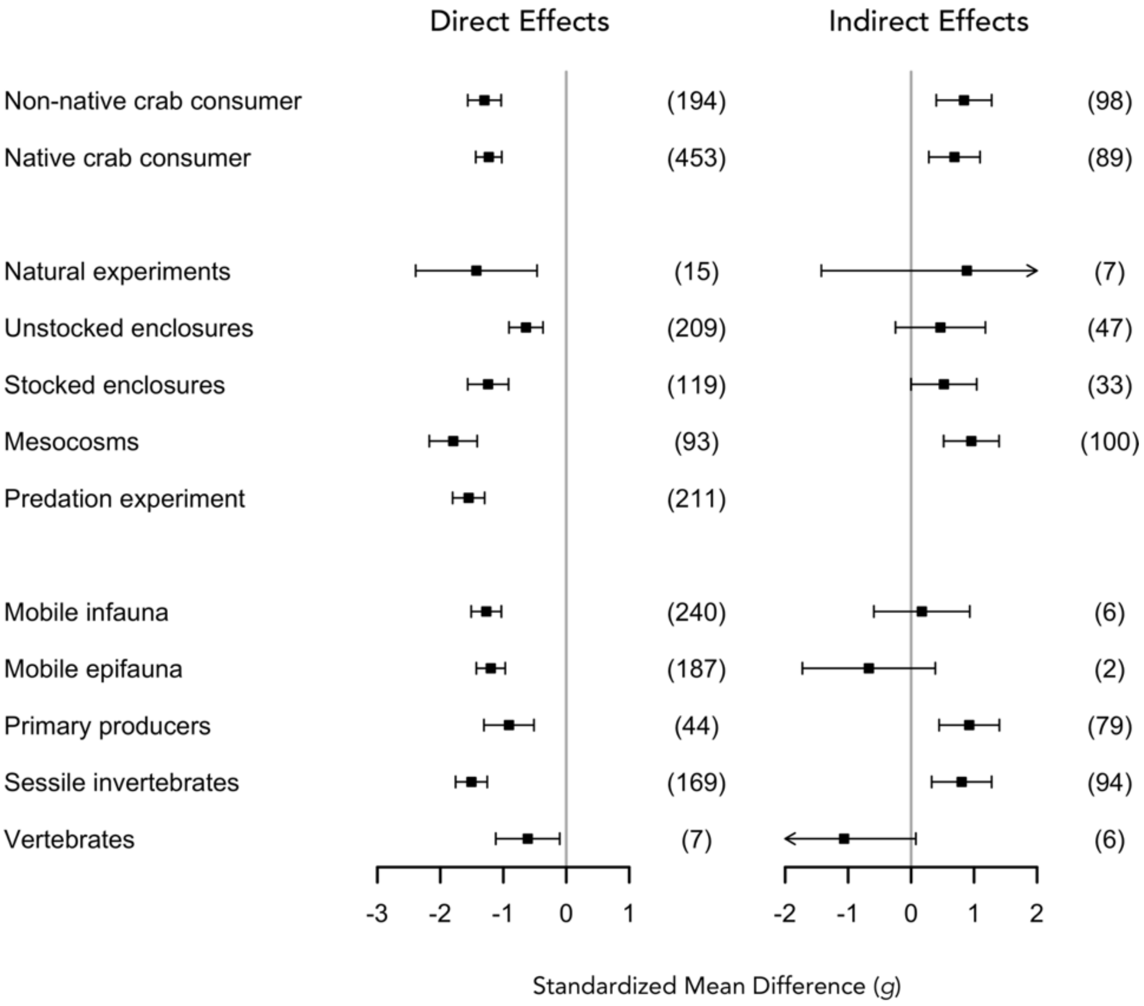

**Figure 2.2 Weighted average effect sizes (Hedge's *g*) and 95% confidence intervals from models of relative abundance of species involved in direct and indirect interactions with crabs.**

Effect sizes for each level of three moderators are shown: crab origin, experimental design, and prey type. Negative effect sizes indicate lower abundance of responding species in treatments with crabs than in treatments without crabs. Effect sizes are considered significant when confidence intervals do not overlap zero.

**Table 2.1 Results of mixed-effects models of species abundance after direct (i.e., consumptive) interactions with crabs.**

| **Moderator** | | ***g*** | **$\text{CI}_{\text{lower}}$** | **$\text{CI}_{\text{upper}}$** | **n** | **$Q_M$** | **p** |
|---|---|---|---|---|---|---|---|
| **Model: Crab origin * Experimental design** | | | | | | | |
| Natural experiments | Non-native | -1.67 | -3.31 | -0.03 | 4 | 0.13 | 0.72 |
| | Native | -1.30 | -2.48 | -0.12 | 11 | | |
| Unstocked field enclosures | Non-native | -0.59 | -0.96 | -0.23 | 57 | <0.01 | 0.95 |
| | Native | -0.61 | -0.93 | -0.28 | 152 | | |
| Stocked field enclosures | Non-native | -1.46 | -1.88 | -1.05 | 59 | 0.59 | 0.44 |
| | Native | -1.29 | -1.69 | -0.88 | 60 | | |
| Lab mesocosms | Non-native | -2.34 | -2.95 | -1.73 | 8 | **4.96** | **0.03** |
| | Native | -1.53 | -1.99 | -1.06 | 85 | | |
| Lab predation experiment | Non-native | -1.52 | -1.88 | -1.16 | 66 | 0.04 | 0.84 |
| | Native | -1.56 | -1.87 | -1.25 | 145 | | |
| **Model: Crab origin * Prey functional group** | | | | | | | |
| Mobile infauna | Non-native | -1.40 | -1.74 | -1.06 | 82 | 3.14 | 0.08 |
| | Native | -1.06 | -1.33 | -0.78 | 158 | | |
| Mobile epifauna | Non-native | -0.75 | -1.11 | -0.39 | 31 | **9.45** | **<0.01** |
| | Native | -1.35 | -1.60 | -1.10 | 156 | | |
| Sessile invertebrates | Non-native | -1.71 | -2.06 | -1.37 | 70 | 1.35 | 0.25 |
| | Native | -1.50 | -1.79 | -1.21 | 99 | | |
| Primary producers | Non-native | -1.37 | -1.94 | -0.79 | 10 | **4.80** | **0.03** |
| | Native | -0.48 | -1.04 | 0.08 | 34 | | |
| Vertebrates | Non-native | 0.00 | -0.62 | 0.63 | 1 | **11.62** | **<0.01** |
| | Native | -1.94 | -2.88 | -1.00 | 6 | | |

All models considered crab origin (non-native or native) and one moderator (experimental design or prey type), and the interaction between the two, with study as a random factor. Weighted average effect sizes (Hedge's *g*), i.e. the standardized mean difference in prey abundance when a crab consumer was present vs absent in an experiment, are considered significant when confidence intervals (CI) do not overlap zero. P-values refer to pairwise Wald-type chi-squared ($Q_M$) comparisons between non-native and native crabs for each moderator level; significant values ($p < 0.05$) are shown in bold.

Although all prey types were significantly negatively affected by crab predation (Fig. 2.2), there were significant differences in effect sizes among prey functional groups ($Q_M$ = 19.96, df = 4, $p < 0.01$). Direct predation by non-native crabs reduced the abundance of primary producers significantly more than direct predation by native crabs, while direct predation by native crabs reduced the abundance of mobile epifauna and vertebrates significantly more than non-native crabs (Table 2.1). However, the effect on vertebrates arises from very small sample sizes (Table 2.1). There were no other differences between native and non-native crabs in consumption of other prey types (Table 2.1).

## Indirect interactions

Overall, the abundance of species interacting indirectly with crabs increased in the presence of crabs (i.e., *g* was positive); however, there was no significant difference in effect sizes between native and non-native crabs ($Q_M = 0.45$, df = 1, $p = 0.50$; Fig. 2.2).

The impact on responding species abundance did not differ significantly among experimental designs ($Q_M = 5.63$, df = 3, $p = 0.13$; Fig. 2.2). Mesocosm experiments yielded the largest and only statistically significant indirect effect on responding species abundance ($p < 0.01$; Fig. 2.2). It was not possible to compare the indirect effects of non-native and native crabs in natural field experiments because of the absence of such studies for native crabs. The only difference in indirect effects between native and non-native crabs was for unstocked field enclosures, where non-native crabs increased the abundance of responding species significantly more than native crabs (Table 2.2).

**Table 2.2 Results of mixed-effects models of species' abundance after indirect (i.e., via trophic cascade) interactions with crabs.**

| Moderator | | g | $CI_{lower}$ | $CI_{upper}$ | n | $Q_M$ | p |
|---|---|---|---|---|---|---|---|
| **Model: Crab origin * Experimental design** | | | | | | | |
| Natural experiments | Non-native | 0.89 | -1.20 | 2.97 | 7 | - | - |
| | Native | - | - | - | 0 | | |
| Unstocked field enclosures | Non-native | 1.66 | 0.75 | 2.57 | 24 | **12.16** | **<0.01** |
| | Native | -0.67 | -1.61 | 0.27 | 23 | | |
| Stocked field enclosures | Non-native | 0.57 | 0.00 | 1.16 | 21 | 2.96 | 0.09 |
| | Native | -0.09 | -0.79 | 0.62 | 12 | | |
| Lab mesocosms | Non-native | 0.83 | 0.32 | 1.33 | 46 | 0.86 | 0.36 |
| | Native | 1.06 | 0.61 | 1.51 | 54 | | |
| **Model: Crab origin * Prey functional group** | | | | | | | |
| Mobile infauna | Non-native | 0.23 | -0.81 | 1.26 | 4 | 0.86 | 0.35 |
| | Native | 0.91 | -0.21 | 2.02 | 2 | | |
| Mobile epifauna | Non-native | -0.33 | -1.43 | 0.77 | 2 | - | - |
| | Native | - | - | - | 0 | | |
| Sessile invertebrates | Non-native | 1.06 | 0.55 | 1.57 | 60 | 0.50 | 0.47 |
| | Native | 1.24 | 0.65 | 1.82 | 34 | | |
| Primary producers | Non-native | 1.95 | 1.21 | 2.69 | 28 | **13.65** | **<0.01** |
| | Native | 0.16 | -0.43 | 0.76 | 51 | | |
| Vertebrates | Non-native | -0.99 | -2.38 | 0.40 | 4 | <0.01 | 0.95 |
| | Native | -1.08 | -3.44 | 1.28 | 2 | | |

All models considered crab origin (non-native or native) and one of either experimental design or prey type, and the interaction between origin and the focal moderator, and study as a random factor. Weighted average effect sizes (Hedge's *g*), i.e. the standardized mean difference in prey abundance when a crab consumer was present vs absent in an experiment, are considered significant when confidence intervals (CI) do not overlap zero. P-values refer to pairwise Wald-type chi-squared ($Q_M$) comparisons between non-native and native crabs for each moderator level; significant values ($p < 0.05$) are shown in bold. Empty cells indicate there were no data available to test the interaction for that particular level of the moderator and origin combination.

The indirect effect of crabs varied among prey types ($Q_M = 18.43$, df = 4, $p < 0.01$; Fig. 2.2). The abundance of both sessile invertebrates (e.g., barnacles) ($p < 0.01$) and primary producers ($p < 0.01$) increased the most in the presence of crabs, compared to treatments without crabs (Fig. 2.2). There was a significant difference between the indirect effects of native and non-native crabs on the abundance of primary producers, with non-native crabs having a larger positive effect than native crabs (Table 2.2).

## Discussion

Non-native consumers were expected to have larger negative impacts on native prey abundance than native ones (Salo et al. 2007, Paolucci et al. 2013, Alexander et al. 2014, Thomsen et al. 2014). In general, our meta-analysis does not support this expectation. Regardless of whether the interactions between crabs and prey species were direct (e.g., predation) or indirect (e.g., via trophic cascades), we could not detect an overall difference in abundance of responding species between native and non-native crabs. Although some differences between native and non-native crabs arose in experiments with specific experimental designs and prey types, they did not consistently point to non-native crabs having greater impacts.

We had predicted that the abundance of species that interact directly with predatory crabs would decrease, but that species interacting indirectly with a crab predator would benefit. These predictions were supported. Direct effects were always strongly negative, regardless of crab origin, prey type, or experimental design (Fig. 2.2), which is consistent with our understanding of marine crabs as important generalist predators in nearshore and intertidal ecosystems (Boudreau & Worm 2012). Overall indirect effects on the abundance of responding species were positive but were more variable among experimental designs and prey types than direct effects (Fig. 2.2). This is consistent with the notion that indirect effects are typically harder to predict, test, and detect than direct effects (White et al. 2006). Furthermore, indirect impacts are not always manifested as changes in prey survival or abundance, which was the metric used here. Indirect effects of consumers are sometimes detectable as size shifts (Peterson et al. 2014) and in phenotypic and behavioural adaptations of prey (Freeman & Byers 2006, Brookes & Rochette 2007, Flynn & Smee 2010, Whitlow 2010), neither of which could be examined here.

Generally, non-native crabs had a similar impact on the abundance of responding species as native crabs, regardless of whether the interaction was direct or indirect. This is contrary to recent meta-analyses comparing other taxa of non-native and native consumers. These studies found that the effects of non-native species were consistently two to three times larger than those of native species and invoked prey naïveté and novelty of the non-native consumer as potential explanations (e.g., Salo et al. 2007; Paolucci et al. 2013). The converse mechanisms, i.e. limited prey naïveté and low distinctiveness of non-native crab species in recipient communities, may explain why non-native and native crabs appear to have similar impacts. Most nearshore marine communities, except at the most polar latitudes, have co-evolved alongside crab-like consumers (Aronson et al. 2015). This ubiquity may make it less likely for a non-native crab to be taxonomically or functionally distinct from native crab species. From the native prey's perspective, a novel crab consumer may therefore not represent a particularly significant adaptive challenge. Indeed, the rapid responses of formerly naïve prey species to novel crab predators has been demonstrated experimentally for both European green crab (Edgell et al. 2009) and Asian shore crab (Freeman & Byers 2006).

Prey type influenced the effect of direct interactions with crabs. The abundance of all prey groups was significantly reduced by direct predation from crabs, but with some variation among groups. Within prey groups, the extent of these reductions was similar regardless of crab origin, with the exception of primary producers and mobile epifauna. Primary producers were disproportionally affected by non-native crabs, although this result is based on a relatively small sample size. In contrast, the abundance of mobile epifauna was more negatively affected by native crabs. Due to the wide variety of prey species encompassed in the 'mobile epifauna' functional group, it is unlikely that this pattern is driven by a single mechanism. However, it could suggest predator naïveté, where non-native crabs are unfamiliar with the anti-predator defenses and escape responses of novel prey species and therefore can consume less than native crabs (Sih et al. 2010). Our prediction that sessile prey would be the most vulnerable to non-native crab predation due to lack of an active behavioural escape response (Vermeij 1987) was not supported. The similarity in direct effects of native and non-native crabs on this group may indicate that sessile prey, particularly those that rely on shells as a mechanical defense (e.g., mussels), are adapted to crushing predators, regardless of crab origin.

Prey type also influenced the effect of indirect interactions with crabs. In contrast to direct interactions, the effects of indirect interactions with crabs were more variable, with some prey types responding positively to the presence of predatory crabs and others not responding at all. Primary producers and sessile invertebrates benefited the most from crab presence. This result is probably explained by the fact that sessile species are particularly susceptible to consumers (Sih et al. 2010) and they were often included in studies focusing on tri-trophic cascades where crabs preyed upon an intermediate consumer, thus relaxing consumption on sessile species at the lowest trophic level. As with direct effects, there was a significant difference between native and non-native crabs in their indirect effect on primary producers, with non-native crabs associated with a larger increase in abundance of primary producers than native crabs (Table 2.2). It is possible that the intermediate predators used in tri-trophic cascade experiments are more responsive to non-native than native crabs, thus releasing primary producers more effectively from herbivory (Sih et al. 2010). However, it is not clear why the same larger indirect impact of non-native crabs is absent when sessile invertebrates are the basal prey (Table 2.2).

The magnitude of the effect of predatory crabs on other species also varied significantly among experimental designs. For direct interactions, laboratory-based experiments on crab predation resulted in the largest reductions in prey abundance, undoubtedly because of the absence of alternative prey and/or the limited biotic interactions experienced by predators. The direct effects of native and non-native crabs were generally similar, except in laboratory mesocosms where non-native crabs reduced prey abundance more than native crabs. This result should be interpreted with some caution, however, given the very small number of mesocosm experiments using non-native crabs (Table 2.1). For indirect interactions, the presence of crabs was associated with increased abundance of responding species, but this effect was only significant in mesocosm experiments, supporting the notion that interactions are easier to detect in simpler systems. However, in contrast to direct interactions, non-native crabs exerted significantly larger, positive indirect effects on responding species abundance than native crabs in unstocked field enclosures but not in any other type of experiment. It is notable that most unstocked field enclosures included primary producers as the basal responding species, and plants and algae responded strongly (negatively for direct interactions, positively for indirect interactions) to the presence of non-native crabs.

Our review has revealed several important research gaps. We found marked geographic and taxonomic biases in the studies available, which reflect a need for more research on non-native crabs outside of North America and Europe. Studies of non-native crabs could also be biased towards species suspected of having strong negative impacts (e.g., green crabs). If this is the case here, then non-native crabs could in fact have smaller impacts than we estimated. The indirect impacts of crab consumers are generally understudied, especially for mobile fauna and vertebrates. The few studies that have attempted to demonstrate indirect linkages between crab consumers and vertebrates (e.g., wading birds or juvenile fish) suggest potentially important competitive interactions (Table 2.1; Estelle and Grosholz 2012). We also noted that there are very few natural field-experiments. This is unfortunate because, although such experiments do not offer the same level of control as mesocosm and other laboratory designs, ecosystem-wide studies are one of the best tools available for understanding the impacts of native and non-native species over large spatial and temporal scales (Carpenter et al. 1995, Sagarin & Pauchard 2010). Most importantly, we found few studies that placed native and non-native crabs in direct competition for single or multiple prey items. Thus, while non-native predators might have different functional responses and impacts on native prey abundance than native predators when held on their own (Dick et al. 2013, Alexander et al. 2014, Dunoyer et al. 2014), these measures of predatory impact might be greatly modified by ecological interactions. Experiments that consider both non-native and native species together will help determine whether mortality imposed by non-native predators simply replaces mortality imposed by native predators, or whether it is additive. The implications of such studies for understanding the effect of non-native predators in the wild are critical and can inform risk assessments and management efforts.

# Chapter 3.

# Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer–resource dynamics[2]

## Abstract

Variability in the ecological impacts of invasive species across their geographical ranges may decrease the accuracy of risk assessments. Comparative functional response analysis can be used to estimate invasive consumer–resource dynamics, explain impact variability, and thus potentially inform impact predictions. The European green crab (*Carcinus maenas*) has been introduced on multiple continents beyond its native range, although its ecological impacts appear to vary among populations and regions. Our aim was to test whether consumer–resource dynamics under standardized conditions are similarly variable across the current geographic distribution of green crabs, and to identify correlated morphological features. Crabs were collected from multiple populations within both native (Northern Ireland) and invasive regions (South Africa and Canada). Their functional responses to local mussels (*Mytilus* spp.) were tested. Attack rates and handling times were compared among green crab populations within each region, and among regions (Pacific Canada, Atlantic Canada, South Africa, and Northern Ireland). The effect of predator and prey morphology on prey consumption was investigated. Across regions, green crab consumed prey according to a Type II (hyperbolic) functional response curve. Attack rates (i.e., the rate at which a predator finds and attacks prey), handling times and maximum feeding rates differed among regions. There was a trend toward higher attack rates in invasive than in native populations. Green crabs from Canada had lower handling times and thus higher maximum feeding rates than those from South Africa and Northern Ireland. Canadian and Northern Ireland crabs had significantly larger claws than South African crabs. Claw size was a more important predictor of the proportion of mussels killed than prey shell strength. The differences in functional response between regions reflect observed

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[2] A version of this chapter appears as Howard, BR, Barrios-O’Neill D, Alexander ME, Dick, JTA, Therriault TW, Robinson TB & Côté IM 2018. Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer–resource dynamics. PeerJ 6:e5634

impacts of green crabs in the wild. This suggests that an understanding of consumer–resource dynamics (e.g., the *per capita* measure of predation), derived from simple, standardized experiments, might yield useful predictions of invader impacts across geographical ranges.

## Introduction

The ever-increasing rate of introductions of species beyond their native ranges and the potential negative impacts on native biodiversity of species that become invasive continue to generate worldwide concern (Seebens et al. 2017). However, the effects of invaders are notoriously difficult to predict, especially across geographical ranges (Simberloff et al. 2013, Doherty et al. 2016). Many predatory invaders are responsible for large declines in the abundance and richness of native species (e.g., Wiles et al. 1995, Medina et al. 2011). These impacts are often attributed to advantages of invasive predators in novel environments, including the lack of prey resistance, release from natural enemies/pathogens, or behavioural, morphological, and physiological pre-adaptations (Alpert 2006, Sih et al. 2010, Weis 2010, Roy et al. 2011). However, not all introduced predators cause notable declines in native populations (Gurevitch & Padilla 2004, Zenni & Nuñez 2013); some have minimal detectable impacts on recipient ecosystems (Simberloff & Gibbons 2004, Hampton & Griffiths 2007, Chapter 2). These variable outcomes may arise because the impacts of an invasive predator are influenced by context-specific biotic and abiotic conditions (Lipcius & Hines 1986, Alcaraz et al. 2008, Robinson et al. 2011, Barrios-O’Neill et al. 2014, Paterson et al. 2015). This variability can make it difficult to accurately predict the impacts of invasive species (Dick et al. 2017), especially when the same invasive species occurs at multiple locations (Melbourne et al. 2007, Kumschick et al. 2015).

Comparative functional response analysis (CFRA) has become a useful tool for elucidating relative variability in consumer–resource interactions among invasive species and under different contexts (Barrios-O’Neill et al. 2014, Alexander et al. 2015, Paterson et al. 2015, Dick et al. 2017). The functional response is the relationship between consumer (e.g., predator) consumption rate and resource (e.g., prey) density (Holling 1959, 1965). This relationship provides information on the ability of a predator to find and consume prey and, by extension, its potential ecological impacts (Dick et al. 2013). Unlike predation studies, which seek to directly measure the impact of an invasive species in a particular location or on a particular species, the CFRA approach uses simplified experimental conditions to generate relative (not absolute) parameters that are comparable across contexts. Functional responses can be linear (Type I), hyperbolic (Type II), or sigmoidal (Type III) (Holling 1965). The magnitude and type of functional response can determine predator–prey coexistence (Holling 1959, Oaten & Murdoch 1975, Hassell 1978). Type II responses in particular may potentially destabilize prey populations and lead to localized prey extinction (e.g., Lipcius & Hines 1986; Rindone & Eggleston 2011; Spencer, Van Dyke & Thompson 2016). Studies using CFRA have consistently demonstrated that invasive species, ranging from plants (Funk & Vitousek 2007) to invertebrates (Dick et al. 2013) and vertebrates (Alexander et al. 2014) consume available resources at a higher rate than analogous native species. While these results support the general concept that successful invasive species do well, in part, because they are more efficient at using resources, context-dependent biotic interactions or abiotic conditions can cause variation in invasive species functional responses (Barrios-O’Neill et al. 2014, 2016, Paterson et al. 2015). It is thus unclear whether we should expect the functional responses of an invasive species to be conserved across geographical ranges or whether context-specific differences between populations will result in variable functional responses. Intraspecific geographic comparisons of functional responses should make it possible to estimate the relative importance of local behavioural and morphological adaptations in determining invader responses to resource availability and their potential ecological impacts.

The European green crab (*Carcinus maenas*) is a well-known invasive species that occurs in intertidal and shallow subtidal habitats around the world (Behrens Yamada 2001) (Fig. 3.1). Green crabs are viewed as highly effective generalist predators (Gillespie et al. 2007), with detrimental effects for native biodiversity in some regions (Welch 1968, Walton et al. 2002, Matheson et al. 2016). However, there is large variation in the reported impacts among green crab populations, which does not simply relate to time since invasion. For example, on the east coast of North America, where green crabs have been established since the 1800s (Say 1817), significant declines in commercially important shellfish stocks have been attributed to green crab predation (Glude 1955, Welch 1968). There are also notable ecological impacts on shellfish species on the west coast of North America, where green crabs have been established since the 1990s (Grosholz et al. 2000, 2011). In contrast, there are limited observed impacts by populations in both Australia (introduced 1880s) and South Africa (introduced 1980s) (Fulton & Grant 1902, Le Roux et al. 1990, Carlton & Cohen 2003, Hampton & Griffiths 2007, Mabin et al. 2017).

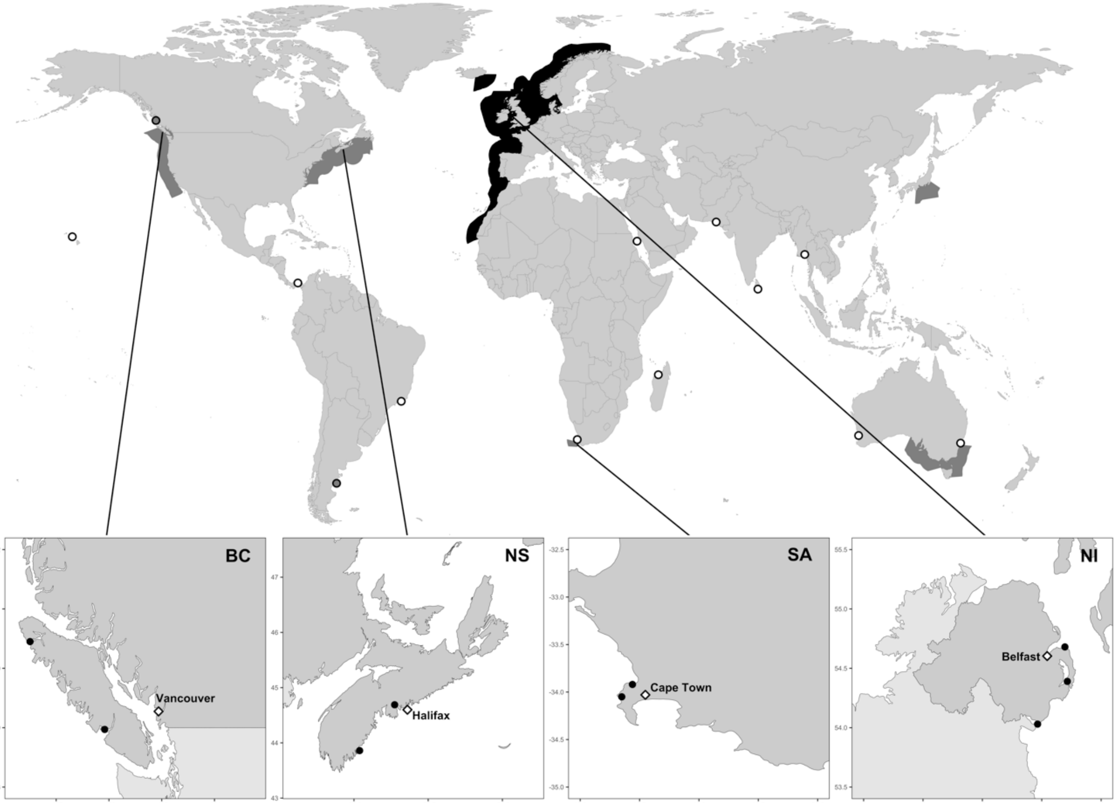

**Figure 3.1 Global distribution of European green crab (*Carcinus maenas*) and sampling locations for green crab populations used in this study.** Native (black) and invaded (dark grey) ranges of European green crab. Locations where green crabs occur in isolated populations are indicated by black dots. Open circles indicate locations where green crabs have been collected but established populations are not yet known to exist (see Carlton & Cohen 2003 for additional details). Insets show the sampling locations (black dots) for populations of green crabs used in this study: BC (British Columbia, Canada), NS (Nova Scotia, Canada), SA (South Africa), and NI (Northern Ireland, UK). White diamonds indicate locations of major cities near sampling locations, for reference.

In this chapter, we investigate variability in consumer–resource dynamics of green crabs from regions within both their invasive and native ranges using CFRA. If green crab functional responses are variable among regions, we expect these differences to reflect local ecological impacts, as demonstrated in interspecific CFRA studies (e.g., Dick et al. 2013, Alexander et al. 2014, Paterson et al. 2015). Thus, crabs from populations within regions should have similar functional responses, but crabs from North American regions (in this chapter, Atlantic and Pacific Canada) might be expected to have higher functional responses than those from regions within the native range (in this chapter, Northern Ireland) and parts of the invaded range where their impacts appear limited (in this chapter, South Africa). We also investigated morphological differences among both crab and prey populations that might potentially cause inter-regional differences in functional responses.

## Materials and methods

### Site selection and animal collection

Green crabs were collected from nine populations from four regions where green crabs have been introduced: British Columbia, Pacific Canada (BC, n = 2 populations), Nova Scotia, Atlantic Canada (NS, n = 2), and South Africa (SA, n = 2), and from the region where they are native: Northern Ireland, UK (NI, n = 3) (Fig. 3.1). A minimum of 18 crabs were collected from each site between July and September 2014 (Table B.1). All crabs collected were males, with carapace widths between 55.0 and 65.0 mm, intact claws, and a firm shell (as springy or soft shells indicate recent moulting). Although the invasive congener *C. aestuarii* was previously recorded as co-occurring in very low densities alongside *C. maenas* in South Africa in the mid 1990s, they were no longer present a decade later (Robinson et al. 2005, 2016). As such, all South African crabs were correctly identified as European green crab. Intertidal mussels of the genus *Mytilus* (BC: *M. trossulus*; NS: *M. edulis*; NI: *M. edulis*; SA: *M. galloprovincialis*) were used as prey because they are widely available in all four regions (Gosling 1992), are readily consumed by green crabs (Elner 1981, Morton & Harper 2008, Behrens Yamada et al. 2010), and are ecologically similar to one another (Seed & Suchanek 1992). Mussels of 25 mm (± 3 mm) length were collected by hand from a single site in each region, which standardized prey across populations within region. A similar standardization (i.e., using the same prey species) was not possible across regions, owing to ethical concerns about non-native species introductions.

Animals were housed in local research laboratories (BC: Bamfield Marine Sciences Centre; NS: Bedford Institute of Oceanography; NI: Queen’s University Belfast; SA: Stellenbosch University). All crabs were housed in indoor tanks, with artificial lighting on day/night cycles similar to local summer conditions. In BC and NS, tanks were supplied with flow-through seawater from adjacent inlets. Tanks in SA and NI used artificial seawater systems. Across all trials, water temperatures varied across a narrow range (9 - 15 °C) suitable for green crab feeding (7 - 26 °C, Behrens Yamada 2001). Salinity range (30 - 36‰) was also well within green crab tolerances (4 - 54‰; Behrens Yamada 2001). Prior to and after being used in experiments, crabs in all locations were fed raw bait fish (e.g., herring) every two to three days. Prey animals were held separately from green crabs but under similar conditions.

## Experimental set-up and methods

At all locations, we used plastic bins (61 cm long x 40.6 cm wide), filled with seawater to a depth of 23 cm, as experimental chambers for all trials. The lids had a mesh screen to prevent escape while allowing light to diffuse inside the bins.

Prior to trials, green crabs were isolated and starved for 48 h to standardize hunger levels. Each crab was used only once. Intact mussels were cleaned of encrusting biota and checked for pre-existing damage. The evening prior to a trial, each bin received a randomly assigned prey density of 2, 4, 8, 16, 32, or 64 mussels, which were scattered across the bottom. The following morning, a single crab was placed into each bin and allowed to forage for eight daylight hours. Each prey density was replicated three times for each of the nine green crab populations tested. We retained, fed, and monitored all crabs for one week after testing to ensure that feeding behaviour had not been affected by imminent moulting. Because no moulting was observed, crabs that had eaten no prey (BC = 1/36 trials, NS = 2/35 trials, SA = 6/36 trials, NI = 15/54 trials) were retained in the analysis to reflect individual variation, and because reduced consumption at low prey densities can be indicative of a Type III functional response. One Nova Scotia trial (at prey density = 2) was omitted owing to crab mortality. One predator-free control bin was run for every prey density and region to measure mussel mortality unrelated to predation.

## Morphological measurements

We evaluated morphological characteristics of both predators and prey that could cause differences in functional responses among populations. Claw size in green crabs is known to vary among populations (Smith 2004, Schaefer & Zimmer 2013), and claw strength is directly proportional to claw size, which has implications for handling times of crabs consuming shelled prey (Behrens Yamada et al. 2010). We therefore measured crusher claw propal height as an index of claw size for each crab (Behrens Yamada & Boulding 1998). Similarly, mussel shell thickness could influence consumption by green crab. We did not measure shell thickness of mussels in each trial, as mussels that were not consumed may have been rejected due to their thickness. Instead, in each region we collected an additional 19 to 30 randomly selected mussels of the same size as used in the trials, euthanized them, and removed the tissue, keeping the valves intact. Shells were air-dried, measured and weighed to the nearest 0.01 g. Following Freeman, Meszaros and Byers (2009), we calculated the shell thickness index ($STI$) as:

$$STI = Shell\ weight/[L * (H^2 + W^2)^{0.5} * \pi/2]$$

where $L$, $H$, and $W$ correspond to linear measurements (in mm) of shell length (maximum anterior-posterior axis), height (maximum dorsal-ventral axis), and width (maximum lateral axis), respectively (Lowen et al. 2013).

## Analysis

All analyses were done using R version 3.3.2 (R Development Core Team 2008). Data were tested for homogeneity of variances and normality prior to statistical analyses to determine possible regional differences. The carapace width data were non-normal so a Kruskal-Wallis test was used, and the claw size data were heteroskedastic, and thus a Welch’s F test was used. We examined the relationship between the number of prey killed and average temperature (i.e., start temperature + end temperature/2) across all 64-mussel trials, using a linear mixed-effect model with region as a random effect. Temperature did not explain a significant amount of variation in number of mussels killed (Likelihood ratio test: $X^2 = 0.618$, df = 1, p = 0.43; Fig. B.1). We therefore did not consider temperature in further analyses.

To determine functional responses as Type II or Type III, we first fit the proportion of prey consumed to prey density for each population using a logistic regression with the package *frair* and function frair_test(). Because the logistic regressions generated negative first-order terms in all cases, indicative of Type II functional responses (Juliano 2001), we then fit the data using the appropriate random predator equation (see Results), without prey replacement (Rogers 1972):

$$N_e = N_0\left(1 - \exp\left(a(N_e h - T)\right)\right)$$

where $N_e$ is the number of prey eaten, $N_0$ is the starting prey density, $a$ is the attack rate, $h$ is the handling time, and $T$ is the experimental duration. Values of $N_e$ and $N_0$ were generated experimentally, while $a$ and $h$ were estimated by fitting the model. Models were fit for each population using maximum likelihood estimation with the package function frair_fit() and bootstrapped ($n$ = 2000) to generate 95% confidence intervals.

Because functional responses were similar within regions (see Results, Figs. B.2 and B.3), we pooled populations within regions to test whether inter-regional differences were driven by differences in attack rate ($a$) or handling time ($h$). We re-fitted Rogers' Type II curves to regional data and bootstrapped the fits (n = 2000) to generate parameter estimates for $a$, $h$ and maximum feeding rates ($1/hT$). The 95% confidence intervals for these parameter estimates were first compared visually and then more formally where necessary (Table B.2).

Finally, to identify factors underpinning regional differences in prey consumption, we used generalized linear mixed-effects models (GLMMs) with a binomial error distribution to predict the proportion of prey consumed by green crabs as a function of claw size, prey STI, and region using a suite of additive candidate models. Mean prey STI for each region was included as a continuous, fixed effect. Because attack rates and handling times by green crabs from both Canadian regions (see Results) were similar, we combined BC and NS into a single region (North America, NA) for comparison with SA and NI. Finally, we included initial prey density as a fixed effect – not as an explanatory variable *per se* but because it is important in functional responses – and population as a random effect in all candidate models. The best-supported model was identified using Akaike's Information Criterion corrected for small sample sizes (AICc), where the top model had the lowest AICc value (Burnham & Anderson 2002). We also determined the relative variable importance (RVI) of each fixed effect, based on the sum of the AICc weights for models that included the focal variable (Burnham & Anderson 2002), and the marginal and conditional $R^2$ values for the top model (Nakagawa & Schielzeth 2013). To display the individual effect of each variable included in the top model on the predicted proportion of mussels killed, we used the *effects* package to calculate effect sizes for each variable, relative to the mean values (continuous data) or proportional distribution (categorical data) of the other factors in the model (Fox 2003, Fox & Hong 2009).

# Results

## Regional patterns of functional responses

In trials without crabs, 100% of mussels survived. All logistic regressions indicated the predation data were best fit using Type II functional response models. Within regions, the confidence intervals around the number of prey killed overlapped between populations at most prey densities, indicating that differences in predatory behaviour within regions were minimal (Figs. B.2 and B.3). Inter-regionally, we found the highest functional response curves for North American green crabs (BC and NS) (Fig. 3.2). Attack rates (*a*) were highest in BC, NS, and SA and the lowest in NI, but there was overlap in confidence intervals between all regions except BC and NI and NS and NI (Fig. 3.3a, Table B.2). Handling times (*h*) were lower in BC and NS than in SA and NI, with no overlap of confidence intervals between these two groups (Fig. 3.3b, Table B.2). By extension, the maximum feeding rates of North American green crabs were considerably higher than those of crabs in SA or NI (Fig. 3.3c).

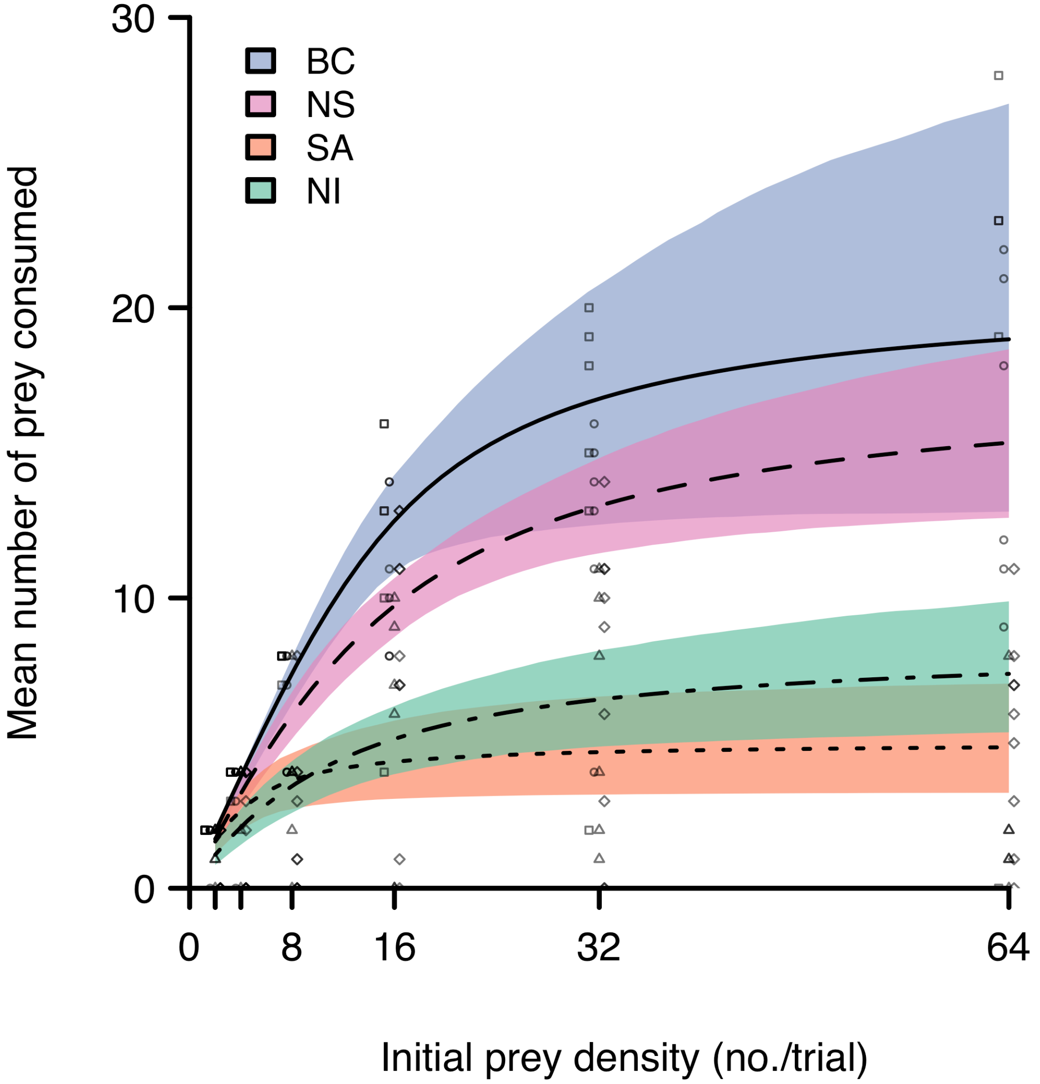

**Figure 3.2 Functional response curves for European green crabs preying on mussels (*Mytilus* spp.) in four regions.**

Functional response curves, modeled from the raw data (open symbols) with a Type II Rogers random predator equation without prey replacement, for European green crabs preying on mussels (*Mytilus* spp.) in four regions: BC (British Columbia, Pacific Canada; solid line; open square), NS (Nova Scotia, Atlantic Canada; dashed line; open circle), SA (South Africa; dotted line; open triangle), and NI (Northern Ireland, UK; dot-dashed line; open diamond). The mean number of prey consumed by green crabs in each region has been averaged across the multiple populations shown in Fig. B.3. Shaded areas represent the 95% bootstrapped confidence intervals.

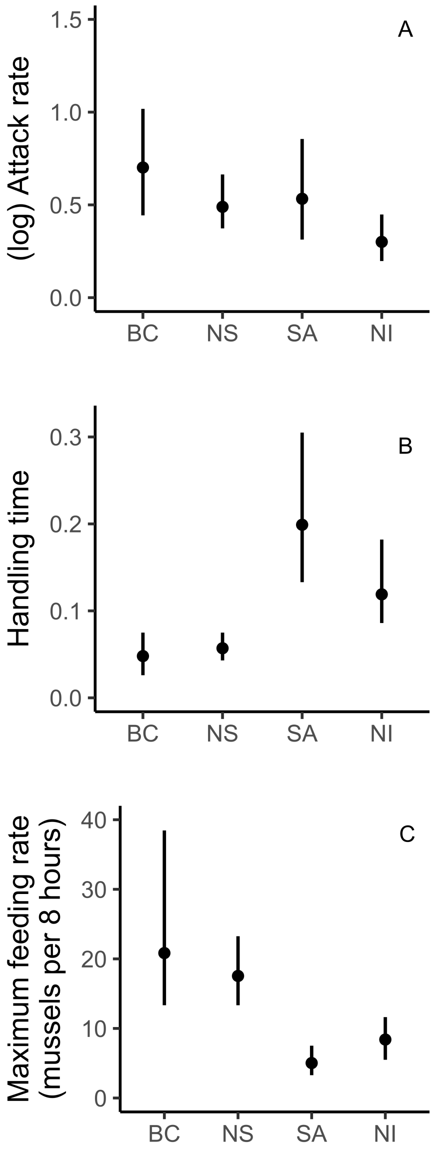

**Figure 3.3 Parameter estimates of attack rate, handling time, and maximum feeding rate for European green crabs feeding on mussels.**
Parameter estimates (± 95% CI) of (A) attack rate *a*, (B) handling time *h*, and (C) maximum feeding rate 1/*h*T, from bootstrapped Type II functional response curves of green crabs preying on varying densities of mussels. Green crabs were collected from BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK).

## Potential drivers of regional variation in prey consumption

Although there was no significant difference in crab carapace width among regions (Kruskal-Wallis test, $p = 0.68$), claw size did differ significantly among regions (Welch's $F_{3,84.55} = 40.28$, $p < 0.01$), with crabs from NI, BC and NS having the largest claws and those from SA, the smallest (Fig. 3.4a). Mussel shell thickness index (STI) also differed significantly among regions (Kruskal-Wallis test, p < 0.01), resulting in a clear regional ranking (SA>NI>BC>NS) of decreasing mussel shell thickness (Fig. 3.4b).

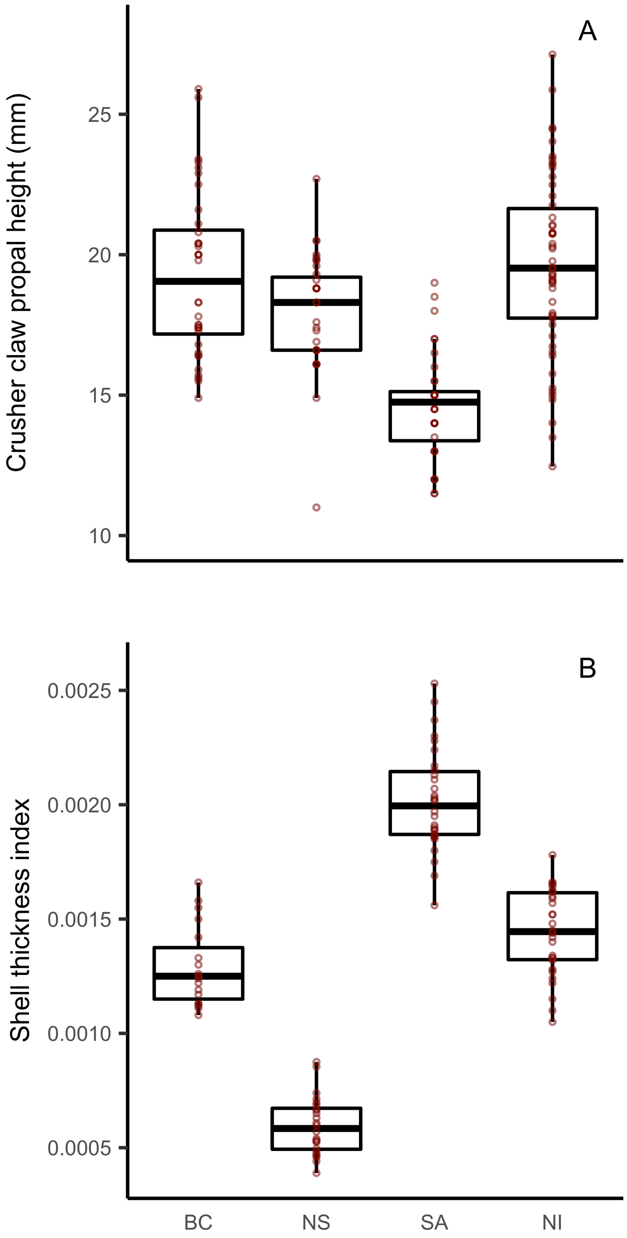

**Figure 3.4 Regional variation in European green crab claw size and *Mytilus* mussel shell thickness for four regions.**
Regional variation in potential determinants of the proportion of mussels killed by European green crabs in four regions: BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK). (A) Claw size (i.e., propal height, in mm) of crabs, and (B) mussel shell thickness index. Raw data indicated by open circles.

Prey density was the most important variable (RVI = 1.0) and was included in all models of proportion of prey consumed by green crabs. Region (RVI = 0.98), claw size (RVI = 0.85) were the next most important variables across all models. Prey STI (RVI = 0.48) was relatively less important.

There was substantial support for two of the candidate models (Table 3.1). Both included claw size and region as important predictors of the proportion of mussels killed. The second-ranked model also included prey STI, but this variable had poor explanatory power: it did not substantially improve the model fit (as indicated by the log-likelihood) or the marginal $R^2$ (Table 3.1).

**Table 3.1 Results of model selection on all candidate binomial generalized linear mixed-effects models predicting the proportion of mussels killed by European green crabs in functional response trials.**

| Model | k | LL | AICc | ΔAICc | $w_i$ | Cumulative $w_i$ | Marginal $R^2$ |
|---|---|---|---|---|---|---|---|
| Density + claw + region | 6 | -474.5 | 961.58 | 0 | 0.44 | 0.44 | 0.29 |
| Density + claw + STI + region | 7 | -473.5 | 961.79 | 0.21 | 0.40 | 0.84 | 0.29 |
| Density + STI + region | 6 | -476.3 | 965.17 | 3.59 | 0.07 | 0.91 | 0.29 |
| Density + region | 5 | -477.4 | 965.17 | 3.59 | 0.07 | 0.98 | 0.28 |
| Density + claw + STI | 5 | -479.5 | 969.47 | 7.89 | 0.01 | 0.99 | 0.23 |
| Density + claw | 4 | -481.3 | 970.83 | 9.26 | 0 | 1.00 | 0.18 |
| Density + STI | 4 | -482.2 | 972.58 | 11.00 | 0 | 1.00 | 0.22 |
| Density-only | 3 | -484.2 | 974.55 | 12.97 | 0 | 1.00 | 0.17 |
| Intercept-only | 2 | -733.88 | 1471.84 | 510.26 | 0 | 1.00 | 0 |

Results of model selection using Akaike's Information Criterion AICc, showing all candidate binomial generalized linear mixed-effects models predicting the proportion of mussels killed by European green crabs in functional response trials. Fixed effects included crab claw size, region (North America, South Africa, or Northern Ireland), and the shell thickness index (STI) of mussels from each region. Prey density per trial (density) was included as a fixed effect, and crab population as a random effect in all models. *k* is the number of parameters in each model; ΔAICc is the difference in AICc value between the focal model and the model with the lowest $AIC_c$; Akaike weight $w_i$ is interpreted as the probability that a given model is the best model of the candidate set given the data at hand. Marginal $R^2$ values are also given as an index of model fit.

The variables in the top model were prey density, claw size, and region (Table 3.1). Increasing prey density resulted in proportionally fewer mussels being killed, as expected from Type II functional responses that reach saturation (Fig. 3.5a). The proportion of mussels killed increased with claw size, as expected, regardless of region and prey density (Fig. 3.5b). At mean prey density and claw size, mussels had a 33% chance of being killed by green crabs in NI and SA (Fig. 3.5c). In contrast, and as predicted, green crabs in North America imposed the highest prey mortality. The probability of a mussel being killed in North America was 67% (Fig. 3.5c). Together, these three fixed effects in the top model explained 29% of variation in the proportion of prey killed (marginal $R^2$). The combination of the fixed effects and random effect (population) explained 31% of this variation (conditional $R^2$). To validate our approach of combining the North American populations we also re-ran the analysis on a modified version of our top model that included all four regions, rather than three, to see if there were any differences in the results. All the trends were consistent with our top model (Fig. B.4), and there were no differences in the marginal and conditional $R^2$ values or the model coefficients for prey density and claw size.

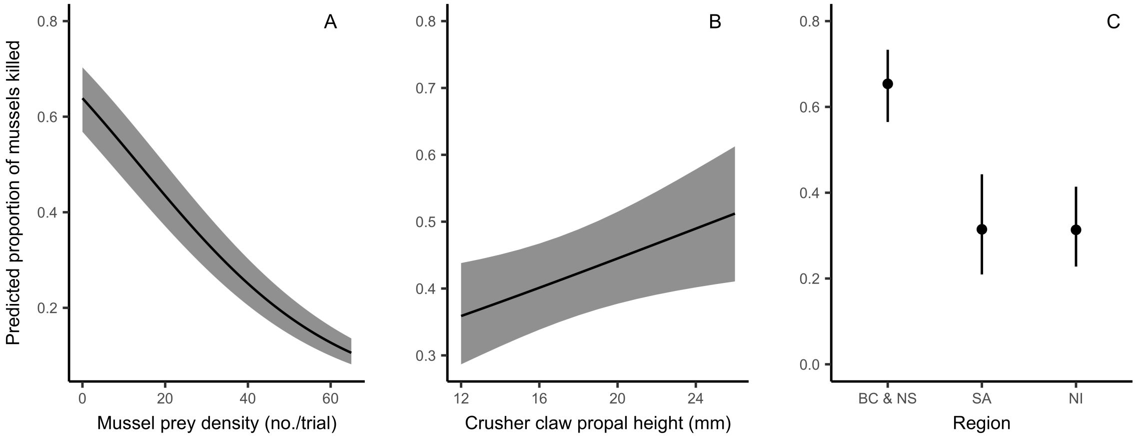

**Figure 3.5 Predicted proportion of mussels killed by European green crabs in relation to prey density, claw size (mm), and the region of origin, derived from top generalized linear mixed-effects model.**
The predicted proportion of mussels killed by European green crabs (with 95% confidence intervals) in relation to (A) prey density, (B) claw size (mm), (C) and the region from which crabs were collected: North America (British Columbia and Nova Scotia, BC & NS), South Africa (SA), and Northern Ireland, UK (NI). Predictions are derived from a generalized linear mixed-effects model (see top model in Table 3.1) and are shown for each factor when the other factors are fixed at their mean or proportional values.

## Discussion

Comparative functional response analysis (CFRA) has consistently demonstrated that the functional responses of invaders reflect their known ecological impacts, but it has traditionally focussed on interspecific comparisons between invasive and native species (e.g., Dick et al. 2013, Alexander et al. 2014, Paterson et al. 2015). CFRA has not previously been used to investigate geographic variation in functional responses of a single, cosmopolitan invader. Here, we did not observe large differences in the functional responses of green crabs from populations within regions: Although it cannot be assumed our results apply to entire ranges, as this would require more extensive sampling in both North America and Europe, crabs from populations several hundred kilometres apart but in the same region showed similar attack rates, prey handling times, and maximum feeding rates. However, differences in functional response curves and parameters among regions were large. Furthermore, the higher functional responses of invasive green crabs from North America compared to South Africa and Northern Ireland appear to reflect, at least qualitatively, their predatory impacts in the wild (see Glude 1955, Welch 1968, Grosholz et al. 2000, 2001, Mabin et al. 2017). Despite their experimental simplicity, functional responses might therefore be a useful, relative estimate of predation that can help inform predictions about the ecological impacts of green crabs in areas where more refined impact predictions are not yet available or impossible to make.

We found regional differences in the green crabs' capacity to kill mussels. These differences stemmed mainly from differences in handling times, and by extension maximum feeding rates (which are mathematically derived from handling times), although some variation in attack rates was also observed. The foraging success of predators depends on their behaviour, morphology, and physiology as they detect, attack, capture, and consume prey (Hassell 1978, Lima 2002). Attack rate (*a*) reflects the first two steps of this foraging sequence. We found some inter-regional differences in attack rates, with invasive crabs from BC demonstrating higher attack rates than those in Northern Ireland. Handling time (*h*), by comparison, reflects the time it takes for a predator to capture and consume prey items and is influenced by physiological and morphological constraints on the predator (Elner & Hughes 1978, Hassell 1978, Vucic-Pestic et al. 2010). Handling times were markedly lower, and maximum feeding rates (1/*h*T) higher, for green crabs from North America than for those from South African and Northern Ireland. Interestingly, higher resource consumption by invasive species, compared to native species, is usually realized either through higher attack rates (e.g., Dick et al. 2013) or lower prey handling times (e.g., Bollache et al. 2008, Haddaway et al. 2012, Alexander et al. 2014), but rarely both. Differences in attack rates among regions might have been driven by differences in individual activity levels, which are often higher in invasive than in native species (Sih et al. 2004). In contrast, differences in claw size likely drove the observed differences in handling times. Green crabs from North America (BC and NS) had significantly larger claws, and shorter handling times, than crabs from South Africa. Crabs with larger claws have a morphological advantage over crabs with smaller claws, because large claws reduce the effort required to break mussels and the risk of claw damage (Behrens Yamada et al. 2010). This suggests that invasive green crabs from North America are morphologically better suited to handling hard-shelled prey than those from South Africa. Contrary to the pattern, however, native green crabs in Northern Ireland had large claws, on par with those of North American green crabs, but their handling times were significantly lower, more closely matching those seen in South African crabs. Because handling time incorporates both breaking time and eating time (Elner & Hughes 1978, Lee & Seed 1992, Smallegange & van der Meer 2003, Calderwood et al. 2016), perhaps crabs in Northern Ireland are under less pressure to ‘eat quickly’ due to less competition or kleptoparasitism (Smallegange et al. 2006, Chakravarti & Cotton 2014), while still requiring large claws to crush thick-shelled local mussels.

There are four possible explanations for inter-regional differences in claw size and prey handling times. First, differences could be primarily driven by genetic variation. While there are detectable founder effects in some green crab populations (Darling et al. 2008), genetic variation does not explain the large phenotypic variation seen, including in claw size, within the native range of green crabs (Brian et al. 2006). It therefore seems unlikely that inter-regional variation in claw size is linked to a variable genetic make-up of founder individuals. Second, claw size could be a highly plastic trait. Green crabs can modify their claw sizes in response to prey shell thickness (Brian et al. 2006, Schaefer & Zimmer 2013). This phenotypic response occurs under laboratory conditions (Baldridge & Smith 2008) and along biogeographic gradients (Smith 2004). In this chapter, claw size did not covary with prey shell thickness. However, the standardized mussel prey we offered might have not always reflected local diets of green crabs. For example, green crabs in British Columbia are currently only found in soft-sediment habitats where their diet consists mainly of infaunal clams (Klassen & Locke 2007), which can have very thick shells (Boulding 1984). In contrast South African green crabs eat predominantly small gastropods and soft-bodied prey (e.g., polychaetes) (Le Roux et al. 1990). Claw size may therefore normally be more closely linked to prey characteristics than our results suggest. Third, differences in water temperatures could affect the calcification of crab exoskeletons and of their molluscan prey. Warmer temperatures lead to decreased calcification, so crabs in warmer habitats may therefore have weaker claws with which to attack shelled prey. However, because the effect of decreased calcification would also make prey shells weaker handling times should be unaffected overall (Landes & Zimmer 2012). Finally, inter-regional variation in claw sizes, and by extension handling times, may reflect selective forces beyond prey defenses, including reproduction (mate competition) and agonistic interactions (interference competition) (Lee & Seed 1992). Claw size is the best determinant of success in intra- and interspecific agonistic interactions between crabs (Lee & Seed 1992, Sneddon et al. 1997). It is notable that green crabs in North America face competition from large-clawed decapods like Dungeness crab (*Metacarcinus magister*) in BC and American lobster (*Homarus americanus*) in NS (McDonald et al. 2001, Rossong et al. 2006). A combination of exposure to thick-shelled prey and a highly competitive environment could explain the especially large claws and fast handling times of green crabs sampled from North America compared to those from other populations.

Globally, the impacts of green crabs seem to vary among regions, with some populations (e.g., North America and Tasmania) appearing to have larger impacts on intertidal communities than others (e.g., South Africa, Australia, or Japan) (Behrens Yamada 2001). The quantitative evidence for this variability is provided by a few large-scale field studies showing that green crabs are effective bivalve predators that have negatively impacted native community composition, trophic interactions, critical habitat, and human economic interests (Welch 1968, Grosholz et al. 2000, Walton et al. 2002, DeRivera et al. 2011, Matheson et al. 2016). Our finding that green crabs sampled from North America have higher attack rates and lower prey handling times than those sampled from other regions is consistent with these field observations. Moreover, North American green crabs have had markedly different patterns of spread than in other regions, including in South Africa where green crabs have a comparatively restricted range despite becoming established decades ago (Mabin et al. 2017). The limited success and impacts of invasive green crabs in South Africa has been attributed to abiotic conditions (e.g., fast-flowing water and highly exposed coasts) being unfavourable to range expansion (Le Roux et al. 1990, Robinson et al. 2005, Hampton & Griffiths 2007). Our results demonstrate that South African green crabs exploit a similar prey less effectively than green crabs from other invasive regions. This suggests that the variable success of different populations of green crabs is partially driven by biotic interactions, not just habitat suitability.

The CFRA approach has been successful because it entails an extreme reduction of the complexity of experimental conditions. Functional response studies do not seek to generate absolute values of foraging parameters under realistic environmental contexts (e.g., habitat structure). Instead, the approach generates relative parameters that are comparable across species and contexts. Thus, high-impact invasive species typically display functional response curves that are steeper and/or have higher asymptotes than similar native species or lower-impact invaders (e.g., Dick et al. 2013, Alexander et al. 2014, Paterson et al. 2015). Our study is the first to establish that there is also marked inter-regional variation in the functional responses of a globally invasive consumer that appears to reflect, at least qualitatively, the regionally variable impacts of green crabs.

CFRA can be a powerful approach with which to compare the relative impacts of invasive consumers both within and among species. As it relates to European green crab, it would be interesting to apply the method used here to populations of green crab we were not able to cover, such as those in Australia, the more southern parts of the North American ranges, and elsewhere in the native range. This method could also be applied to native decapod species that co-occur with green crabs to help identify how much competition influences foraging behaviours. Finally, while we make the inference that the functional responses described here may reflect impacts of green crabs in the field, data gaps in the literature make it difficult to be more definitive about that relationship or use these functional response results predictively. Methods to link experimental functional responses to field impacts exist (e.g., Parker et al. 1999, Dick et al. 2017), but at a minimum require data on abundance that is largely unavailable for European green crab. Where this information is available, functional responses offer a simplified, standardized metric of *per capita* impact that can be used to predict the ecological impacts of invasive species.

# Chapter 4.

# Habitat alteration by invasive European green crab (*Carcinus maenas*) causes eelgrass loss in British Columbia, Canada

## Abstract

Dominant, habitat-forming plant species, such as seagrasses, are key components of coastal ecosystems worldwide. Multiple stressors threaten these ecosystems, including the introduction of invasive species that directly alter, remove, or replace foundation plant species. On the Atlantic coast of North America, the loss of some eelgrass (*Zostera marina*) beds has been linked to bioturbation by invasive European green crabs (*Carcinus maenas*). However, the interaction of these same co-occurring species on the Pacific coast has not previously been investigated. We conducted an enclosure experiment in Barkley Sound, British Columbia, to determine if the impacts of green crabs on Pacific eelgrass ecosystems mirror those previously identified on the Atlantic coast. Eelgrass shoot density declined rapidly over four weeks, with a 73 - 81% greater loss in enclosures with the highest crab density compared to the low-density and control treatments. The low ratio of eelgrass blades to rhizomes in the high-density treatment as well as genetic barcoding of green crab stomach contents suggest that shredding and/or consumption, rather than bioturbation of whole plants, were the main mechanisms of eelgrass loss. Crab density did not have a detectable effect on the biomass or community composition of benthic fauna over the duration of the experiment. The eelgrass loss we observed was consistent with losses detected on the Atlantic coast, which raises management concerns on the Pacific coast, particularly in areas where green crabs and eelgrass co-occur with other coastal stressors and with ecologically and economically important species such as Pacific salmon (*Oncorhynchus* spp.).

## Introduction

Estuarine and coastal ecosystems such as saltmarshes, mangroves, and seagrass beds are collectively some of the most ecologically and economically important ecosystems in the marine environment (Barbier et al. 2011). These ecosystems are created by habitat-forming marine plants that provide significant ecosystem services, including acting as carbon sinks, attenuating wave action, and providing shelter for juvenile fish and invertebrates (Costanza et al. 1997). However, these ecosystems are threatened globally by a multitude of anthropogenic stressors, including habitat loss and species invasions (Ewel et al. 2001, Levin et al. 2001, Duarte 2002, Williams 2007). Estuaries and bays are particularly susceptible to invasive species introductions because they are readily accessible and heavily used by people, aquaculture, and recreational and commercial vessels (Ruiz et al. 1997, Wasson et al. 2001). Hundreds of invasive species have been identified in coastal ecosystems worldwide (Ruiz et al. 1997, Bax et al. 2003, Bouma et al. 2009, Romero et al. 2015, Mach et al. 2017).

In addition to modifying interactions between species, invasive species can also physically alter habitat. Habitat alteration may be autogenic, where the species itself creates or replaces habitat, or allogenic, where the habitat is transformed by the invasive organism through its activities (Jones et al. 1994, Fei et al. 2014). If habitat alteration results in significant changes to native community composition or resource availability, the invasive species is considered an ecosystem engineer (Jones et al. 1994). In coastal ecosystems, invasive autogenic species like marine flowering plants can become dominant in their invasive ranges (Fei et al. 2014). For example, the introduction and spread of red mangrove (*Rhizophora mangle*) throughout the Hawaiian archipelago since the early 1900s has replaced algae and saltmarsh plant-dominated intertidal habitats with monospecific mangrove forests (Allen 1998). In contrast, allogenic invasive species in coastal ecosystems are often mobile invertebrates that bioturbate, erode, or otherwise alter existing habitat (Fei et al. 2014, Romero et al. 2015). For example, along the east coast of North America, the invasive herbivorous European periwinkle (*Littorina littorea*) can sufficiently disrupt sedimentation while grazing such that saltmarshes are converted into rocky intertidal habitat (Bertness 1984). Similarly, in California, bioturbation by the invasive isopod *Sphaeroma quoianum* causes bank collapse and erosion, leading to the loss of marshland (Talley et al. 2001).

The ecosystem-level impacts of an invasive species are often inconsistent across invaded regions due to context-specific factors (Molnar et al. 2008, de Moura Queirós et al. 2011, Guy-Haim et al. 2018). An invasive species considered to be an ecosystem engineer in one location may have much less consequential impacts in a different setting. For example, the Pacific oyster (*Crassostrea gigas*), native to the Pacific coast of

Asia, has a global introduced or invasive range, and is often considered an autogenic ecosystem engineer (Molnar et al. 2008, Padilla 2010). In high densities, Pacific oyster form reefs that can replace native habitats, attract new species, displace others, and change local biogeochemical cycling (Padilla 2010). However, the impacts of Pacific oyster are geographically variable. In British Columbia (Canada) and Washington (USA), Pacific oyster can result in both the direct loss of eelgrass habitat through conversion to oyster beds, and indirect shifts in both epibenthic and nektonic communities (Kelly et al. 2008, Wagner et al. 2012). In other regions, Pacific oyster may replace a functionally similar native species such as the native European flat oyster (*Ostrea edulis*) or remain in low densities after establishment, resulting in negligible ecosystem impacts (Padilla 2010, Green & Crowe 2014, Zwerschke et al. 2018). Therefore, it cannot be assumed that the observed ecosystem impacts of an invasive species will be consistent among invaded regions.

The European green crab (*Carcinus maenas*) has become invasive in coastal ecosystems around the globe, including eelgrass beds on both the Atlantic and Pacific coasts of North America. To date, research on the interaction between green crabs and eelgrass ecosystems has been focused on the Atlantic coast, where green crabs are considered a likely allogenic ecosystem engineer of eelgrass beds (Klassen & Locke 2007, Matheson et al. 2016). Davis et al. (1998) first showed that green crabs foraging in transplanted eelgrass mesocosms shredded blades and dislodged whole plants i.e., through bioturbation – a major concern for eelgrass restoration efforts. The density of green crabs was an important predictor of eelgrass damage, with densities of 4 green crabs $m^{-2}$ or more having a significant impact after just one week (Davis et al. 1998). Subsequently, widespread eelgrass declines in the USA (Maine and New Hampshire) and Canada (Nova Scotia and Newfoundland) coincided with observed high densities of green crabs, and experimental work in these areas supported a causal link (Malyshev & Quijón 2011, Garbary et al. 2014, Neckles 2015, Matheson et al. 2016). In addition to causing the loss of eelgrass shoots by bioturbation and shredding, juvenile green crabs are thought to directly consume shoots (Malyshev & Quijón 2011). Green crab activity in eelgrass beds has also been linked to direct and indirect impacts on biotic communities associated with eelgrass. By reducing eelgrass shoot density, green crabs indirectly affect species that use eelgrass as cover or habitat, including small fish and invertebrates (Thompson 2007, Matheson et al. 2016). Moreover, green crabs can directly compete with other foragers, such as native decapods or migrating birds (Boudreau & Hamilton 2012, Rossong et al. 2012). Thus, multiple lines of evidence support the conclusion that green crabs can act as allogenic ecosystem engineers in eelgrass habitats along the Atlantic coast of North America. However, whether this is also true of green crabs in eelgrass beds on the Pacific coast has not previously been assessed.

There are reasons to believe that the impact of green crabs on eelgrass on the Pacific coast of North America could be different based on geographic differences in climate, disturbance regime, and biodiversity. Although eelgrass beds on both coasts are similar in that they are dominated by *Zostera marina*, a marine angiosperm (Short et al. 2007), *Z. marina* on the Pacific coast typically occurs at shallower depths, experiences less frequent annual disturbance, and flowers earlier in the summer than it does at the same latitude on the Atlantic coast of North America (Phillips et al. 1983a, Robertson & Mann 1984, Moore & Short 2006). *Zostera marina* on the Pacific also frequently co-occurs with an invasive species of eelgrass, *Z. japonica* (dwarf eelgrass), which is not present on the Atlantic coast of North America (Shafer et al. 2014). While eelgrass beds on both coasts are important feeding, spawning, and nursery habitats for many species, including economically important and threatened fish and bird species (Gotceitas et al. 1997, Heck et al. 2003, Kennedy et al. 2018), these regions support very different species assemblages and species interactions. On the Pacific coast, eelgrass beds function as both spawning ground and shelter for Pacific herring (*Clupea pallasii*) (Hosack et al. 2006, Pikitch et al. 2014, Shelton et al. 2014), and as foraging grounds for out-migrating juveniles of several species of Pacific salmon, including the critically important Chinook salmon (*Oncorhynchus tshawytscha*) (Moore et al. 2016, Kennedy et al. 2018). Migrating waterfowl are twice as abundant in wetlands, including eelgrass beds, on the Pacific than the Atlantic coast (Bellrose & Trudeau 1988). Finally, while the Pacific coast of North America is typically more species rich and has a greater diversity of macroalgae and marine plants (Archambault et al. 2010, Costello et al. 2010), it is also more heavily invaded than the Atlantic coast (Ruiz et al. 2000, Molnar et al. 2008). The differences between these two bioregions may result in different impacts of green crabs in eelgrass ecosystems on the Atlantic and Pacific coasts.

To determine the potential impacts of green crabs on Pacific coast eelgrass ecosystems, we conducted an enclosure experiment in an eelgrass bed in Barkley Sound, British

Columbia, Canada. If green crabs are allogenic ecosystem engineers, eelgrass loss should increase over time and with increasing densities of green crabs, consistent with similar experiments done on the Atlantic coast (e.g., Davis et al. 1998, Garbary et al. 2014, Neckles 2015). We also examined the mechanism of habitat alteration by green crabs. If eelgrass is lost primarily due to bioturbation, as we might expect based on other allogenic species (Fei et al. 2014), we hypothesized that the ratio of eelgrass blades to rhizome biomass would not differ significantly across treatments, as both shoots and rhizomes would be lost at a similar rate. In contrast, if eelgrass is lost primarily due to above-ground shredding or tearing, as observed on the Atlantic coast (Davis et al. 1998, Malyshev & Quijón 2011, Garbary et al. 2014), then the ratio of eelgrass blades to rhizomes should be smaller in treatments with green crabs present, as blades would be lost at a faster rate than rhizomes. Finally, to meet the definition of ecosystem engineer, habitat modification by green crabs should impact native species diversity (Jones et al. 1994). Other studies have linked direct predation on infaunal organisms by green crabs to eelgrass loss, caused by bioturbation while foraging. This loss of eelgrass habitat is linked in turn to indirect changes in the abundance and composition of infaunal and nektonic species (e.g., Thompson 2007, Matheson et al. 2016). Thus, we estimated the abundance and size of benthic fauna in enclosures, to test if higher densities of green crabs would result in decreasing biomass of eelgrass-associated benthic fauna and shifts in community composition.

## Methods

### Field site

Our field site was located at the head of an unnamed embayment in the southeast corner of Mayne Bay, Barkley Sound, British Columbia, Canada (latitude 48.974, longitude -125.288) (Fig. 4.1a). The site was sheltered and there were no obvious anthropogenic or natural stressors (i.e., sedimentation, disease, aquaculture, etc.) in the immediate area. The embayment is approximately 1 km long with a continuous intertidal area of approximately 0.03 km$^2$, one-third of which consists of eelgrass (British Columbia Marine Conservation Analysis Project Team 2011). The eelgrass band extends from the high intertidal to 1.1 m below mean low water (MLW) at its deepest point. The slope of the eelgrass bioband ranges from 3.1 – 8.0% along the steeper southern shore and flattens out at the head of the embayment to 0.9%. While the highest part of the bioband consists of non-native *Zostera japonica*, most of the bed, including the area used for this experiment, is predominantly or exclusively *Z. marina*. This is consistent with the expected vertical zonation in mixed beds with steep slopes, where *Z. japonica* is restricted to the high intertidal zone (Shafer et al. 2016).

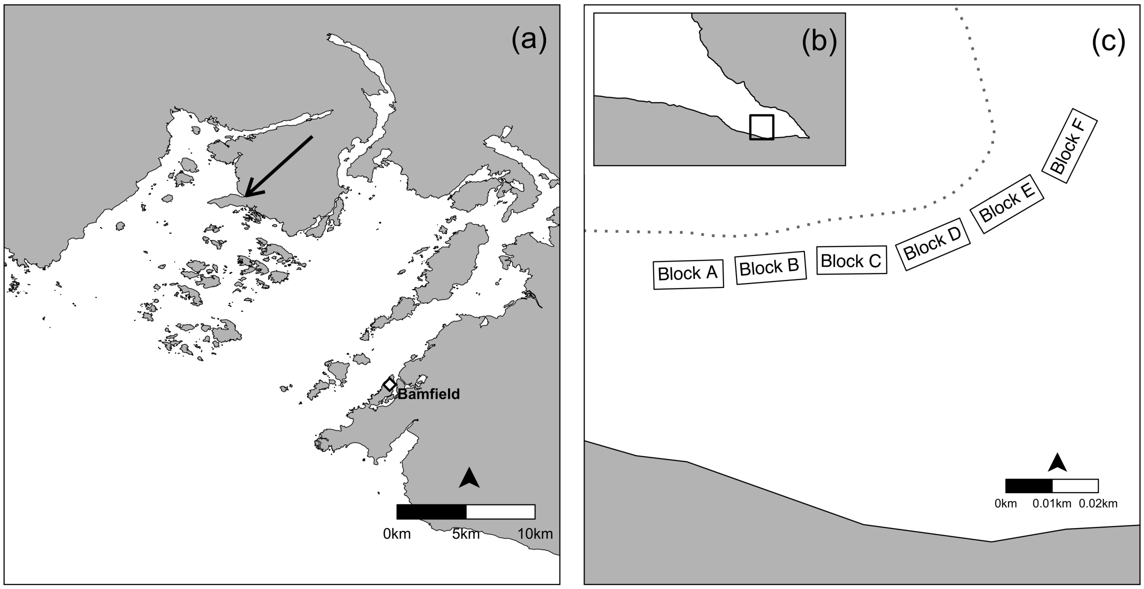

**Figure 4.1 Map of study region and experimental design.**
(**a**) Map of Barkley Sound, British Columbia, Canada. The arrow indicates the southeast corner of Mayne Bay where this study was conducted. The white diamond indicates the town of Bamfield. White indicates sea, grey indicates land; (**b**) Embayment where green crab enclosure experiment was established; (**c**) location and arrangement of experimental blocks. Each block contained one plot of each of four treatments: exclosure (0 crabs $m^{-2}$), low density (1.4 crabs $m^{-2}$), high density (5.6 crabs $m^{-2}$), and a no-cage control plot. Continuous dotted line indicates mean low low water (MLLW).

Green crabs were first detected in Barkley Sound in 1999 and specifically in Mayne Bay in 2006 (Gillespie et al. 2007). The catch-per-unit-effort in Mayne Bay over three consecutive summers (2013-2015) ranged from 0.18 to 0.56 crabs/trap-day, which represents 100 to 339 crabs caught in a day. This density is moderate compared to catch rates for the most heavily invaded sites in Barkley Sound, which are as high as 2.5 crabs/trap-day, representing over 1,400 crabs caught per day (see Chapter 5).

## Enclosure design and sampling

We installed experimental enclosures along the low intertidal zone of the eelgrass bed (~1.0 m above MLW) (Fig. 4.1b-c). Enclosures measured 1.2 m x 1.2 m x 1 m and were constructed of rebar and plastic deer fencing with a mesh size of 2.54 cm, which prevented the movement of large, mobile epifauna including crabs of 50 mm carapace width (CW) or larger. The tops of the enclosures were also covered with the fencing material to prevent crabs from escaping by climbing out or being predated. The walls of the enclosures were buried approximately 15 cm into the sediment to prevent crabs from escaping by burrowing. There was sufficient vertical height in the enclosures that the eelgrass was not impeded at high tide when the enclosures were fully submerged. The top of each enclosure also had a small mesh (2.0 cm) collar that functioned as an access point for data collection. The collar was held closed with cable ties between sampling events. We arranged enclosures in a randomized block design, with a total of six blocks along the south- and east-facing shoreline. Each block included three enclosure plots, one per treatment (described below) and one no-enclosure plot marked by cedar stakes (to estimate the enclosure effect), for a total of 24 plots. Plots (enclosed or not) in a block were spaced 1 m apart and blocks were spaced a minimum of 5 m apart (Fig. 4.1c). No enclosures were lost during the experiment, which ran for four weeks (1-29 August 2015).

Our experimental treatments included high density (5.6 green crabs m$^{-2}$), low density (1.4 green crabs per m2), and empty exclosures (0 green crabs m$^{-2}$). The first two densities approximated the extreme high and average densities, respectively, of green crabs at sites in Barkley Sound, based on observations (BRH, TWT, and IMC). The green crabs used were caught on-site using baited Fukui fish traps and were all males with intact claws, between 50-72 mm CW (notch-to-notch). We chose to use males to control for differences in behaviour and activity levels between sexes during the breeding season (Behrens Yamada 2001). To distribute evenly the range of crab sizes caught, the low-density treatment consisted of two average-sized crabs (approximately 50-65 mm CW), and the high-density treatment contained six crabs, two large (>65 mm CW) and six average-sized crabs. Crab densities were largely maintained throughout the experiment as 33 out of 60 crabs were recovered from the enclosures at the end of the month (see Results).

We surveyed eelgrass shoot density in all plots by snorkeling at high tide every 4-6 days over the course of the experiment, for a total of six site visits. We haphazardly tossed a circular frame (201 cm$^2$) into each plot and counted the shoots inside the frame. This subsampling was repeated three times per plot on our first site visit, which took place over two days (August 4 and 5), after which we increased sampling to five subsamples per plot for all following visits. After counting shoots, we counted the number of crabs in each enclosure to ensure that densities were being maintained.

At the end of the experiment, we recovered all the remaining crabs we could find (33 out of 60) and took five replicate sediment cores, 5.5 cm in diameter and 10 cm in depth (238 $cm^3$), including the associated above-ground blades of eelgrass, in each plot. The locations of the cores were predetermined using randomized x-y coordinates and were at least 10 cm from the perimeter of the plots to avoid edge effects. Green crabs and cores were placed in separate sealed plastic bags and frozen for processing at Simon Fraser University.

## Sample processing

Cores were defrosted and sieved over a fine mesh screen and all eelgrass and benthic fauna visible to the naked eye were retained for further analysis. Fauna were stored in 95% ethanol until further processing. Remaining organic detritus in each core (e.g., shells, terrestrial plant material, etc.) was also removed. Individual eelgrass plants were cleaned of gravel and sand by rinsing them with fresh water and then cut at the sheath to separate the blades from rhizomes. Both blades and rhizomes were dried to constant weight for a minimum of 48 h at 60 ºC and we took the total dry weight of blades and, separately, of rhizomes (to the nearest 0.0001 g) for each core. Benthic fauna were weighed individually (wet weight to the nearest 0.001 g) and identified to the lowest taxonomic level possible based on macroscopic characteristics.

## Analysis

All analyses were done using R (version 3.3.2) (R Development Core Team 2008). Generalized linear mixed-effects models (GLMMs) were generated using the *lme4* package for three response variables: average eelgrass shoot density, average blade to rhizome dry weight ratio, and average benthic fauna wet weight. In all cases, the within-plot variance of the samples was first analysed using Bartlett's or Levene's test, as appropriate, and determined to be non-significant. This allowed us to average samples within each plot without losing statistically important variance (Murtaugh 2007). We opted to analyse averages rather than raw data as a means to deal with the true-zero-inflated fauna and eelgrass weight data, as recommended by Bolker (2008).

To determine if average eelgrass shoot density differed among treatments over time, we included treatment (categorical), time (days since onset of experiment; continuous), and the interaction between the two as fixed effects. To account for heterogeneity in the residuals, we included a weighting term for the treatment variable (Zuur et al. 2009). Although we resampled shoot density in the enclosures over time, there was no auto-correlation between sampling dates so no correlation structure was needed (Zuur et al. 2009). The average ratio of blades to rhizomes was calculated for each plot based on dry weights. We modelled this response using treatment as the only fixed effect. The model was fitted using logged ratios to account for heteroscedastic residuals. To determine if there was a difference in benthic fauna biomass among treatments, we calculated the average wet weight per cage by summing weights of individual taxa per core and then averaging across cores per plot. As above, we included treatment as the only fixed effect and logged the response variable to correct the heteroscedasticity. All models included block as a random effect. The final model for each response variable was tested against a null model using a likelihood ratio test to determine the significance of the fixed effects.

We used non-metric multi-dimensional scaling (nMDS) to determine if community composition of benthic fauna varied with treatment, using the package *vegan* (Oksanen et al. 2017). Due to the low taxonomic resolution and low numbers of fauna collected (see Results), we used functional groups and relative size, rather than taxonomic groupings, to create a Bray-Curtis dissimilarity matrix based on abundance. In doing so, we assumed that taxa in the same functional group might respond similarly to the risk of crab predation (Langerhans & DeWitt 2004, Sih et al. 2010). We conducted an analysis of similarity (ANOSIM) to determine if the dissimilarity between treatments was significant.

Finally, we dissected out the stomachs of green crabs collected on the last day of the experiment to determine if and how many crabs ate eelgrass, and whether crab size affected eelgrass consumption. After inspecting the contents visually, we homogenized each sample by agitation in 99% ethanol with a sterilized tungsten bead. After centrifuging and decanting the excess ethanol, the remaining tissue samples were sent to the Canadian Centre for DNA Barcoding (University of Guelph, Ontario) for metabarcoding (see Appendix C for details). Samples were compared to a custom BOLD (Barcode of Life Database) reference library for rbcLa marker in plants and assigned an identity using the BLAST algorithm. This allowed us to potentially detect both *Z. marina* and *Z. japonica*. Taxonomic identifications for species detected in each sample were accepted as genuine if they were supported by at least 100 reads that matched a reference sequence with at least 98% identity across at least 100 base pairs.

## Results

Over the course of the experiment we observed crabs actively digging in the sediment in the enclosures and consuming eelgrass rhizomes and detritus. Observations of fresh remnants of bivalves and small (< 50 mm CW) green crabs (i.e., small enough to enter and exit enclosures) also suggest the enclosed green crabs were eating, although we cannot definitively attribute this physical evidence of predation exclusively to our experimental green crabs. At the end of the experiment, we recaptured 33 out of 60 crabs: 22 (of 48) from the high-density plots and 11 (of 12) from the low-density plots.

Eelgrass shoot density decreased over the course of the experiment in all treatments, from an initial estimated average bed density of 796 shoots $m^{-2}$, based on our undisturbed open plots. Average eelgrass shoot density was better predicted by the model including treatment than by the null model (Likelihood ratio test: $X^2 = 110.93$, df = 7, $p < 0.001$). Average eelgrass shoot density declined at an average rate of 4.09 to 7.47 shoots $m^{-2}$ $day^{-1}$ across the open plots, empty exclosures, and low-density treatments, with extensive overlap among these treatments (Fig. 4.2). However, in the high-density treatment eelgrass, shoot density declined 2.4 to 4 times faster, by an average of 17.56 shoots $m^{-2}$ $day^{-1}$ (Fig. 4.2).

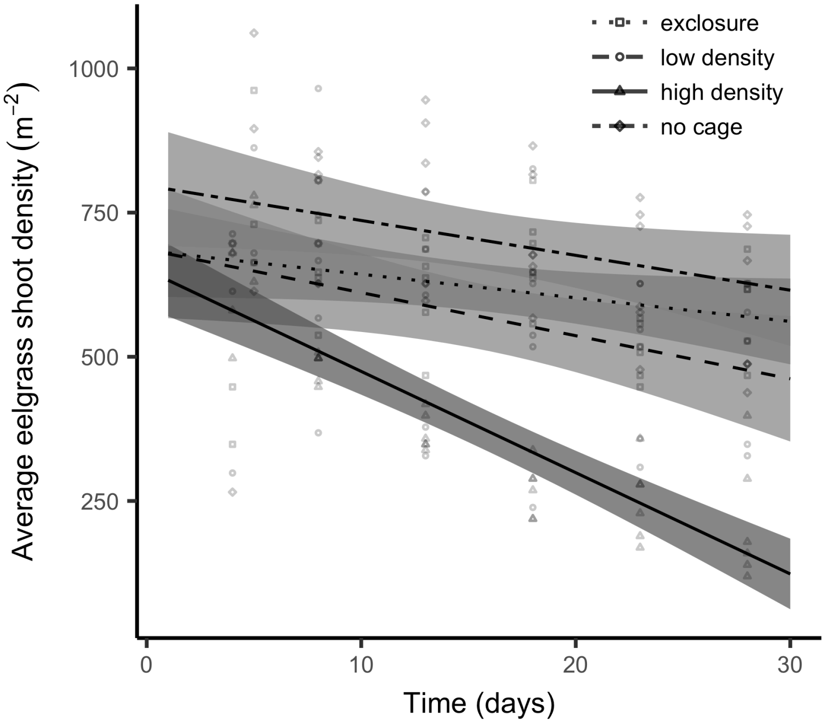

**Figure 4.2 Change in eelgrass shoot density over time.**
Change in average eelgrass shoot density (scaled to $m^{-2}$) in Mayne Bay, British Columbia, over a four-week period in plots containing variable numbers of invasive green crabs. Lines represent the predicted average derived from the generalized linear mixed-effects model. Shaded areas represent 95% confidence intervals. Raw data (average of all samples per plot) are indicated by open points. In addition to low and high green crab density treatments (1.4 and 5.6 green crabs $m^{-2}$, respectively), there was an exclosure treatment (0 crabs $m^{-2}$), and an unenclosed (no cage) treatment, which experienced the ambient density of green crab present at the field site.

The average ratio of blades to rhizome biomass was also better predicted by the treatment model than the null model (Likelihood ratio test: $X^2 = 14.19$, df = 6, p = 0.003). The ratios for all treatments were below 1, meaning that above-ground (blade) biomass was consistently less than below-ground (rhizome) biomass. The average ratio of blades to rhizomes in the open plots was 0.47, which was the highest of the four treatments. In contrast, the average ratio of blades to rhizomes for the high crab density treatment was 0.13, which represents a 72.3% relative decrease in the amount of eelgrass blade biomass compared to the open plot treatment and a 38.1% relative decrease compared to the exclosure treatment (0 crabs $m^{-2}$) (Fig. 4.3a).

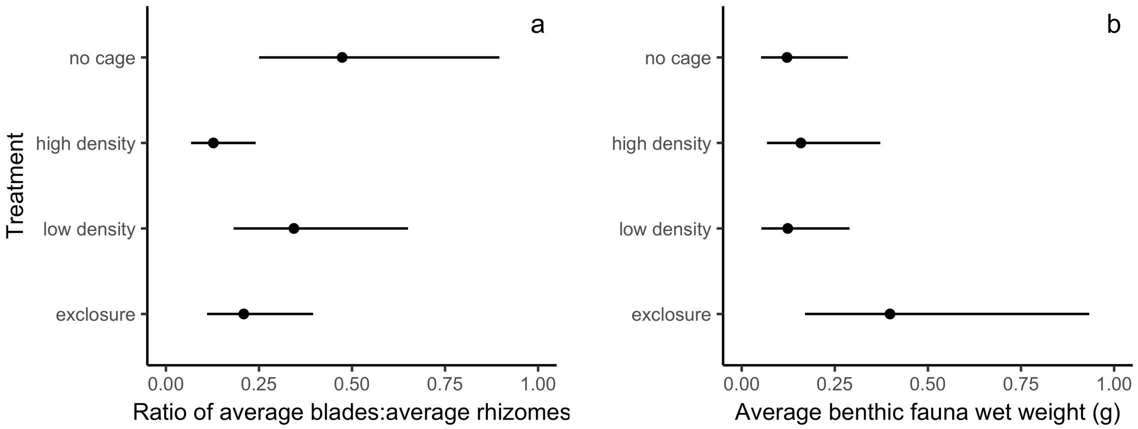

**Figure 4.3 Change in eelgrass and benthic fauna biomass for each of four green crab density treatments.**
Regression coefficients of the (**a**) average ratio of dry weights of eelgrass blades to rhizomes, and (**b**) average benthic fauna wet weight, from plots containing variable densities of invasive green crabs at the end of a four-week period. Points are the unlogged predicted coefficients from the generalized mixed-effects models and errors bars the 95% confidence interval (n = 6 in all cases). In addition to low and high green crab density treatments (1.4 and 5.6 green crabs m$^{-2}$, respectively), there was an exclosure treatment (0 crabs m$^{-2}$), and an unenclosed (no cage) treatment, which experienced the ambient density of green crab present at the field site.

The model of average benthic fauna wet weight that included a treatment effect was not significantly better than the null model (Likelihood ratio test: $X^2$ = 5.06, df = 6, p = 0.17). There was no significant difference in benthic fauna weight among treatments (Fig. 4.3b). Moreover, the nMDS plot (Fig. 4.4, stress = 0.15) and ANOSIM results indicate there is no significant dissimilarity in community composition between treatments (R = - 0.05, p = 0.80).

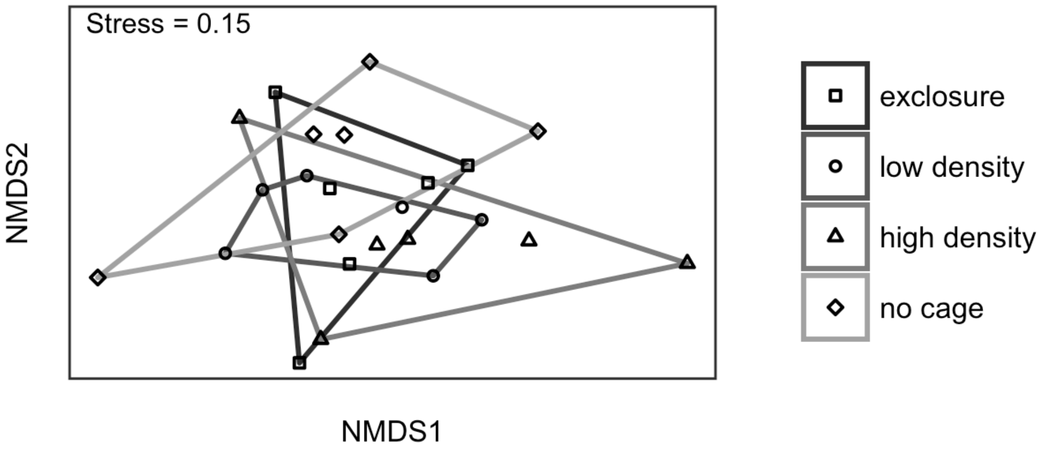

**Figure 4.4 Non-metric multidimensional scaling ordination of benthic faunal communities in eelgrass after exposure to green crabs.**
Non-metric multidimensional scaling (nMDS) plot of benthic fauna community composition in plots containing variable densities of invasive green crabs at the end of a four-week period. Fauna were classified based on functional group and relative size class, rather than taxonomy (Appendix C). Each point represents a plot (n = 6 plots per treatment). In addition to low and high green crab density treatments (1.4 and 5.6 green crabs $m^{-2}$, respectively), there was an exclosure treatment (0 crabs $m^{-2}$), and an unenclosed (no cage) treatment, which experienced the ambient density of green crab present at the field site. Stress value indicates degree of distortion required to plot multidimensional dissimilarity rankings in two dimensions; a stress value of <0.2 is considered acceptable (Clarke & Ainsworth 1993).

A total of 12 crabs (out of 33) had eelgrass contents in their stomach that we visually identified as eelgrass rhizomes. This was consistent with observations of crabs eating rhizomes during the experiment and barcoding, which also detected eelgrass in the crabs' stomach contents. Of the 19 individual stomach samples successfully barcoded, 42% contained *Z. marina* and 26% contained *Z. japonica*, with one crab stomach containing both species. There was 75% agreement between our visual identification of eelgrass rhizomes and the barcoding. Barcoding also detected *Zostera* in an additional 10 stomachs where material was too digested for visual identification. *Zostera* was found in a significantly higher proportion of crabs from high-density cages (88%, n = 8 processed samples) than in low-density cages (45%, n = 11 processed samples) ($X^2$ (2) = 9.68, $p < 0.01$). There was no significant difference in the size of crabs (CW) with or without *Zostera* in their stomach contents ($t_{17}$ = -0.75, p = 0.46).

## Discussion

Anthropogenic stressors such as introduced species can cause drastic declines of habitat-forming species in coastal ecosystems, but the severity of these impacts may vary geographically (Molnar et al. 2008, Padilla 2010, Guy-Haim et al. 2018). We tested this geographic variability by examining the impacts of green crabs on eelgrass ecosystems on the Pacific coast of Canada, to compare them to patterns previously observed on the Atlantic coast. To date, studies on the interaction between invasive green crabs and eelgrass are limited to the Atlantic coast of North America, and most focus on post-hoc mechanistic explanations of observed bed losses (Malyshev & Quijón 2011, Garbary et al. 2014, Neckles 2015). Broadly speaking, we found that invasive green crabs in the Pacific are capable of significantly altering eelgrass habitats and, as observed on the Atlantic coast (Davis et al. 1998), eelgrass loss was related to green crab density. Eelgrass shoot loss was three times greater than natural, seasonal senescence in our high crab density treatment. We also observed that the removal of above-ground eelgrass material, through shredding or direct consumption by green crabs, was more common than removal of whole plants (i.e., bioturbation). Both mechanisms have previously been observed (Davis et al. 1998, Malyshev & Quijón 2011, Garbary et al. 2014); however, our additional observations of direct consumption of below-ground material (rhizomes) by large adult male crabs is novel. Contrary to Thompson (2007) who found that enclosed green crabs had significant direct and indirect effects on invertebrate fauna in Atlantic eelgrass beds (with no change in eelgrass biomass) over a four-week period, we did not detect changes in benthic fauna biomass or community composition for any density of green crab. The rapid loss of eelgrass caused by high densities of green crabs indicates these invaders may have a similar, and potentially greater long-term, negative impact on eelgrass ecosystems on the Pacific coast than has been observed in the Atlantic.

The density of an invasive species is a well-established predictor of impact severity (Parker et al. 1999, Thomsen et al. 2011). While green crabs had no discernable effect on shoot density in low-density enclosures or open plots exposed to ambient densities of green crab, the rate of eelgrass loss in our high-density treatment was rapid. After accounting for, natural, site-wide declines in eelgrass due to seasonal effects (i.e., an average of 4.09 shoots $m^{-2}$ $day^{-1}$ in our no-crab exclosures), we estimated that green crabs in high-density plots removed an average of 13.47 eelgrass shoots $m^{-2}$ $day^{-1}$. This is a much faster rate of eelgrass loss than has previously been detected on the Atlantic coast, where similar densities of enclosed green crabs (4.4 crabs $m^{-2}$) reduced shoot density by only 4.1 shoots $m^{-2}$ $day^{-1}$ on average over seven days (Garbary et al. 2014). While differences in eelgrass loss between the two studies may be due in part to variations in study duration, there were also large differences in estimated initial bed densities, with the Atlantic bed in Garbary et al. (2014) being only 20% as dense as the bed in this chapter (Garbary et al. 2014: 172 shoots $m^{-2}$; this chapter: 796 shoots $m^{-2}$). When described in terms of percent bed loss our results are comparable to Garbary et al. (2014). After seven days, the number of eelgrass shoots in high crab density enclosures in our study declined by an average of 14% (after accounting for 4% loss due to natural senescence) (Fig. 4.2), while Garbary et al. (2014) estimated a decline of 15% of shoots over the same duration on the Atlantic coast. The rate of eelgrass loss in our high crab density treatment confirms that green crabs at high densities on the Pacific coast can remove eelgrass at a much faster rate than natural senescence. This suggests that over prolonged exposure to consistently high densities of green crabs, which occur at several invaded sites in the region (BRH, unpublished data), eelgrass beds on the Pacific coast are at risk of severe degradation and loss.

In addition to shoot loss, changes in the ratio of below and above ground eelgrass biomass revealed that the mechanism of green crab disturbance predominately affected above-ground material (i.e., blade shredding or consumption) instead of bioturbation of the entire plant (blades and rhizomes). Due to variability in *Z. marina* phenology, the retention of rhizomes may have varying importance to the persistence of eelgrass beds (Boese et al. 2009). On both the east and west coasts of North America, *Z. marina* displays a range of life-history traits, both within and between beds, in response to local disturbance regimes (Phillips et al. 1983a, Phillips et al. 1983b, Ruesink et al. 2010). In environments with greater natural disturbance (i.e., temperature or salinity fluctuations, ice scouring, grazing), *Z. marina* tends to be an annual plant, flowering and releasing seeds which regrow the bed each year. In more stable environments, *Z. marina* is a perennial plant that maintains beds predominantly through clonal growth (propagation), making the retention of rhizomes particularly important to the persistence of these beds (Boese et al. 2009). Both reproductive strategies occur on the Pacific coast in response to stress and disturbance regimes (e.g., temperature fluctuations, tidal height, etc.)

(Ruesink et al. 2010). The impact of green crabs on eelgrass bed persistence may therefore be related to the dominant reproductive strategy of a bed. Because bioturbation is a disturbance that uproots whole plants including the rhizomes, this mechanism of eelgrass loss is potentially more detrimental to perennial bed persistence than shredding, which shears off the above-ground blades only (Harrison 1979). Our observations that invasive green crabs on the Pacific coast, at high densities, favour shredding above-ground blades over dislodging whole plants (Fig. 4.2a) are consistent with behavioural observations of green crabs on the Atlantic coast where shredding is also the more common mechanism of disturbance (Davis et al. 1998, Malyshev & Quijón 2011).

Shredding may be an indirect consequence of foraging (Davis et al. 1998) or caused directly when crabs consume eelgrass blades and meristems (Malyshev & Quijón 2011). We detected *Zostera* both visually and genetically in crab stomachs, especially in the high-density treatment, indicating that green crabs on the Pacific coast also consume eelgrass. Whether green crabs prefer specific parts of the plant has not been established. However, for the first time, we were able to confirm that green crabs consume rhizomes in addition to blades, and that eelgrass consumption is not limited to juvenile green crabs. We visually identified rhizomes in a third of crab stomachs and incidentally observed rhizome consumption during our field surveys. Typical foregut retention time for green crab is 12-15 h at 15 °C, although may be longer for plant material (McGaw & Curtis 2013). This short retention time indicates that crabs were still readily consuming eelgrass at the end of the experiment despite reductions in eelgrass availability. A more rigorous test of green crab consumption preferences and rates may be an important avenue of future research, especially if green crab have a preference for (or against) invasive *Z. japonica*, as has been shown for ducks and geese (Baldwin & Lovvorn 1994). Even if eelgrass rhizome mats are left largely intact by green crab, overgrazing of above-ground blades alone can still cause population collapses of habitat-forming plants (Nowicki et al. 2018). For example, in Maine (USA), cordgrass (*Spartina alterniflora*), which is the primary habitat-forming plant in saltmarshes, has been overgrazed by herbivorous crabs for decades, resulting in widespread habitat loss and conversion of saltmarsh creekbanks to unstable mudflats (Holdredge et al. 2009).

Despite evidence of active predation by green crabs on benthic fauna in our enclosures, we did not detect a significant effect, whether direct or indirect, on the biomass or composition of benthic fauna. This is contrary to other enclosure experiments, both inside and outside of eelgrass beds and on both coasts, which found significant effects of green crabs on a wide range of invertebrate species (Grosholz et al. 2001, Thompson 2007, Whitlow 2010). We also expected the loss of eelgrass habitat to indirectly affect the community composition of benthic fauna. Our inability to detect a community shift in benthic fauna as a result of green crab activity might be caused by the low faunal density at our site (Table C.1) or the low taxonomic resolution of the data. In addition, there may have also been changes to epifauna on the eelgrass itself and nektonic fauna, including fish, that were not tested here. On the Pacific coast, critically important fish species, including Pacific salmon species and herring, rely on eelgrass habitats extensively for survival and reproduction (Hosack et al. 2006, Kennedy et al. 2018). The loss of eelgrass habitat may contribute to declines in salmon abundance, as the growth of out-migrating juveniles in these estuarine ecosystems predicts future adult abundance (Tomaro et al. 2012). When juvenile salmon are forced to forage in less productive, more risky ecosystems their growth rates are slower, potentially resulting in worse survival outcomes (David et al. 2016, Kennedy et al. 2018).

An invasive species is thought to have ecosystem-wide impacts if there is evidence that they change some or all of the following: nutrient resource availability and supply; consumer–resource dynamics resulting in food web shifts; or physical resources such as space (Vitousek 1990, Crooks 2002). Where these impacts are the result of the species' creation, modification, or maintenance of physical habitat, the species is also considered an ecosystem engineer (Jones et al. 1994). On the Atlantic coast, large declines in eelgrass and subsequent changes to local biodiversity indicate that European green crabs are ecosystem engineers, capable of ecosystem-wide impacts (Klassen & Locke 2007, Matheson et al. 2016). Our study indicates that on the Pacific, green crab impacts on eelgrass should be similar to those observed on the Atlantic coast, especially in sites with high densities of green crabs. However, green crabs have been established at high densities in areas on the Pacific coast for more than two decades and declines in eelgrass beds coincident with high green crab densities have not been reported to date. This may be due to a failure of detection rather than a true difference in Atlantic and Pacific green crab impacts as the largest population densities of green crabs on the Pacific coast are found in remote areas of British Columbia and therefore less closely observed than populations on the Atlantic coast. For example, in Nova Scotia, eelgrass losses in Benoit Cove were noted by local residents prior to the start of formal research in the area (Garbary et al. 2014). Therefore, it is possible that high population densities of green crabs in British Columbia may have already had a significant impact on eelgrass habitat, but that this habitat shift has gone unobserved (or at least unreported). On the other hand, isolation from human populations may mean that invaded Pacific eelgrass beds are under less anthropogenic stress from other sources (e.g., anchors, pollution, shading) than their Atlantic counterparts. Fewer overall stressors could increase the resilience of Pacific eelgrass beds to green crab disturbance. As green crabs on the Pacific coast of North America spread to more populated areas, it is possible that the combined effect of high green crab densities with other coastal stressors will result in observations of ecosystem-wide impacts of green crabs in eelgrass habitats, as has been observed on the Atlantic coast.

# Chapter 5.

# Native crab abundance predicts invasive European green crab (*Carcinus maenas*) hotspots better than habitat

## Abstract

As an invasive species spreads, variation in biotic and abiotic characteristics of habitat patches can lead to large site-level variability in invader distribution and abundance, as demonstrated by the invasive European green crab (*Carcinus maenas*) along the west coast of Vancouver Island, Canada. While green crabs typically occur in low to moderate abundances in this region, some sites have become 'hyper-abundant' with catches orders of magnitude greater than adjacent sites. Because these hotspots are the most likely to experience severe impacts from green crabs, I determined the combination of site-specific abiotic and biotic factors that facilitate these 'hyper-abundant' sites. The occupancy (presence/absence), abundance (catch-per-unit-effort, CPUE), and recruitment success (proportion of the catch that were less than one year old) of green crabs on Vancouver Island were modelled using gradient boosted regression trees (BRTs) and mixed-effects modelling. Eight years (2010-2017) of CPUE data from 72 sites along the west coast of Vancouver Island were analyzed, along with site-specific physical and biological characteristics that could influence propagule pressure, survival, and prey availability, including the CPUE of three co-occurring native crab species. Few abiotic factors showed strong effects on green crab distribution. Freshwater outflow had a non-linear effect on both green crab occupancy and abundance, suggesting a preference for sites with intermediate flows, while sites with soft sediments and a large intertidal area were good predictors of hotspots. The most consistent predictor of green crabs across all models was the CPUE of native crab species. The probability of green crab occupancy at a site was reduced by 50% when any Dungeness crabs (*Metacarcinus magister*) co-occurred there, and green crab abundance was greatly reduced with increasing CPUE of any of the three native species. Although some abiotic site-level characteristics may be helpful in detecting green crab hotspots on the west coast of Vancouver Island, this chapter finds that it is the distribution of native crab

species which appears to contribute most significantly to the regional variability in green crab abundance and distribution on the Pacific coast.

## Introduction

The spread of invasive species is a conservation issue worldwide, as range expansion increases both the risk to native biodiversity and the challenges for management (Lockwood et al. 2007). How to best predict the current and future distributions of invasive species to inform management is therefore one of the most important questions in invasion ecology (Elton 1958). Because management efforts typically target individual colonies or populations, predictive models that improve detection at the site-level scale are the most useful for determining how to apply limited management resources (de Rivera et al. 2007, Epanchin-Niell et al. 2012). However, predictions become difficult in spatially heterogeneous environments, as populations establish non-uniformly across the landscape, making them harder to detect (Melbourne et al. 2007, Epanchin-Niell et al. 2012). The influence of factors such as site isolation, area, quality, and community composition, in determining species distributions is often dealt with using species distribution models (SDMs), which characterize a species' distribution over a patchy landscape in relation to the complex abiotic and biotic features of that landscape (Guisan & Zimmermann 2000). In invasive species management, SDMs are often used to construct predictive tools to help direct limited management resources to the sites most likely to support an invasive species (Guillera-Arroita et al. 2015).

Historically, SDMs used for invasive species management have relied on presence/absence data to predict the occurrence of an invasive species in new environments (Guisan & Thuiller 2005). However, invasive species rarely spread uniformly across sites. Both habitat quality and biotic interactions affect site-level population growth rates of invaders (Hirzel & Le Lay 2008), creating variation in population densities among sites that has important implications for both management and future rates of spread (Crooks 2005). Larger or denser populations of invaders are often of greater concern for management, as the severity of impacts by invasive species scales, often non-linearly, with abundance (Parker et al. 1999, Byers et al. 2002, Dick et al. 2017). For example, in southeast Australian eucalyptus forests there is a density threshold beyond which invasive lantana (*Lantana camara*) causes rapid loss of native plant biodiversity (Gooden et al. 2009). Thus, patches most suitable to the invader might also be sites with the largest negative impact on native biodiversity. Understanding the context-dependent biotic and abiotic factors that create high-density sites for invaders can improve local efforts for detecting and managing new and growing populations of invasive species (e.g., Gooden et al. 2009, Chan & Bendell 2013).

The European green crab (*Carcinus maenas*) is a common shore crab native to Europe and invasive in parts of Africa, Asia, Australia, and both coasts of North America (Behrens Yamada 2001). Significant negative impacts of this species on native bivalve populations and eelgrass habitat have been reported, often occurring in areas where green crab abundance was especially high (e.g., Glude 1955, Grosholz et al. 2000, Neckles 2015, Chapter 4). European green crabs were introduced to the west coast of North America, initially in San Francisco Bay around 1990 (Cohen et al. 1995), and have continued to spread along the spatially complex coastline of the Pacific Northwest. By 2007 this species was present in estuaries and soft-sediment bays all along the west coast the United States and Vancouver Island, British Columbia (BC) (Klassen & Locke 2007). Subsequent surveys and genetic testing of populations from California to Quatsino Sound, BC have shown this species to be genetically well mixed, indicating there is enough long-distance dispersal for the species to function as one large meta-population originating from a single introduction event (Tepolt et al. 2009). This scenario is consistent with their populations elsewhere, including their native European range (Darling et al. 2008).

The distribution of European green crabs on the west coast of North America is potentially influenced by the abundance, distribution, and behaviour of several species of native crabs. European green crabs spread almost exclusively by larval dispersal, and as adults (minimum carapace width (CW) at maturity = 30 mm) have high site-fidelity making them unlikely to travel between sites separated by depths of more than 10 m (Klassen & Locke 2007, Silva et al. 2013, Yamada et al. 2015). In contrast, two common large epibenthic crab species that co-occur with green crabs in BC, Dungeness crab (*Metacarcinus magister*) and red rock crab (*Cancer productus*), regularly migrate between subtidal and intertidal habitats, following the tides. As juveniles, Dungeness crabs rely on soft-sediment littoral habitats, where they co-occur with and are outcompeted by green crabs (McDonald et al. 2001, Armstrong et al. 2003), but adult Dungeness crabs (minimum CW at maturity = 100 mm) can occur at depths >80 m and may travel significant distances between foraging habitats (Higgins et al. 1997; Stone and O'Clair 2001; Holsman et al. 2006). Similarly, red rock crabs (minimum CW at maturity = 65 mm) also undertake large vertical migrations, typically into rocky intertidal habitats to forage during high tides (Boulding & Hay 1984, Carroll & Winn 1989, Yamada & Groth 2016). Because red rock crabs are predators and competitors of green crabs, it is thought that they serve a biotic resistance role and prevent the establishment of green crabs in rocky habitats (Hunt et al. 2003). The only other large crab species that co-occurs regularly with green crabs in BC is the graceful crab (*Metacarcinus gracilis*). This species appears to overlap the most with green crabs in size (minimum CW at maturity = 77 mm) and habitat preference, but far less is known about their movement, dietary niche, or behaviours in general (Orensanz et al. 1995).

Green crabs show patchy occupancy along the west coast of Vancouver Island (WCVI). Most sites with established populations yield low to moderate catches. However, a handful of sites consistently have population densities orders of magnitude larger than neighbouring sites (Gillespie et al. 2007, Klassen & Locke 2007, pers. obs.). It is not clear why some sites along the WCVI maintain moderate populations of green crabs while others have become 'hyper-abundant' hotspots. There is a wide range of site-level variation in the abiotic habitat characteristics and biotic assemblages among sites occupied by green crabs, however what combination of site-level characteristics drives the formation of a green crab hotspot has not previously been modelled for British Columbia. Given that higher densities of green crabs are expected to have greater ecological impacts and act as source populations for further spread of green crabs around Vancouver Island and beyond, knowing how to identify a potential hotspot could greatly improve management strategies.

In this chapter, I modeled the distribution and abundance of green crab on Vancouver Island using ensemble machine learning, specifically gradient boosted regression trees (BRTs). Gradient boosting iteratively builds 'weak' trees and compares the error from each tree with that preceding it, in a stepwise process (De'ath 2007). To make predictions about the types of sites on Vancouver Island that could be green crab hotspots, two BRT models, one using green crab occupancy data (i.e., presence/absence) and a second using catch-per-unit-effort (CPUE) from trapping data were constructed and evaluated. I hypothesized that green crab distribution and abundance would be most strongly influenced by a few abiotic characteristics, particularly those that favour the settlement and survival of juvenile green crabs like intertidal area and the presence of cover, followed by biotic interactions with red rock crabs in particular.

# Methods

## Data collection: Crab catch per unit effort

Trapping surveys for European green crabs have been conducted since 2006 by the Department of Fisheries and Oceans Canada to better understand invasion dynamics of this species in British Columbia. Green crabs were reported in BC as early as 1999 and subsequently confirmed as present at locations all along the WCVI, including in Barkley Sound in 2006 and in Quatsino Sound in 2007 (Gillespie et al. 2007, Klassen & Locke 2007). Between 2010 and 2017, a total of 72 sites were trapped at least once in these two target areas (Fig. 5.1).

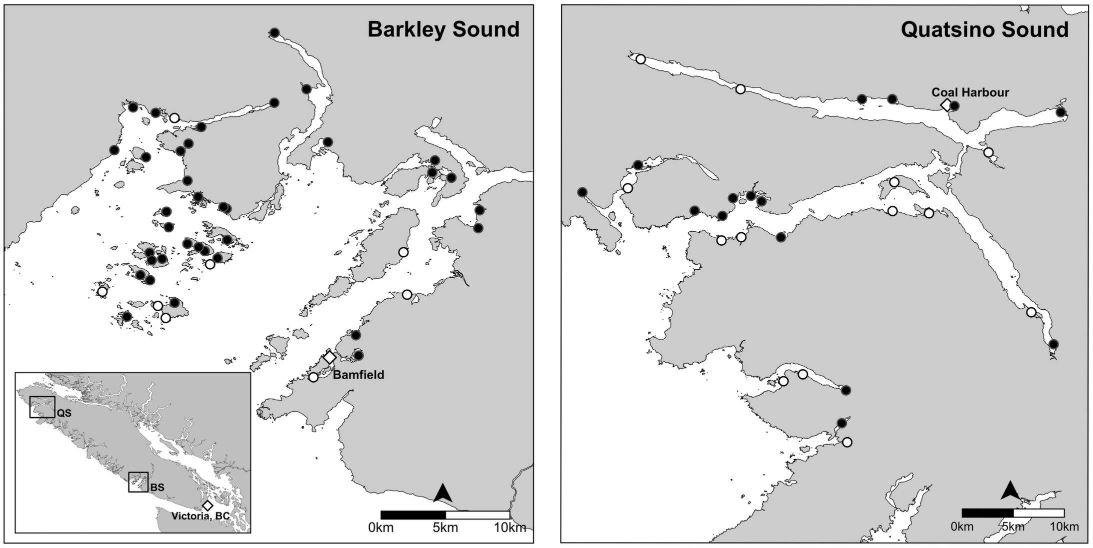

**Figure 5.1 Locations of green crab trapping surveys that occurred between 2010-2017.**
Sites were not surveyed in every year. Filled circles indicate sites where green crabs were detected at least once. Open circles indicate site where green crabs were never detected. White diamonds indicate local cities and towns for reference. The inset shows the locations of Barkley Sound (BS) and Quatsino Sound (QS) on Vancouver Island, British Columbia.

The same trapping method was used consistently, with some variation in effort (i.e., number of sets per site). A single set consisted of six Fukui fish traps, baited with frozen herring, strung on a 60 m groundline with 10 m spacing between traps. At each site, a trapping event typically consisted of two sets placed parallel to shore, 1 meter above mean low water (MLW), and one or two sets placed perpendicular to shore to assess the depth range across which green crabs occur. Sets were retrieved the next day, on the high tide (average soak duration: 23.1 h ± 2.6 h SD) and the trap contents enumerated, identified to species, and measured (notch-to-notch carapace width to the nearest mm). Additional details on the type and method of data collection can be found in Gillespie et al. (2007). Like all trap-based methods of estimating animal abundance, baited Fukui traps are imperfect (Bergshoeff et al. 2018). Both water temperature and agonistic interactions among crabs are likely to affect crab behaviour and therefore CPUE (Murray & Seed 2010, Bergshoeff et al. 2018). Despite these limitations, using CPUE from baited traps to distinguish between sites with a low or average abundance of green crabs from hotspots is appropriate, particularly if the focus is on inter-annual variability (Murray & Seed 2010).

## Data collection: Abiotic variables

Information was compiled on invariant site-level abiotic characteristics that could affect local green crab survival and population size (Table 5.1). The characteristics chosen were those that could affect larval propagule pressure, shelter and prey availability, and overall site-level temperature and salinity profiles. Most of these data were derived from GIS data layers (Table 5.1) using the program QGIS (v.2.18).

Inlet length and intertidal area were included as they are expected to have implications for propagule pressure. Inlet length is a measure of site isolation, as newly arriving larvae have to travel further to reach a suitable site to settle and larvae released are more likely to be retained locally if an inlet is especially long (Byers & Pringle 2006, Banas et al. 2009). In the absence of a standard method for measuring inlet length, I defined the head of the inlet as the low water mark at each site and the mouth of the inlet as the point at which the opposing banks were a minimum of 2 km apart. Although arbitrary, this distance worked well as a general rule to approximate the point at which the inlet or bay joined the nearest main channel. This approximation effectively distinguished long inlets from bays and coves. Intertidal area was included, as sites with larger areas are expected to have higher colonization rates and larger populations (Hanski 2001). Intertidal area was calculated as the area between the high and low water marks at each site that encompassed all trapping events at that site, based on Canadian Hydrographic Service (CHS) data.

Sediment type, presence of eelgrass (*Zostera* spp.), and the presence of Pacific oyster (*Crassostea gigas*) aquaculture were included as each could affect the survival of green crabs, through provision of cover and prey. Sediment type at each site was designated by the CHS, on a numerical scale ranging from rocky cliffs to estuary or marshland (Howes et al. 1995). There were two sites in Effingham Inlet, Barkley Sound for which the CHS data did not provide a classification, so these were assigned based on site visits. In Europe, the presence of eelgrass (predominately *Zostera marina*) is considered important shelter habitat for juvenile green crabs (Moksnes 2002). The presence of eelgrass at each site on the WCVI was determined from province-wide eelgrass survey data compiled by Tides Canada for the British Columbia Marine Conservation Analysis (2009). The data represent the occurrence of eelgrass at surveyed sites prior to 2010 (i.e., the start of the surveys presented here). Finally, the presence of Pacific oyster aquaculture facilities was included because near-shore oyster aquaculture tenures frequently inadvertently seed nearby beaches with feral oyster populations, which increases the structural complexity of the benthic habitat (Kelly et al. 2008). The cover provided by bivalve beds and shell hash has been shown to provide better cover for settling and juvenile green crabs than other types of benthic habitat (Hedvall et al. 1998, Moksnes 2002). Additionally, Pacific oysters are both a common vector for the human-mediated transport of invasive species, including green crabs, and are a known prey source for green crabs (Ruesink et al. 2005, Curtis et al. 2015). Locations of oyster aquaculture licenses issued for Barkley and Quatsino Sounds between 2010 and 2015 were obtained from the Department of Fisheries and Oceans Canada. A site was considered to have experienced Pacific oyster aquaculture if its location overlapped with or was immediately adjacent (< 1 km) to an aquaculture lease. While the license information itself does not definitively indicate whether or for how long oyster aquaculture was carried out at a site, I was able to confirm the operations of several tenures while conducting green crab trapping surveys. The data also do not exclude the possibility of feral populations of Pacific oyster resulting from natural spread.

The last set of characteristics, freshwater outflow magnitude and aspect, were included as proxies for site-level variation in salinity and temperature. Individual site-level measures of water temperatures and salinities could not be obtained for all sites, and more common measures, such as air temperature and rainfall data from weather monitoring stations or sea surface temperature from satellite data, were not at scales appropriate for detecting site-level differences (Lowen et al. 2016). Freshwater outflow magnitude was determined from data on the freshwater stream networks in British Columbia (Table 5.1), which provides a value for the known or estimated number of tributaries that join together to form a freshwater source (Gray 2010). The more tributaries contributing to a single freshwater input at a site, the larger the volume of freshwater discharge is expected to be, causing the salinity to be lower than at a site with a very small or non-existent freshwater input. To get an approximation of temperature at a site, the aspect for each site was recorded as the dominant cardinal or intercardinal direction (e.g., north, northeast, east, etc.). I used aspect as a proxy for temperature because south and west-facing slopes in the northern hemisphere typically receive more solar radiation than north and east-facing slopes.

Collinearity among site characteristics was low, with all two-way interactions having a correlation coefficient < 0.43. I initially included an approximate measure of slope for each site, but this was highly positively correlated with intertidal area (Pearson’s $r = 0.76$, $p < 0.001$), so slope was not retained as a site characteristic.

**Table 5.1 Abiotic site-level characteristics included in the BRT models, grouped by the hypothetical dominant mechanism of effect on green crab populations.**

| Abiotic variable | Units and observed range | Sources |
|---|---|---|
| **Propagule pressure and settlement** | | |
| Intertidal area | Measured in km$^2$<br>(207 m$^2$ – 1.59 km$^2$) | Canadian Hydrographic Service (CHS) High Water Mark Lines and Low Water Mark Lines shapefiles<br><br>Downloaded from the GeoBC Data Catalogue on June 9, 2017. |
| Inlet length | Measured to nearest km<br>(0 km – 30 km) | Using QGIS (v.2.18) measured as the shortest route from the low-water edge at the head of the inlet to mouth. |
| **Shelter and prey availability** | | |
| Sediment type | Types defined on a numerical scale with categories ranging from 3 (rock cliff) to 14 (estuary/marsh). Increasing values indicate a decrease in particle size and wave energy. | Canadian Hydrographic Service (CHS) *High Water Mark Lines* and *Low Water Mark Lines* shapefiles<br><br>Downloaded from the GeoBC Data Catalogue on June 9, 2017. |
| Eelgrass (categorical) | Presence/absence | British Columbia Marine Conservation *Analysis Eelgrass Polygons* shapefile<br><br>Downloaded from the BCMCA GIS database on September 7, 2017. |
| Oyster aquaculture (categorical) | Presence/absence | Based on the locations of oyster licenses issued by DFO between 2010-2015. |
| **Temperature and salinity** | | |
| Freshwater outflow magnitude | Count of the number of upstream 'nodes' (tributaries) contributing to single outflow.<br>(0 – 1477 nodes) | Province of British Columbia *Freshwater Atlas Stream Network* shapefile<br><br>Downloaded from the GeoBC Data Catalogue on August 23, 2018. |
| Slope aspect (categorical) | Classified by cardinal and intercardinal directions. | Visually determined as main direction the beach slopes. |

Measurement units, data ranges (in parentheses), and data sources given.

## Analysis

### *Trapping data requirements*.

Catchability refers to the proportion of standing population that can be caught with a particular fishing method. It is both difficult to quantify and control for but is critical for determining how well a fishing method approximates standing stock biomass (Francis et al. 2003). Variation in catchability in this dataset was primarily minimized by using standardized trapping protocols (e.g., set locations, bait, trap spacing). I also limited the analysis to the years 2010-2017 and to the months of May through September (Duncombe & Therriault 2017), and removed four individual sets for which the GPS coordinates of sets showed inconsistencies with the standard trapping protocol. At one site, Pipestem Inlet (40.038, -125.202), green crabs were trapped and removed annually between 2010 and 2014 as part of a separate reduction trapping experiment for invasive population control. I did not use the reduction trapping data. However, as Duncombe and Therriault (2017) concluded that reduction trapping had no net interannual effect on green crab populations in Pipestem Inlet, I opted to include two non-reduction trapping events that occurred several months prior to annual reduction trapping.

### *Calculating CPUE of green crab and other crab species*

To analyse trends in the trapping data, I first calculated the catch-per-unit-effort for each of four crab species (European green crab, Dungeness crab, red rock crab, and graceful crab), for each trapping event (n = 272). CPUE is the number of crabs of a species caught, divided by trapping time (i.e., the number of traps set multiplied by total average soak time of the set).

Because colder water temperatures are likely to slow crab metabolism and therefore movement, catchability of green crabs is thought to vary with season (Duncombe & Therriault 2017). A second-order polynomial model fit to the average daily green crab CPUE (all years combined) over Julian day (JD) was significantly better than a linear model (Likelihood ratio test: $X^2 = 1.62$, df = 1, p = 0.01), confirming a drop in catches in the shoulder months. To correct for this seasonal effect in catchability, I first determined the average peak trapping day for green crabs across all years from the polynomial model (July 18-19 or $JD_{peak} = 199.817$). Presence-only green crab CPUE was then modeled as a function of the absolute difference between $JD_{peak}$ and the actual trapping

Julian day, the slope of which was used to calculate an adjusted green crab CPUE that removes the variability driven by trapping day ($\text{CPUE}_{\text{adj}}$). No correction was made if green crab CPUE was zero, as it cannot be assumed that these are failures to detect green crabs due to catchability, rather than true absences.

### *Boosted regression trees*

To model CPUE data, the R package *gbm* was used in conjunction with the *caret* wrapper to produce gradient boosted regression trees (BRTs) (Elith & Leathwick 2011, Kunh 2008). BRT models combine the predictions from many weak models, called trees, to optimize the predictive performance of a final, average model. Each successive tree minimizes the error of the preceding tree following the loss function, which specifies the error distribution (Elith et al. 2008). As a result, trees become successively better at predicting the response variable while also minimizing error (De'ath 2007, Elith et al. 2008). Ensemble methods like BRTs also permit multiple variables, both categorical and continuous, to interact in complex and non-linear ways, and have relaxed assumptions around data structure, units, interactive effects, and missing values (Elith et al. 2008). This makes ensemble methods preferable when working with species abundance data (i.e., catches), as these are often zero-inflated, and habitat characteristics, which can be measured on very different scales.

As BRT models are prone to overfitting (De'ath 2007), two additional steps were taken during pre-processing to prevent and test for model overfitting. First, the data were initially randomly split into testing (20%) and training (80%) sets. Because sites were typically included multiple times in the data, sites were clustered together so that they occurred in one set or the other, but not both. This grouping allows the final model to encounter 'new' sites during model testing and addresses the issue of non-independence of site within the data (De'ath 2007). Second, all models were run with 10-fold cross-validation. The same use of grouping by site was applied when creating cross-validation folds in the training set. During cross-fold validation, 10 models were generated, each built on data from nine of the 10 'folds'. The average error across these models was used to determine the optimal number of trees and learning rate needed to produce the best model, i.e., that with the minimum predictive error (Elith et al. 2008). Both the use of testing and training sets and cross-fold validation were meant to ensure that the final model was not overfit to a particular subset of data, but that it could be generally applied to all the data. Finally, using the *caret* package, I was able to tune several hyperparameters that affect the learning algorithm, to find the optimal combination of learning rate, interaction depth, and number of trees needed to minimize overfitting (Kuhn 2008). Once the BRT models were optimized, I averaged the output across five runs of the model using these same hyperparameter settings (Greenberg et al. 2017).

Because the green crab $CPUE_{adj}$ data were zero-inflated, analysis was based on a two-step delta-lognormal approach and two BRT models were produced (Dedman et al. 2015, Froeschke & Froeschke 2016). The first model used green crab presence or absence (0/1) as the dependent variable. The second model used as the dependent variable the $\log(CPUE_{adj})$ for trapping events in which green crabs were caught. Both models used the full suite of seven site-level characteristics (Table 5.1), plus the year of the trapping event, and the CPUE for the three native crab species for each trapping event, for a total of 11 predictor variables. For the BRT analyses, the categorical predictors were dummy-encoded prior to running the models.

The first BRT modeled the probability of green crab occupancy using a binomial (Bernoulli) loss function. Due to the strong class imbalance toward sites with green crabs, an additional pre-processing step was needed to even out the representation of the classes in the training dataset. Following the Synthetic Minority Over-sampling Technique (SMOTE), the training dataset was resampled through a combination of oversampling the absence data and undersampling the presence data, such that the two conditions both occurred in trees roughly 50% of the time (Chawla et al. 2002). Hyperparameter tuning on the resampled training data determined the best model based on 900 trees, a learning rate of 0.002, and interaction depth of 7. These hyperparameters were used to rerun the model (n = 5 times) and determine the average relative influence of predictor variables and the average predicted probability of green crab occupancy for all trapping events (n = 420 events, with SMOTE over-sampling).

The second BRT model predicted the $\log(CPUE_{adj})$ of green crabs across all presence-only sites and trapping events (n = 192 events). Because there were so few sites with aspects facing east and northeast (n = 2 sites each), there were insufficient data for these aspects to be equally represented in both the testing and training data sets. As such these two levels of the aspect variable were dropped as predictors. A BRT with a

Gaussian loss function was run on the processed training data. The final model was parameterized on 600 trees, a learning rate of 0.005, and an interaction depth of 7. These parameters were then used to predict average log($CPUE_{adj}$) for all 192 presence-only trapping events and average relative variable importance over five iterations of the model.

## Results

Over eight years of trapping (n = 272 trapping events), effort was concentrated in Barkley Sound (72%) and was highest overall in 2014 and 2015 (Fig. 5.2a). The average $CPUE_{adj}$ over all trapping events and all years was 0.40 green crab per trap-day (± 0.64 SD), which equates to approximately 165 green crabs caught, if back-calculated using the standard effort of 18 traps set for 23 hours. The highest $CPUE_{adj}$ recorded was 5.07 crabs per trap-day (n = 1925 green crabs) at Hillier Island (49.032, -125.325) in 2016. Green crabs were consistently present at 29 sites (40%) and consistently absent at 21 sites (29%), while the remainder fluctuated between presence and absence over eight years (Fig. 5.2b).

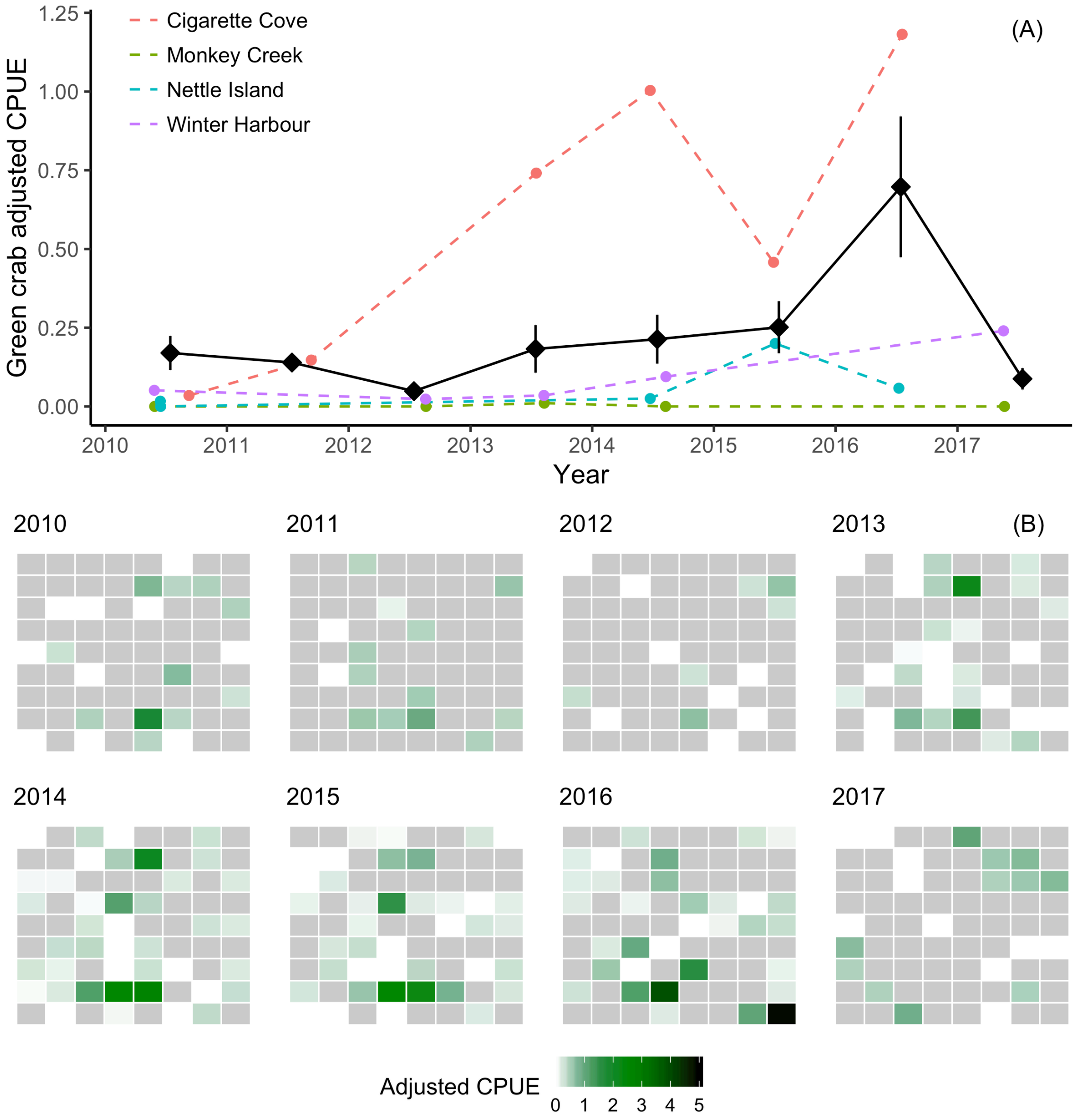

**Figure 5.2 Summary of CPUE for European green crab, adjusted for seasonal variation in catchability (see text), for 72 sites surveyed between 2010 and 2017 on the west coast of Vancouver Island.**

(A) Average green crab CPUE$_{adj}$ (± SE) for all trapping events per year (black solid line) and CPUE$_{adj}$ over time for four representative sites to depict some common trends in green crab abundance. (B) Maximum annual CPUE$_{adj}$ for green crab for each of 72 sites surveyed. Sites are represented in the same place in the grid every year. Greyed out cells indicate the site was not surveyed that year; white indicates that a site was trapped but no green crabs were caught.

In most years, sites were only trapped once, if at all, but repeated trapping events within a year did occur. The most frequently trapped sites overall, excluding reduction trapping in Pipestem Inlet, were Hillier Island (32 trapping events, 12%), followed by Useless Inlet

(48.993, -125.029; 11 trapping events, 4.0%). On average, sites were trapped 3.78 (± 3.95 SD) times over eight years. No site was visited every year, but Hillier Island was only missed in 2017. Of the 72 sites trapped, 14 (19%) were only ever visited once.

## Probability of green crab occupancy

The final BRT model for probability of green crab occupancy resulted in an average model accuracy of 0.85 over all cross-validation folds. When used to predict green crab occupancy on the testing set, the overall accuracy was 0.77 (lower 95% CI = 0.61, upper 95% CI = 0.88), which was significantly better than random classification (p = 0.001). Across the five re-run models, model accuracy ranged from 0.82 to 0.84. Relative variable importance for predicting green crab occupancy was highest for the CPUE of the native Dungeness crab (average relative importance = 33.5 ± 0.04% SE), followed by intertidal area (average relative importance = 9.99 ± 0.12% SE) (Fig. 5.3, Table D.1).

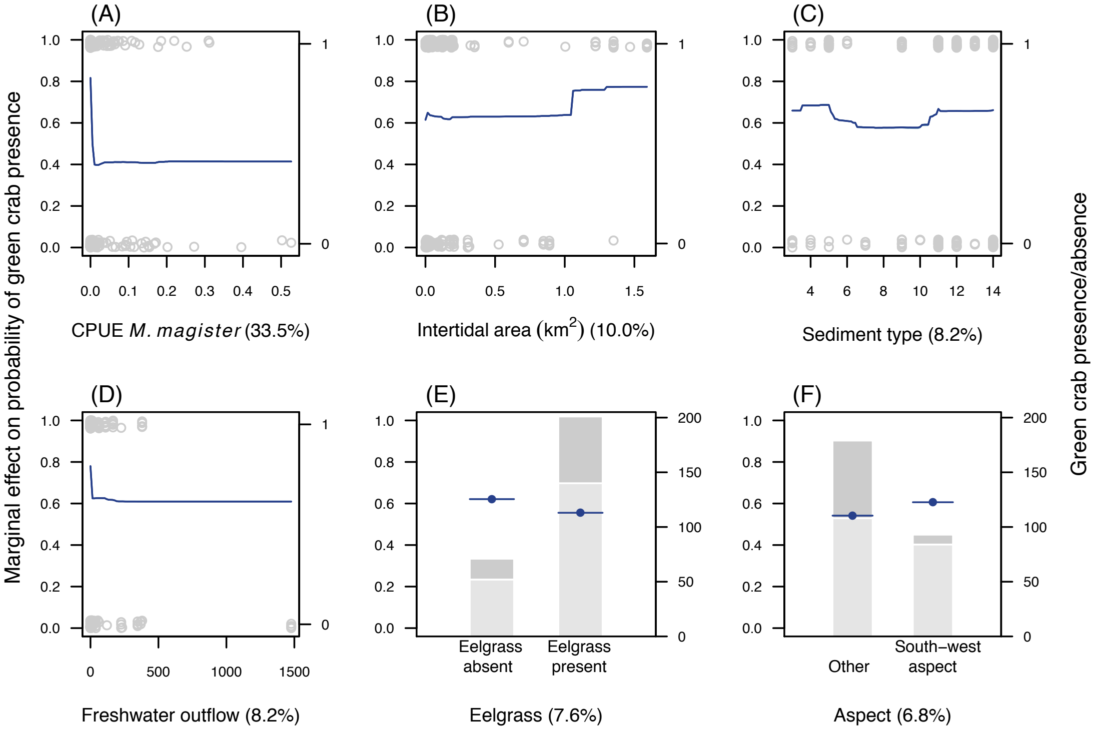

**Figure 5.3 Partial dependency plots of the marginal effect of the predictor variable (when all other predictors are averaged) on the probability of invasive green crab occurring at a site.**
Only the top 6 predictors of green crab occupancy are shown, as determined by relative variable importance (indicated in parentheses). Lines indicate the average fitted response and shading the maximum and minimum fitted response, over five model runs. Note the model fit was very consistent among all runs so shaded region is not visible. Grey points (A-D) indicate trapping events where green crabs were present (1) or absent (0) over the range of the predictor variable. For the categorical predictors eelgrass (E) and aspect (F) the grey bars indicate the total number of trapping events where green crab were absent (light grey) or present (dark grey) at sites, for each level of the categorical predictor.

## Predicted green crab log(CPUE$_{adj}$)

The final BRT model for green crab log(CPUE$_{adj}$) had an R$^2$ of 0.40 and root mean squared error (RMSE) of 0.65 over all cross-validation folds. When used to predict the log(CPUE$_{adj}$) of the test set, there was no significant difference between the predictions and observed values (paired t-test, t = 1.56, df = 37, p = 0.13), indicating that the model was not overfit to the training data. Across all five models used to predict the log(CPUE$_{adj}$) for all 192 trapping events, model R$^2$ ranged from 0.39 to 0.41, and RMSE from 0.64 to 0.65. Freshwater outflow magnitude had the greatest average importance (20.0 ± 0.31% SE), followed by the year the crabs were trapped (16.9 ± 0.26% SE) and the CPUE of graceful crab (16.2 ± 0.16% SE) (Fig. 5.4, Table D.2).

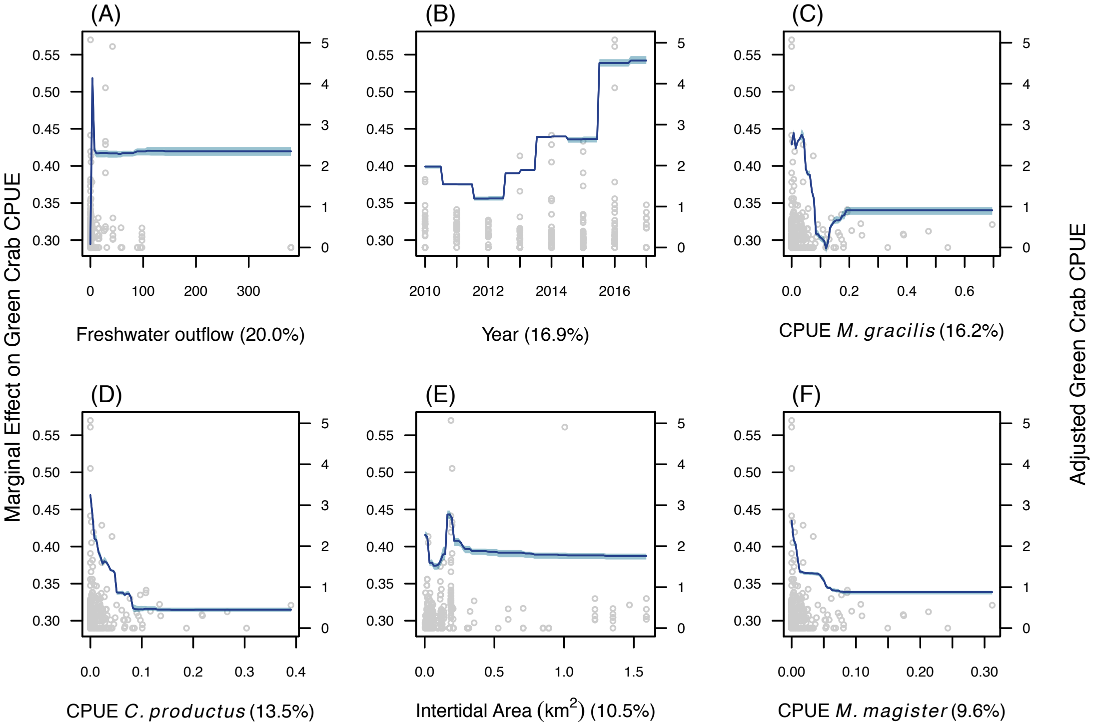

**Figure 5.4 Partial dependency plots of the marginal effect of the predictor variable (when all other predictors are averaged) on the adjusted green crab CPUE$_{adj}$ (unlogged) at a site.**

Only the top 6 predictors of green crab CPUE$_{adj}$ are shown, as determined by relative variable importance (indicated in parentheses). Lines indicate the average fitted response and shading the maximum and minimum fitted response, over five model runs. Grey points indicate the presence-only green crab CPUE$_{adj}$ over the range of the predictor variable.

## Discussion

After an invasive species has established, effective management requires an understanding of the distribution of that species. Species distribution modelling in invasion ecology can be a powerful tool to predict spread, though only if predictions are made at relevant scales. Further, because the impacts of invasive species are often density-dependent, these models should go beyond occupancy alone and consider abundance. For invasive European green crab on the WCVI, I found that very large populations were associated with soft-sediment habitats with large intertidal areas, as expected. Persistent low and medium abundances of green crab occurred across a much wider range of habitat characteristics. This result presumably reflects the species' generalist life history and broad physiological tolerances, as elsewhere in the world green crabs occur in diverse habitats that range from the rocky subtidal to brackish lakes and mangrove forests (Behrens Yamada 2001, Klassen & Locke 2007, Breen & Metaxas 2008, Garside & Bishop 2014). More surprisingly, my results also indicate that green crab abundance on the WCVI is significantly negatively associated with the abundance and distribution of the large crab species native to the region. This finding highlights a previously understudied role of interspecific interactions in controlling invasive green crabs in British Columbia.

The overall accuracy of the green crab occupancy BRT model (Fig. 5.3) suggest it could be used to predict the presence of green crabs in parts of the WCVI not yet surveyed. However, the model also revealed that detecting green crabs would be most effective if predictions are based on *a priori* knowledge of the abundance of Dungeness crabs in the area of interest. Indeed, the addition of any Dungeness crab at a site reduced the probability of green crab occurring at that site by half (Fig. 5.3a). This effect on green crab site occupancy was stronger than that of any physical habitat characteristic or other biotic interaction. In the absence of pre-existing information on Dungeness crab abundance however, the physical characteristics that best predict green crab occupancy are sites with more than 1 $km^2$ of intertidal area, with soft sediments consisting of sand, mud, or fine sediment, and low to intermediate freshwater input (Fig. 5.3b-d). Although these findings generally concur with pre-existing knowledge about green crab habitat preferences in British Columbia, sediment type was less important as a predictor than expected, only increasing or decreasing the probability of green crab occupancy by ~10%, as green crabs were found over the whole range of sediment types (Fig. 5.3c). While the occurrence of green crabs in rocky intertidal habitats was unexpected for the WCVI, the species is capable of living in rocky habitats elsewhere in their native and invasive ranges (Klassen & Locke 2007).

The presence-only BRT model was less accurate than the occupancy model. This was particularly evident at the extreme values of the site characteristics where there were fewer data points. Because the model had less information on which to form predictions about how or if these extreme values had any effect on green crab abundance, some model fits plateau around the global average $CPUE_{adj}$ (0.40 crabs per trap-day) (Fig. 5.4a,e). The strongest predictor of green crab abundance was freshwater outflow magnitude. Green crabs were present in very low abundances at sites without a source of fresh water but were up to 1.5 times more abundant with the addition of any fresh water (Fig. 5.4a). Abundance declined again as the volume of fresh water continued to increase, similar to the pattern observed for probability of occurrence (Fig. 5.4a; Fig. 5.3d). This non-linear relationship may reflect the upper and lower salinity limits for larvae, which have a narrower tolerance for salinity than adult green crabs (Nagaraj 1993, Behrens Yamada 2001). The only other informative physical characteristic for predicting green crab abundance was intertidal area. Larger sites generally predicted more green crabs, as expected, up to a threshold around 0.20 km$^2$ (Fig. 5.4e). The largest catches of green crabs were not associated with the largest sites, possibly because the biggest intertidal areas also had large freshwater sources, such as the Marble River estuary in Quatsino Sound (0.8 km$^2$). These sites may have been less suitable habitats for green crabs due to lower salinity or high tidal exchange ratios that made it more difficult for larvae to remain in the estuary long enough to settle before being flushed out again (Grindley 1972, Banas et al. 2009). There was an overall lack of strong effects of any other abiotic or biogenic habitat characteristics on green crab abundance. Rather, the model shows that increasing the abundance of any of the three native crab species was associated with significant decreases in green crab CPUE (Fig. 5.4c-d, f). There was also a noticeable increase in green crab CPUE over time, with a particularly large jump in 2016 (Fig. 5.4b), which coincides with the anomalously warm sea surface temperatures of the preceding two years (Cavole et al. 2016).

If predation and competition with native crabs is the best explanation for the consistently negative impact of native crabs on both green crab abundance, it is possible that green crab behaviour is also affected. If so, green crab CPUE at sites with high abundances of large, native crabs, may have been underestimated if green crabs were less active or warier of entering traps (Hunt et al. 2003, Bergshoeff et al. 2018). It is not possible to know definitively how or if this affected my analysis, as the effect is either masked by or confounded with depth. I regularly observed large native crabs in traps set below MLW, while green crabs dominated above. This pattern could mean that subtidal green crabs were less likely to be caught because they were modifying their behaviour to avoid predators. Alternatively, it could mean that large native crabs exclude green crabs in the subtidal entirely. There is some evidence for the latter as visual transects done on SCUBA at Pipestem Inlet demonstrated zonation, with European green crabs being replaced by graceful crabs with increasing depth (IM Côté 2013, pers. comm.).

Every introduction of a non-native species to a novel ecosystem, whether at the regional or site level, produces new context-dependent biotic associations. This context-dependency is one of the most challenging aspects of invasive species management because there is usually little to no specific information available about these associations. By building species distribution models that include the distribution and abundance of native species it is possible to develop some general understanding about where an invasive species might spread, where it will become most abundant, and whether there is the potential for some biotic resistance (*sensu* Stachowicz et al. 2002). On the WCVI, a continuous time series of trapping data for multiple crab species provided the opportunity to model invasive green crab distribution at a scale appropriate for the species' management, while incorporating abiotic and biotic characteristics important to the species' ecology. There are some challenges to using long-term fisheries survey datasets, like this one, including inconsistencies in the methods that cannot be accounted for (e.g., set depth, age of bait, experience of the operator), the large variation in habitat characteristics and scales, and both temporal and behavioural stochasticity. However, ensemble learning methods provide a statistical tool that can adapt to these complex datasets and still generate useful predictions about how species distribute themselves over heterogenous landscapes.

For European green crabs on the west coast of Vancouver Island, physical parameters like intertidal area, sediment type, and freshwater outflow magnitude provide some idea of where green crabs might be present. While abundance was also tied to some physical characteristics, particularly freshwater outflow magnitude, annual variation and biotic associations with native crab species were the strongest predictors of green crab abundance. If this pattern is underpinned by a relationship between water temperature and green crab reproduction, then warmer summers will increase green crab reproductive output and recruitment. As such, we should expect already dense sites to continue to grow exponentially, leading to 'hyper-abundant' (hotspot) sites, especially in warm years. From a management perspective, this suggests survey efforts should increase during and immediately after anomalously warm summers to detect these rapidly expanding populations. The most consistent pattern demonstrated here was the importance of native crab abundance, not physical characteristics, in determining green crab occupation at a site. This result highlights the potential importance of maintaining native crab populations, particularly Dungeness crab which have declined in abundance since the 1990s (Orensanz et al. 1998), to provide some biotic resistance against expanding invasive European green crab populations in British Columbia.

# Chapter 6.

# General discussion

Applying ecological research to real world problems will always involve uncertainty arising from the absence of context-specific information. To fill these gaps in knowledge we often rely on our collective understanding of similar problems. Given enough case studies, we can find reliable general principles, theories, and concepts that apply across ecosystems and ecological disciplines. Generalizations like the theory of island biogeography (MacArthur & Wilson 1967), metapopulation dynamics (Levins 1969), or keystone species (Paine 1969) are now fundamental to ecological understanding. Invasion ecology relies on all of these generalizations to understand the risk of species transport, introduction, establishment, population growth, and spread (Fig. 6.1). However, the last step of the invasion process, itself a generalization (Lockwood et al. 2007), is impact; a step that is largely specific to invasion ecology. There is to date no unifying framework for impact prediction that has been singularly adopted, although many have been proposed (e.g., Parker et al. 1999, Blackburn et al. 2014, Dick et al. 2017). Reliable generalizations remain elusive because of context dependency, as each new introduction event creates a unique ecological community, resulting from the interactions between the introduced species, the native species, and the environment (Chapter 1).

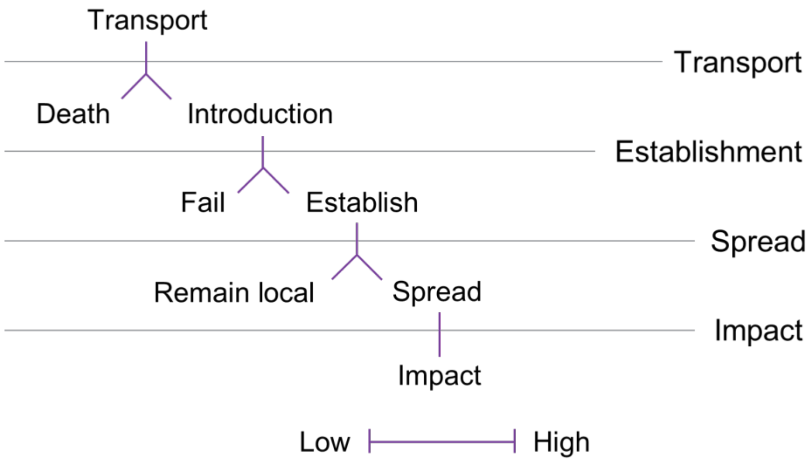

**Figure 6.1 Theoretical model of the invasion process.**
Adapted from Lockwood et al. 2007.

While I think it is unlikely that there will ever be a theory that can completely underpin impact prediction, there do need to be some useful generalizations (or rules of thumb) to proceed with impact prediction and invasive species management. In this thesis, I have explored three of the more common general principles of invaded systems invoked in the literature: that invasive consumers will have a larger impact than native ones (Chapter 2), that past invasions of the same or similar species can inform new invasions (Chapter 3), and that the abundance of invasive species is the best predictor of impact magnitude (Chapters 4 and 5). In these chapters I tested the reliability of these assumptions for a specific group of invasive animals, marine true crabs. However, because the ultimate goal is to find general principles that can apply across invaded systems, I put these same general principles to the test in a very different context.

African hippopotamuses (*Hippopotamus amphibius*) were introduced to Colombia by the drug lord Pablo Escobar in the late 1980s. Four hippos were imported and left to roam throughout his compound, and beyond, about 100 km outside the city of Medellín. There are now 60-70 hippos in Colombia living both within and around the Magdalena River. While locals see them as a mascot, there are a handful of scientists and government officials who are concerned by both the public safety risk posed by roaming hippos and their potential ecological impact (Aguilera 2018, Wilcox 2018). Because the latter has not been studied sufficiently to appear in the literature, impact assessment must be predicted based on what we know from other invaded systems.

To determine what impacts an invasive population of hippos might have on a Colombian freshwater ecosystem, I first considered whether it could have different or larger impacts than similar native species. From Chapter 2, we know the assumption that invasive crabs consistently have a larger effect on native prey abundance than native crabs does not hold, likely because the role of co-evolution and prey naïveté in each specific system need to be considered. This is connected to the distinctiveness hypothesis, which predicts that the more novel an invasive species is, the less likely it is that native species in the recipient ecosystem have evolved appropriate defenses or co-existence strategies, hypothetically leading to larger impacts (Ricciardi & Atkinson 2004, Sih et al. 2010). This begs the question, how novel is novel enough? The most scientifically rigorous distinction draws the line taxonomically (Ricciardi & Atkinson 2004). However, functional similarity/dissimilarity is often thought to be sufficient; the more functionally similar the invasive species is to the native species, the less significant its impacts (e.g., Salo et al. 2007; Paolucci et al. 2013), although this does not exclude the possibility that the invasive species outcompetes and replaces the native one in the process (e.g., the invasive grey squirrel, *Sciurus carolinensis*, and native red squirrel *S. vulgaris* in Europe [Kenward & Holm 1993, Bertolino et al. 2014]). There have never been any species in the family Hippopotamidae in South America, and the next nearest native ancestors are the llamas and guanacos (family Tylopoda). However, there are two species of large, unrelated, herbivorous aquatic or semi-aquatic mammals that are functionally similar to hippos: Amazonian manatee (*Trichechus inunguis*), which structure aquatic angiosperm communities and habitats, and capybara (*Hydrochoerus hydrochaeris*), an important contributor of terrestrial nutrients to aquatic ecosystems (Bakker et al. 2016). In their native range of sub-Saharan Africa, hippos serve both of these functions in freshwater ecosystems. Their movements through wetlands and river channels, and between freshwater and terrestrial habitats, disturb aquatic plants, create new waterways, and redistribute nutrients so comprehensively that they are considered ecosystem engineers (Bakker et al. 2016). If the aquatic plant life of Colombia can withstand similar disturbance from large native herbivores, perhaps the freshwater ecosystem will also be resilient to the impacts of hippos. This prediction would contradict the expectation made on the basis of a taxonomically-based assessment.

An interesting addendum to the generalization that functionally similar species should have similar effects on a shared ecosystem is that the invasive species does not have to be similar to an extant native species for it to apply. This idea posits that North and South American ecosystems initially evolved in the presence of megafauna such as mastodon, giant armadillos, and sabre-toothed cats, which were driven to extinction, possibly by human exploitation, in the early Holocene (Svenning & Faurby 2017). The idea of trophic re-wilding proposes that replacing extinct prehistoric megafauna with functionally equivalent extant species should restore ecosystem functioning that was lost 11,000 years ago (Svenning & Faurby 2017). While the intentional replacement of long-extinct fauna by invasive species like hippos seems unreasonably risky, re-wilding efforts with large, extant, native mammals, such as wolves (*Canis lupus*) in North America and bison in both North America (*Bison bison*) and Europe (*B. bonasus*), have been successful and had significant, largely positive, impacts on the function of these ecosystems (Laundré et al. 2001, Cromsigt et al. 2017).

Another general property of invaded systems that we can use to predict impact is comparing impacts intraspecifically by considering the species' invasion history. Ironically, the reliability of the intraspecific comparative approach increases with replication, making it easier to apply to the handful of species with a long history of being moved around the globe by people. Eurasian species in particular have historically followed patterns of European exploration, trade, and colonialism (Simberloff 2013). The relatively small suite of Eurasian invasive species that includes rats (*Rattus rattus*), common starlings (*Sturnus vulgaris*), and European green crabs (*Carcinus maenas*) are all well-studied. Green crabs have been successfully introduced at least five times that we know of, and likely many more if re-introductions are included (Behrens Yamada 2001, Carlton & Cohen 2003). In Chapters 3 and 4 I investigated the impacts of green crabs through the lens of historical invasion events. On one hand, these results demonstrated the predictive power of intraspecific comparison for predicting impacts, as the North American green crabs on both coasts were highly efficient predators (Chapter 3) and had similar ecosystem impacts on eelgrass beds (Chapter 4). On the other hand, the assumption that an invasive species' impacts will be similar among regions breaks down when comparing North American invasive green crabs with those from South Africa (Chapter 4).

However, modern trade routes, immigration patterns, and the global climate are changing, and so are the species being introduced. More Asian and Mediterranean species are establishing in North America (e.g., grass carp [*Ctenopharyngodon idella*], Burmese python [*Python bivittatus*], Indo-Pacific lionfish [*Pterois volitans*]), and North and West African species are establishing in Australia and the United States (e.g., buffel grass [*Cenchrus ciliaris*], West Nile virus). Many of these species have no known previous history as an invasive, making it impossible to make predictions about their impacts in this manner. The same applies to African hippopotamus, which have no known successful introductions, other than that in Colombia.

The last general approach to predicting impact of an invasive species that I examined in this thesis is based on abundance in the invaded range. I expect that this is the most consistently useful metric for predicting impact severity of an invasive species in a new ecosystem. However, the drawback is that without a *per capita* or density-dependent measure of impact for a specific interaction of interest, abundance cannot be used to predict the actual effects of an invasive species. In Chapter 4, the strong relationship between abundance (measured as density of green crabs) and impact (measured as the loss of eelgrass shoots) makes it possible to use measures of green crab abundance or density in other eelgrass beds to specifically predict impact. In Chapter 5, on the other hand, the model only predicts abundance (i.e., catch-per-unit-effort) of green crabs in British Columbia, Canada. This is still useful, so long as impact scales with abundance. As it applies to hippos, if the assumption holds that the larger the herd the greater their ecological effect, then the current growth rate of the Colombian hippo population is a cause for concern, especially considering these hippos may be reaching maturity sooner and reproducing faster than they do in Africa (Mosendz 2014). However, currently there is no direct empirical evidence for a relationship between hippo abundance and ecological impacts in Colombia, and there are suggestions from other systems that the relationship does not always hold. For example, invasive Japanese skeleton shrimp (*Caprella mutica*) can occur in densities over 100,000 $m^{-2}$ on subtidal marine structures, yet there is little or no evidence of impacts to the native fouling community (Howard et al. 2018).

In the first year of my PhD program I was fortunate enough to travel to southern Africa on CAISN II funding for a workshop on invasive species. Afterwards, while travelling in Zimbabwe and Botswana, I saw hippos in their natural (and native) habitat. During the trip, I also happened to read Daniel Simberloff's book, *Invasive Species: What Everyone Needs to Know* (2013). The book reviews a staggering number of case studies, from every corner of the invasion literature. The diversity of invasive species, interactions, and impacts must have made an impression because I proceeded to build the issues of context-dependency and impact prediction into my thesis. From my work, I believe that context dependency will always lead to unpredictable exceptions. There will be species assumed to be benign that will transform ecosystems, and presumed high-impact invaders that will make no difference at all. Within just the body of work presented here, I found the potential for both outcomes in one species, the European green crab.

In an ideal world, it would be possible to conduct contemporaneous research alongside each introduction or range expansion to make context-specific, informed management decisions. This will never be the case, whether because of social, political, or practical reasons like funding. The ability to do comprehensive research on the hippopotamuses in Colombia is hindered by all three. Until these circumstances change, the Colombian government has two options: ignore the problem and hope the species has no significant impact or apply a general understanding of invasive species impacts to predict and proactively manage for possible outcomes. Using just the generalizations discussed here, an argument could be made that hippos should have a minimal impact. There are already native species in Colombia that restructure freshwater ecosystems, so invasive hippos may not be so functionally novel as to have major impacts. However, while there are no other invasive populations of hippos to use as a comparison, looking at the importance of hippos as ecosystem engineers in Africa, I think it is more likely that hippos represent a greater habitat disturbance to Colombian freshwater ecosystems than manatees and capybaras combined. If this is the case and significant impacts are predicted, how many hippos it will take make those impacts detectable? As long as the answer to this remains unknown, the assumption that impacts scale with abundance means that limiting the population growth of invasive hippos is the most precautionary management approach. Whether it be for hippopotamuses in Colombia or European green crabs in Barkley Sound, impact prediction will continue to rely on general principles like those presented here to inform management. The only given therefore is that in invasion ecology, like in life, there is an exception to every rule.

Hippopotamus on the Zambezi River, Zimbabwe © Brett R. Howard 2013

# References

Aguilera MC (2018, April) A Drug Lord and the World’s Largest Invasive Animal. UC San Diego News Center. Retrieved from https://ucsdnews.ucsd.edu/feature/a-drug-lord-and-the-worlds-largest-invasive-animal

Alcaraz C, Bisazza A, García-Berthou E (2008) Salinity mediates the competitive interactions between invasive mosquitofish and an endangered fish. Oecologia 155:205–213

Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biol Lett 10:20130946

Alexander ME, Kaiser H, Weyl OLF, Dick JTA (2015) Habitat simplification increases the impact of a freshwater invasive fish. Environ Biol Fishes 98:477–486

Allen JA (1998) Mangroves as alien species: the case of Hawaii. Glob Ecol Biogeogr Lett 7:61–71

Alpert P (2006) The advantages and disadvantages of being introduced. Biol Invasions 8:1523–1534

Archambault P, Snelgrove PVR, Fisher JAD, Gagnon JM, Garbary DJ, Harvey M, Kenchington EL, Lesage V, Levesque M, Lovejoy C, Mackas DL, McKindsey CW, Nelson JR, Pepin P, Piché L, Poulin M (2010) From sea to sea: Canada’s three oceans of biodiversity. PLoS One 5:e12182

Armstrong DA, Rooper C, Gunderson D (2003) Estuarine production of juvenile Dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. Estuaries 26:1174–1188

Aronson RB, Frederich M, Price R, Thatje S (2015) Prospects for the return of shell-crushing crabs to Antarctica. J Biogeogr 42:1–7

Bakker ES, Pagès JF, Arthur R, Alcoverro T (2016) Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. Ecography 39:162–179

Baldridge AK, Smith LD (2008) Temperature constraints on phenotypic plasticity explain biogeographic patterns in predator trophic morphology. Mar Ecol Prog Ser 365:25–34

Baldwin JR, Lovvorn JR (1994) Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. Mar Ecol Prog Ser 103:119–127

Banas NS, McDonald PS, Armstrong DA (2009) Green crab larval retention in Willapa Bay, Washington: an intensive Lagrangian modeling approach. Estuaries and Coasts 32:893–905

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ, Alexander ME, Bovy HC (2014) Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. J Anim Ecol 83:693–701

Barrios-O'Neill D, Kelly R, Dick JTA, Ricciardi A, MacIsaac HJ, Emmerson MC (2016) On the context-dependent scaling of consumer feeding rates. Ecol Lett 19:668–678

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313–323

Behrens Yamada S (2001) Global Invader: The European Green Crab. Oregon State University, Corvallis, OR

Behrens Yamada S, Boulding EG (1998) Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. J Exp Mar Bio Ecol 220:191–211

Behrens Yamada S, Davidson TM, Fisher S (2010) Claw morphology and feeding rates of introduced European green crabs (*Carcinus maenas* L, 1758) and native Dungeness crabs (*Cancer magister* Dana, 1852). J Shellfish Res 29:471–477

Behrens Yamada S, Gillespie GE (2008) Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? ICES J Mar Sci 65:725–729

Behrens Yamada S, Peterson WT, Kosro PM (2015) Biological and physical ocean indicators predict the success of an invasive crab, *Carcinus maenas*, in the northern California Current. Mar Ecol Prog Ser 537:175–189

Behrens Yamada S, Groth SD (2016) Growth and longevity of the red rock crab *Cancer productus* (Randall, 1840). J Shellfish Res 35:1045–1051

Bellrose FC, Trudeau NM (1988) Wetlands and their relationship to migrating and winter populations of waterfowl. In: Hook DD (ed) The Ecology and Managment of Wetlands. London, UK, p 183–194

Bergshoeff JA, McKenzie CH, Best K, Zargarpour N, Favaro B (2018) Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada. PeerJ 6:e4223

Bertness MD (1984) Habitat and communty modification by an introduced herbivorous snail. Ecology 65:370–381

Bertness MD, Coverdale TC (2013) An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. Ecology 94:1937–1943

Bertolino S, Cordero di Montezemolo N, Preatoni DG, Wauters LA, Martinoli A (2014) A grey future for Europe: *Sciurus carolinensis* is replacing native red squirrels in Italy. Biol Invasions 16:53–62

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12:e1001850

Boese BL, Kaldy JE, Clinton PJ, Eldridge PM, Folger CL (2009) Recolonization of intertidal *Zostera marina* L. (eelgrass) following experimental shoot removal. J Exp Mar Bio Ecol 374:69–77

Bolker BM (2008) Modeling variance. In: Ecological Models and Data in R. Princeton University Press, Princeton, NJ, p 316–336

Bollache L, Dick JT, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. Biol Lett 4:166–169

Borenstein M, Hedges LV, Higgins JPT, Rothstein H (2009) Introduction to Meta-analysis. John Wiley & Sons Ltd., Chichester, UK

Boudreau ML, Boudreau MR, Hamilton DJ (2013) The influence of body size on foraging facilitation and kleptoparasitic behavior in the green crab (*Carcinus maenas*). J Exp Mar Bio Ecol 449:330–334

Boudreau MR, Hamilton DJ (2012) Seasonal variation in effects of multiple predators on an intertidal mussel bed: implications for interpretation of manipulative experiments. Mar Ecol Prog Ser 465:137–153

Boudreau S, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. Mar Ecol Prog Ser 469:195–213

Boulding EG (1984) Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. J Exp Mar Bio Ecol 76:201–223

Boulding EG, Hay TK (1984) Crab response to prey density can result in density-dependent mortality of clams. Can J Fish Aquat Sci 41:521–525

Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol Mar Res 63:95–106

Breen E, Metaxas A (2008) A comparison of predation rates by non-indigenous and indigenous crabs (juvenile *Carcinus maenas*, juvenile *Cancer irroratus*, and adult *Dyspanopeus sayi*) in laboratory and field experiments. Estuaries and Coasts 31:728–737

Breen E, Metaxas A (2012) Predicting the interactions between "ecologically equivalent" indigenous and nonindigenous brachyurans. Can J Fish Aquat Sci 69:983–995

Brian JV, Fernandes T, Ladle RJ, Todd PA (2006) Patterns of morphological and genetic variability in UK populations of the shore crab, *Carcinus maenas* Linnaeus, 1758 (Crustacea: Decapoda: Brachyura). J Exp Mar Bio Ecol 329:47–54

British Columbia Marine Conservation Analysis (2011) Marine Atlas of Pacific Canada: a product of the British Columbia Marine Conservation Analysis (BCMCA). Victoria, BC

Brookes JI, Rochette R (2007) Mechanism of a plastic phenotypic response: Predator-induced shell thickening in the intertidal gastropod *Littorina obtusata*. J Evol Biol 20:1015–1027

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York, NY

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie J-C, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Byers JE, Pringle JM (2006) Going against the flow: retention, range limits and invasions in advective environments. Mar Ecol Prog Ser 313:27–41

Byers JE, Reichard S, Randall JM, Parker IM, Carey S, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. Conserv Biol 16:630–640

Byers JE, Smith RS, Pringle JM, Clark GF, Gribben PE, Hewitt CL, Inglis GJ, Johnston EL, Ruiz GM, Stachowicz JJ, Bishop MJ (2015) Invasion expansion: time since introduction best predicts global ranges of marine invaders. Sci Rep 5:12436

Calderwood J, O'Connor NE, Roberts D (2016) Breaking and entering: examining the role of stress and aerial exposure in predator-prey relationships between the common shore crab (*Carcinus maenas*) and cultivated blue mussels (*Mytilus edulis*). Aquaculture 452:217–223

Carlton JT, Cohen AN (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. J Biogeogr 30:1809–1820

Carlton JT, Newman WA, Pitombo FB, Melorose J, Perroy R, Careas S, Galil BS, Clark PF, Carlton JT, Boos K, Ashton G V, Cook EJ (2011) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. In: Galil BS, Clark PF, and Carlton JT (eds). Springer Netherlands, Dordrecht, Netherlands

Carpenter SR, Chisholm SW, Krebs CJ, Schindler DW, Wright RF (1995) Ecosystem experiments. Science 269:324–327

Carroll JC, Winn RN (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)--brown rock crab, red rock crab, and yellow crab. US Fish Wildl Serv Biol Reports 82:iii-16

Cavole L, Demko A, Diner R, Giddings A, Koester I, Pagniello C, Paulsen M-L, Ramirez-Valdez A, Schwenck S, Yen N, Zill M, Franks P (2016) Biological Impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 29:273–285

Chakravarti LJ, Cotton PA (2014) The effects of a competitor on the foraging behaviour of the shore crab *Carcinus maenas*. PLoS One 9:e93546

Chan K, Bendell LI (2013) Potential effects of an invasive bivalve, *Nuttallia obscurata*, on select sediment attributes within the intertidal region of coastal British Columbia. J Exp Mar Bio Ecol 444:66–72

Chawla NV, Bowyer KW, Hall LO, Kegelmyer WP (2002) SMOTE: Synthetic Minority Over-sampling Technique. J Artif Intell Res 16:321–357

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser 92:205–219

Clavero M, Brotons L, Pons P, Sol D (2009) Prominent role of invasive species in avian biodiversity loss. Biol Conserv 142:2043–2049

Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110

Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225–237

Costanza R, D’Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O’Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world’s ecosystem services and natural capital. Nature 387:253–260

Costello MJ, Coll M, Danovaro R, Halpin P, Ojaveer H, Miloslavich P (2010) A census of marine biodiversity knowledge, resources, and future challenges. PLoS One 5:e12110

Cristescu ME (2015) Genetic reconstructions of invasion history. Mol Ecol 24:2212–2225

Cromsigt JPGM, Kemp YJM, Rodriguez E, Kivit H (2017) Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? Restor Ecol 26:891–899

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 297:153–166

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions. Ecoscience 12:316–329

Curtis LF, Curtis D, Matkin H, Thompson M, Choi F, Callow P, Gillespie G, Therriault T, Pearce C (2015) Evaluating transfers of harvested shellfish products, from the west to the east coast of Vancouver Island, as a potential vector for European green crab (*Carcinus maenas*) and other non-indidenous species. Can Sci Advis Secr:vi-74

Darling JA, Bagley MJ, Roman J, Tepolt CK, Geller JB (2008) Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. Mol Ecol 17:4992–5007

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife - threats to biodiversity and human health. Science 287:443–449

David AT, Simenstad CA, Cordell JR, Toft JD, Ellings CS, Gray A, Berge HB (2016) Wetland loss, juvenile salmon foraging performance, and density dependence in Pacific Northwest estuaries. Estuaries and Coasts 39:767–780

Davis R, Short F, Burdick D (1998) Quantifying the effects of green crab damage to eelgrass transplants. Restor Ecol 6:297–302

De'ath G (2007) Boosted regression trees for ecological modeling and prediction. Ecology 88:243–251

Dedman S, Officer R, Brophy D, Clarke M, Reid DG (2015) Modelling abundance hotspots for data-poor Irish Sea rays. Ecol Modell 312:77–90

de Moura Queirós A, Hiddink JG, Johnson G, Cabral HN, Kaiser MJ (2011) Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. Biol Invasions 13:1059–1075 de Rivera CE, Grosholz ED, Ruiz GM, Larson A, Kordas RL, Sytsma MD (2007) Green crab management: reduction of an invasive population. In: Proceedings of Coastal Zone 2007. Portland, OR, p 1–6

de Rivera CE, Grosholz ED, Ruiz GM (2011) Multiple and long-term effects of an introduced predatory crab. Mar Ecol Prog Ser 429:145–155

Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol Invasions 16:735–753

Dick JTA, Gallagher K, Avlijas S, Clarke HC, Lewis SE, Leung S, Minchin D, Caffrey J, Alexander ME, Maguire C, Harrod C, Reid N, Haddaway NR, Farnsworth KD, Penk M, Ricciardi A (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biol Invasions 15:837–846

Dick JT, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Robert Britton J, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OL, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017), Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J Appl Ecol, 54: 1259-1267.

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. Proc Natl Acad Sci 113:11261–11265

Dowding JE, Murphy EC (2001) The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. Biol Conserv 99:47–64

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192–206

Duncombe LG, Therriault TW (2017) Evaluating trapping as a method to control the European green crab, *Carcinus maenas*, population at Pipestem Inlet, British Columbia. Manag Biol Invasions 8:235–24619

Dunoyer L, Dijoux L, Bollache L, Lagrue C (2014) Effects of crayfish on leaf litter breakdown and shredder prey: are native and introduced species functionally redundant? Biol Invasions 16:1545–1555

Duval S, Tweedie R (2000) Trim and Fill: a simple funnel-plot–based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56:455-463

Edgell TC, Lynch BR, Trussell GC, Palmer AR (2009) Experimental evidence for the rapid evolution of behavioral canalization in natural populations. Am Nat 174:434–440

Elith J, Leathwick J (2011) Boosted regression trees for ecological modeling. Retrieved from https://cran.r-project.org/web/packages/dismo/vignettes/brt.pdf

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Elner RW (1981) Diet of green crab *Carcinus maenas* (L.) from Port Hebert, southwestern Nova Scotia. J Shellfish Res 1:89–94

Elner RW, Hughes RN (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. J Anim Ecol 47:103–116

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Springer, Boston, MA

Epanchin-Niell RS, Haight RG, Berec L, Kean JM, Liebhold AM (2012) Optimal surveillance and eradication of invasive species in heterogeneous landscapes. Ecol Lett 15:803–812

Estelle V, Grosholz ED (2012) Experimental test of the effects of a non-native invasive species on a wintering shorebird. Conserv Biol 26:472–481

Ewel KC, Cressa C, Kneib RT, Lake PS, Levin LA, Palmer MA, Snelgrove P, Wall DH (2001) Managing critical transition zones. Ecosystems 4:452–460

Fei S, Phillips J, Shouse M (2014) Biogeomorphic impacts of invasive species. Annu Rev Ecol Evol Syst 45:69–87

Fernandes TF, Huxham M, Piper SR (1999) Predator caging experiments: a test of the importance of scale. J Exp Mar Bio Ecol 241:137–154

Flynn AM, Smee DL (2010) Behavioral plasticity of the soft-shell clam, *Mya arenaria* (L.), in the presence of predators increases survival in the field. J Exp Mar Bio Ecol 383:32–38

Fox J (2003) Effect displays in R for generalised linear models. J Stat Softw 8:1–9

Fox J, Hong J (2009) Effect displays in R for multinomial and proportional-odds logit models: extensions to the effects package. J Stat Softw 32:1–24

Francis RC, Hurst RJ, Renwick JA (2003) Quantifying annual variation in catchability for commercial and research fishing. Fish Bull 101:293–304

Freeman AS, Byers JE (2006) Divergent induced responses to an mussel populations. Science 58:831–833

Freeman AS, Meszaros J, Byers JE (2009) Poor phenotypic integration of blue mussel inducible defenses in environments with multiple predators. Oikos 118:758–766

Froeschke JT, Froeschke BF (2016) Two-stage boosted regression tree model to characterize southern flounder distribution in Texas estuaries at varying population sizes. Mar Coast Fish 8:222–231

Fulton SW, Grant FE (1902) Some little known Victorian decapod Crustacea with description of a new species. Proc R Soc Victoria 14:55–64

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Glob Chang Biol 22:151–163

Garbary DJ, Miller AG, Williams J, Seymour NR (2014) Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). Mar Biol 161:3–15

Garside CJ, Bishop MJ (2014) The distribution of the European shore crab, *Carcinus maenas*, with respect to mangrove forests in southeastern Australia. J Exp Mar Bio Ecol 461:173–178

Gillespie GE, Phillips AC, Paltzat DL, Therriault TW (2007) Status of the European green crab, *Carcinus maenas*, in British Columbia - 2006. Can Tech Rep Fish Aquat Sci 2700:vii-39

Glude JB (1955) The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans Am Fish Soc 84:13–26

Gooden B, French K, Turner PJ (2009) Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia. For Ecol Manage 257:960–967

Gosling EM (1992) Systematics and geogaphic distribution of *Mytilus*. In: Gosling EM (ed) The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Elsevier, Amsterdam, Netherlands, p 1-20

Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 54:1306–1319

Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. Ecology 89:3413–3422

Grason EW, Buhle ER (2016) Comparing the influence of native and invasive intraguild predators on a rare native oyster. J Exp Mar Bio Ecol 479:1–8

Gray M (2010) Freshwater Water Atlas User Guide. GeoBC, Victoria, BC

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS One 7:e32596

Green DS, Crowe TP (2014) Context- and density-dependent effects of introduced oysters on biodiversity. Biol Invasions 16:1145–1163

Greenberg DA, Palen WJ, Mooers A (2017) Amphibian species traits, evolutionary history and environment predict Batrachochytrium *dendrobatidis* infection patterns, but not extinction risk. Evol Appl 10:1130–1145

Greenlees MJ, Brown GP, Webb JK, Phillips BL, Shine R (2006) Effects of an invasive anuran [the cane toad (*Bufo marinus*)] on the invertebrate fauna of a tropical Australian floodplain. Anim Conserv 9:431–438

Griffen B, Byers J (2009) Community impacts of two invasive crabs: the interactive roles of density, prey recruitment, and indirect effects. Biol Invasions 11:927–940

Griffen BD, Riley ME (2015) Potential impacts of invasive crabs on one life history strategy of native rock crabs in the Gulf of Maine. Biol Invasions 17:2533–2544

Griffin JN, De La Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. Ecology 89:298–305

Grindley JR (1972) The vertical migration behaviour of estuarine plankton. Zool Africana 7:13–20

Grosholz E, Lovell S, Besedin E, Katz M (2011) Modeling the impacts of the European green crab on commercial shellfisheries. Ecol Appl 21:915–924

Grosholz E, Olin P, Williams B, Tinsman R (2001) Reducing predation on manila clams by nonindigenous European green crabs. J Shellfish Res 20:913–919

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biol Conserv 78:59–66

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, McCarthy MA, Tingley R, Wintle BA (2015) Is my species distribution model fit for purpose? Matching data and models to applications. Glob Ecol Biogeogr 24:276–292

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470–474

Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queirós AM, Chatzinikolaou E, Arvanitidis C, Como S, Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G (2018) Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. Glob Chang Biol 24:906–924

Haddaway NR, Wilcox RH, Heptonstall REA, Griffiths HM, Mortimer RJG, Christmas M, Dunn AM (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. PLoS One 7:e32229

Hampton SL, Griffiths CL (2007) Why *Carcinus maenas* cannot get a grip on South Africa’s wave-exposed coastline. African J Mar Sci 29:123–126

Hanski I (2001) Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372–381

Harrison PG (1979) Reproductive strategies in intertidal populations of two co-occurring seagrasses (*Zostera* spp.). Can J Bot 2:2635–2638

Hassell MP (1978) The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton, NJ

Heck KLJ, Hays G, Orth RJ (2003) Critical evaluation of nursery hypothesis for seagrasses. Mar Ecol Prog Ser 253:123–136

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hedvall O, Moksnes P-O, Pihl L (1998) Active habitat selection by megalopae and juvenile shore crabs *Carcinus maenas*: a laboratory study in an annular flume. Hydrobiologia 376:89–100

Higgins K, Hastings A, Sarvela JN, Botsford LW (1997) Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. Science 276:1431–1435

Hill JM, Weissburg MJ (2013) Habitat complexity and predator size mediate interactions between intraguild blue crab predators and mud crab prey in oyster reefs. Mar Ecol Prog Ser 488:209–219

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. J Appl Ecol 45:1372–1381

Holdredge C, Bertness MD, Altieri AH (2009) Role of crab herbivory in die-off of New England salt marshes. Conserv Biol 23:672–9

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Entomol 91:385–398

Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. Mem Entomol Soc Canada 97:5–60

Holsman K, McDonald P, Armstrong D (2006) Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. Mar Ecol Prog Ser 308:183–195

Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA (2006) Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. Estuaries and Coasts 29:1150–1160

Howard BR, Tamburello N, Francis F (2018) Risk Assessment for Marine Invasive Species in Haida Gwaii. ESSA Technologies Ltd., Vancouver, BC

Howes D, Harper J, Owens E (1995) Physical shore-zone mapping system for British Columbia. Resources Inventory Committee, Victoria, Canada

Hunt CE, Behrens Yamada S (2003) Biotic resistance experienced by an invasive crustacean in a temperate estuary. Biol Invasions 5:33–43

Jensen G, McDonald P, Armstrong D (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. Mar Ecol Prog Ser 225:251–262

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: A global review. Conserv Biol 22:16–26

Juliano SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and Analysis of Ecological Experiments, 2nd edn. Oxford University Press, New York, NY, p 159-182

Kelly JR, Proctor H, Volpe JP (2008) Intertidal community structure differs significantly between substrates dominated by native eelgrass (*Zostera marina* L.) and adjacent to the introduced oyster *Crassostrea gigas* (Thunberg) in British Columbia, Canada. Hydrobiologia 596:57–66

Kennedy LA, Juanes F, El-Sabaawi R (2018) Eelgrass as valuable nearshore foraging habitat for juvenile Pacific salmon in the early marine period. Mar Coast Fish 10:190–203

Kenward RE, Holm JL (1993) On the replacement of the red squirrel in Britain: a phytotoxic explanantion. Proc R Soc B Biol Sci 251:187–194

Klassen G, Locke A (2007) A biological synopsis of the European green crab, *Carcinus maenas*. Can Manuscr Rep Fish Aquat Sci 2818:vii-75

Kraemer GP, Sellberg M, Gordon A, Main J (2007) Eight-year record of *Hemigrapsus sanguineus* (Asian shore crab) invasion in Western Long Island Sound Estuary. Northeast Nat 14:207–224

Kuhn, M. (2008). Caret package. J Stat Softw 28:1-26

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. Bioscience 65:55–63

Landes A, Zimmer M (2012) Acidification and warming affect both a calcifying predator and prey, but not their interaction. Mar Ecol Prog Ser 450:1–10

Langerhans RB, DeWitt TJ (2004) Shared and unique features of evolutionary diversification. Am Nat 164:335–349

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Can J Zool 79:1401–1409

Lee SY, Seed R (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. Mar Ecol Prog Ser 84:151–160

Le Louarn M, Clergeau P, Strubbe D, Deschamps-Cottin M (2018) Dynamic species distribution models reveal spatiotemporal habitat shifts in native range-expanding versus non-native invasive birds in an urban area. J Avian Biol 49:1–16

Lepori F, Benjamin JR, Fausch KD, Baxter CV (2012) Are invasive and native trout functionally equivalent predators? Results and lessons from a field experiment. Aquat Conserv Mar Freshw Ecosyst 22:787–798

Le Roux PJ, Branch GM, Joska MAP (1990) On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. South African J Mar Sci 9:85–93

Leung B, Roura-Pascual N, Bacher S, Heikkilä J, Brotons L, Burgman MA, Dehnen-Schmutz K, Essl F, Hulme PE, Richardson DM, Sol D, Vilà M (2012) TEASIng apart alien species risk assessments: a framework for best practices. Ecol Lett 15:1475–1493

Levin LA, Boesch DF, Covich A, Dahm C, Erséus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P, Strayer D, Weslawski JM (2001) The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4:430–451

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lima SL (2002) Putting predators back into behavioral predator – prey interactions. Trends Ecol Evol 17:70–75

Lipcius RN, Hines AH (1986) Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67:1361–1371

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion Ecology, 1st edn. Blackwell Publishing Ltd., Oxford, UK

Lowen JB, Innes DJD, Thompson RJR (2013) Predator-induced defenses differ between sympatric *Mytilus edulis* and *M. trossulus*. Mar Ecol Prog Ser 475:135–143

Lowen J, McKindsey C, Therriault T, DiBacco C (2016) Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments. Mar Ecol Prog Ser 556:17–30

Mabin C, Wilson J, Le Roux J, Robinson TB (2017) Reassessing the invasion of South African waters by the European shore crab, *Carcinus maenas*. African J Mar Sci 39:259-267

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ

Mach ME, Levings CD, Chan KMA (2017) Nonnative species in British Columbia eelgrass beds spread via shellfish aquaculture and stay for the mild climate. Estuaries and Coasts 40:187–199

Magrach A, Laurance WF, Larrinaga AR, Santamaria L (2014) Meta-analysis of the effects of forest fragmentation on interspecific interactions. Conserv Biol 28:1342–1348

Malyshev A, Quijón PA (2011) Disruption of essential habitat by a coastal invader: new evidence of the effects of green crabs on eelgrass beds. ICES J Mar Sci 68:1852–1856

Martin CW, Valentine MM, Valentine JF (2010) Competitive interactions between invasive Nile tilapia and native fish: the potential for altered trophic exchange and modification of food webs. PLoS One 5:e14395

Matassa CM, Trussell GC (2011) Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. Ecology 92:2258–2266

Matheson K, McKenzie CH, Gregory RS, Robichaud DA, Bradbury IR, Snelgrove PVR, Rose GA (2016) Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. Mar Ecol Prog Ser 548:31–45

McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. J Exp Mar Bio Ecol 258:39–54

McGaw IJ, Curtis DL (2013) A review of gastric processing in decapod crustaceans. J Comp Physiol B Biochem Syst Environ Physiol 183:443–465

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Donlan CJ, Keitt BS, Le Corre M, Horwath SV, Nogales M (2011) A global review of the impacts of invasive cats on island endangered vertebrates. Glob Chang Biol 17:3503–3510

Melbourne BA, Cornell H V., Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol Lett 10:77–94

Moksnes PO (2002) The relative importance of habitat-specific settlement, predation and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J Exp Mar Bio Ecol 271:41–73

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Front Ecol Environ 6:485–492

Moore JW, Gordon J, Carr-Harris C, Gottesfeld AS, Wilson SM, Russell JH (2016) Assessing estuaries as stopover habitats for juvenile Pacific salmon. Mar Ecol Prog Ser 559:201–215

Moore KA, Short FT (2006) *Zostera*: biology, ecology, and management. In: Larkum AWD, Orth RJ, Duarte C (eds) Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, Netherlands, p 361–386

Morton B, Harper EMM (2008) Predation upon *Mytilus galloprovincialis* (Mollusca: Bivalvia: Mytilidae) by juvenile *Carcinus maenas* (Crustacea: Decapoda) using mandibular chipping. J Mar Biol Assoc United Kingdom 88:563–568

Mosendz P (2014, June 27) Pablo Escobar's Hippos Run Amok in Colombia. The Atlantic. Retrieved from: https://www.theatlantic.com/international/archive/2014/06/pablo-escobars-hippos-run-amok-in-colombia/373584/

Murray LG, Seed R (2010) Determining whether catch per unit effort is a suitable proxy for relative crab abundance. Mar Ecol Prog Ser 401:173–182

Murtaugh PA (2007) Simplicity and complexity in ecological data analysis. Ecology 88:56–62

Mutze G, Cooke B, Jennings S (2016) Density-dependent grazing impacts of introduced European rabbits and sympatric kangaroos on Australian native pastures. Biol Invasions 18:2365–2376

Nagaraj M (1993) Combined effects of temperature and salinity on the zoeal development of the green crab, *Carcinus maenas* (Linnaeus, 1758)(Decapoda: Portunidae). Sci Mar 57:1–8

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Neckles HA (2015) Loss of eelgrass in Casco Bay, Maine, linked to green crab disturbance. Northeast Nat 22:478–500

Nowicki R, Fourqurean J, Heithaus M (2018) The role of consumers in structuring seagrass communities: direct and indirect mechanisms. In: Larkum A, Kendrick G, Ralph P (eds) Seagrasses of Australia. Springer, Switzerland, p 491–540

Oaten A, Murdoch WW (1975) Functional response and stability in predator-prey systems. Am Nat 109:289–298

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan

Orensanz JM, Armstrong J, Armstrong D, Hilborn R (1998) Crustacean resources are vulnerable to serial depletion - The multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev Fish Biol Fish 8:117–176

Orensanz JM, Parma AM, Armstrong DA, Armstrong J, Wardrup P (1995) The breeding ecology of *Cancer gracilis* (Crustacea: Decapoda: Cancridae) and the mating systems of cancrid crabs. J Zool 235:411–437

Padilla DK (2010) Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. Integr Comp Biol 50:213–225

Paine R. (1969) A note on trophic complexity and community stability. Am Nat 103:91–93

Paolucci EM, MacIsaac HJ, Ricciardi A (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. Divers Distrib 19:988–995

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle B Von, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. J Anim Ecol 84:453–463

Peterson BJ, Fournier AM, Furman BT, Carroll JM (2014) *Hemigrapsus sanguineus* in Long Island salt marshes: experimental evaluation of the interactions between an invasive crab and resident ecosystem engineers. PeerJ 2:e472

Phillips RC, McMillan C, Bridges KW (1983a) Phenology of eelgrass, *Zostera marina* L., along latitudinal gradients in North America. Aquat Bot 15:145–156

Phillips RC, Grant WS, McRoy CP (1983b) Reproductive strategies of eelgrass (*Zostera marina* L.). Aquat Bot 16:1–20

Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, Cury P, Heppell SS, Houde ED, Mangel M, Plagányi É, Sainsbury K, Steneck RS, Geers TM, Gownaris N, Munch SB (2014) The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish 15:43–64

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol Lett 7:781–784

Richards MG, Huxham M, Bryant A (1999) Predation: a causal mechanism for variability in intertidal bivalve populations. J Exp Mar Bio Ecol 241:159–177

Rindone RR, Eggleston DB (2011) Predator–prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea virginica*). J Exp Mar Bio Ecol 407:216–225

Robertson AI, Mann KH (1984) Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. Mar Biol 80:131–141

Robinson TB, Alexander ME, Simon CA, Griffiths CL, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P, Sink KJ (2016) Lost in translation? Standardising the terminology used in marine invasion biology and updating South African alien species lists. African J Mar Sci 38:129–140

Robinson TB, Griffiths CL, McQuaid CD, Rius M (2005) Marine alien species of South Africa — status and impacts. African J Mar Sci 27:297–306

Robinson EM, Smee DL, Trussell GC (2011) Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. PLoS One 6:e21025

Rodda GH, Fritts TH, Conry PJ (1992) Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. Pacific Sci 46:46–57

Rogers DJ (1972) Random search and insect population models. J Anim Ecol 41:369–383

Romero GQ, Gonçalves-Souza T, Vieira C, Koricheva J (2015) Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. Biol Rev 90:877–890

Rossong MA, Quijón PA, Snelgrove PVR, Barrett TJ, McKenzie CH, Locke A (2012) Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada. Biol Invasions 14:659–669

Rossong MA, Williams PJ, Comeau M, Mitchell SC, Apaloo J (2006) Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). J Exp Mar Bio Ecol 329:281–288

Roy HE, Lawson Handley L-J, Schönrogge K, Poland RL, Purse BV (2011) Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? BioControl 56:451–468

Ruesink JL, Hong JS, Wisehart L, Hacker SD, Dumbauld BR, Hessing-Lewis M, Trimble AC (2010) Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary. Biol Invasions 12:1773–1789

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. Annu Rev Ecol Evol Syst 36:643–689

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Am Zool 37:621–632

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annu Rev Ecol Syst 31:481–531

Sagarin R, Pauchard A (2010) Observational approaches in ecology open new ground in a changing world. Front Ecol Environ 8:379–386

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Skykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc Biol Sci 274:1237–1243

Say T (1817) An account of the Crustacea of the United States. J Acad Nat Sci Philadelphia 1:57–63

Schaefer G, Zimmer M (2013) Ability of invasive green crabs to handle prey in a recently colonized region. Mar Ecol Prog Ser 483:221–229

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nat Commun 8:1–9

Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling E (ed) The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Elsevier, Amsterdam, Netherlands, p 171–222

Shafer DJ, Kaldy JE, Gaeckle JL (2014) Science and management of the introduced seagrass *Zostera japonica* in North America. Environ Manage 53:147–162

Shafer DJ, Swannack TM, Saltus C, Kaldy JE, Davis A (2016) Development and validation of a habitat suitability model for the non-indigenous seagrass *Zostera japonica* in North America. Manag Biol Invasions 7:141–155

Shelton AO, Francis TB, Williams GD, Feist B, Stick K, Levin PS (2014) Habitat limitation and spatial variation in Pacific herring egg survival. Mar Ecol Prog Ser 514:231–245

Shine R (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. Q Rev Biol 84:253–291

Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208

Short F, Carruthers T, Dennison W, Waycott M (2007) Global seagrass distribution and diversity: a bioregional model. J Exp Mar Bio Ecol 350:3–20

Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621

Sih A, Crowley P, Mcpeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Silliman BR, Bertness MD (2002) A trophic cascade regulates salt marsh primary production. Proc Natl Acad Sci 99:10500-10505

Silva ACF, Boaventura DM, Thompson RC, Hawkins SJ (2013) Spatial and temporal patterns of subtidal and intertidal crabs excursions. J Sea Res 85: 343-348

Simberloff D (2013) Invasive Species: What Everyone Needs to Know. Oxford University Press, Oxford, UK

Simberloff D, Gibbons L (2004) Now you see them, now you don't! - Population crashes of established introduced species. Biol Invasions 6:161–172

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Smallegange IM, van der Meer (2003) Why do shore crabs not prefer the most profitable mussels? J Anim Ecol 72:599–607

Smallegange IM, van der Meer J, Kurvers RHJM (2006) Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. Oikos 1:157–167

Smith LD (2004) Biogeographic differences in claw size and performance in an introduced crab predator Carcinus maenas. Mar Ecol Prog Ser 276:209–222

Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). Behav Ecol Sociobiol 41:237–242

Spencer R-J, Van Dyke JU, Thompson MB (2016) The ethological trap: functional and numerical responses of highly efficient invasive predators driving prey extinctions. Ecol Appl 26:1969–1983

Spencer CN, McClelland BR, Stanford JA (1991) Shrimp stocking, salmon collapse, and eagle displacement. Bioscience 41:14–21

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology, 83: 2575-2590

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17:866–880

Stewart G (2010) Meta-analysis in applied ecology. Biol Lett 6:78–81

Stone RP, O'Clair CE (2001) Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. Mar Ecol Prog Ser 214:167–176

Svenning JC, Faurby S (2017) Prehistoric and historic baselines for trophic rewilding in the Neotropics. Perspect Ecol Conserv 15:282–291

Talley TS, Crooks JA, Levin LA (2001) Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. Mar Biol 138:561–573

Tepolt CK, Darling JA, Bagley MJ, Geller JB, Blum MJ, Grosholz ED (2009) European green crabs (*Carcinus maenas*) in the northeastern Pacific: genetic evidence for high population connectivity and current-mediated expansion from a single introduced source population. Divers Distrib 15:997–1009

Thompson WJ (2007) Population-level effects of the European green crab (*Carcinus maenas*, L.) in an eelgrass community of the sourthern Gulf of St. Lawrence. University of New Brunswick, Fredericton, NB

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Mar Ecol Prog Ser 495:39–47

Thomsen MS, Wernberg T, Olden JD, Griffin JN, Silliman BR (2011) A framework to study the context-dependent impacts of marine invasions. J Exp Mar Bio Ecol 400:322–327

Tina FW, Jaroensutasinee M, Jaroensutasinee K (2015) Effects of sexual dimorphism and body size on feeding behaviour of the fiddler crab, *Uca bengali* Crane, 1975. Crustaceana 88:231–242

Tomaro LM, Teel DJ, Peterson WT, Miller JA (2012) When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Mar Ecol Prog Ser 452:237–252

Trussell GC, Ewanchuk PJ, Bertness MD, Biology E (2003) Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. Ecology 84:629–640

Trussell GC, Ewanchuk PJ, Matassa CM (2006) Habitat effects on the relative importance of trait- and density-mediated indirect interactions. Ecol Lett 9:1245–52

Tyrrell MC, Guarino PA, Harris LG (2006) Predatory impacts of two introduced crab species: inferences from microcosms. Northeast Nat 13:375–390

Vermeij GJ (1987) Evolution and Escalation: An Ecological History of Life. Princeton University Press, Princeton, NJ

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36:1–48

Villamagna AM, Murphy BR (2010) Ecological and socio-economic impacts of invasive water hyacinth (*Eichhornia crassipes*): a review. Freshw Biol 55:282–298

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. J Anim Ecol:249–256

Wagner E, Dumbauld BR, Hacker SD, Trimble AC, Wisehart LM, Ruesink JL (2012) Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. Mar Ecol Prog Ser 468:149–160

Walton WC, MacKinnon C, Rodriguez LF, Proctor C, Ruiz GM (2002) Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid clam, *Katelysia scalarina*, in Tasmania (Australia). J Exp Mar Bio Ecol 272:171–189

Wasson K, Zabin CJ, Bedinger L, Cristina Diaz M, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol Conserv 102:143–153

Weis JS (2010) The role of behavior in the success of invasive crustaceans. Mar Freshw Behav Physiol 43:83–98

Welch WR (1968) Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. Fish Bull 67:337–345

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. Divers Distrib 12:443–455

Whitlow WL (2010) Changes in survivorship, behavior, and morphology in native soft-shell clams induced by invasive green crab predators. Mar Ecol 31:418–430

Wilcox C (2018, September 26) Could Pablo Escobar's Escaped Hippos Help the Environment? Natl Geogr Mag. Retrieved from: https://www.nationalgeographic.com/animals/2018/09/colombia-cocaine-hippos-rewilding-experiment-news/

Wiles GJ, Aguon CF, Davis GW, Grout DJ (1995) The status and distribution of endangered animals and plants in Northern Guam. Micronesica 28:31–49

Williams SL (2007) Introduced species in seagrass ecosystems: status and concerns. J Exp Mar Bio Ecol 350:89–110

Zenni RD, Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos 122:801–815

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY

Zwerschke N, Hollyman PR, Wild R, Strigner R, Turner JR, King JW (2018) Limited impact of an invasive oyster on intertidal assemblage structure and biodiversity: the importance of environmental context and functional equivalency with native species. Mar Biol 165:1–13

# Appendix A.

# Supporting Information for Chapter 2

## Supplementary tables

### Table A.1 Survey of invasive marine and euryhaline crab introductions.

Available online at http://get.sfu.ca/UlLxwJ

### Table A.2 Table of individual experiments used for meta-analysis.

Available online at http://get.sfu.ca/UlLxwJ

### Table A.3 Descriptive table of moderator levels.

| Moderator | Level | Description | n (overall dataset) |
|---|---|---|---|
| Interaction type | Direct | Experiment tests a direct, consumptive interaction between a crab and responding species. Interaction either known or strongly expected to be direct by the original authors. | 647 |
|  | Indirect | Experiment tests an indirect interaction between a crab and responding species. Interaction either known or strongly expected to be indirect by the original authors. Mechanism of interaction typically assumed to be a trophic cascade, however we did not require this to be demonstrated. | 187 |
| Crab origin | Native | Crab species is confirmed to be native to the region. | 292 |
|  | Non-native | Crab species is introduced, invasive, or otherwise being tested against responding species that is does not co-occur with naturally. | 542 |
| Prey functional group | Mobile infauna | Clams, marine worms, and infaunal crustaceans (amphipods and isopods). | 246 |
|  | Mobile epifauna | Surface-dwelling decapods (including hermit crabs, shrimps, etc.), gastropods, scallops, and mobile echinoderms. | 189 |
|  | Primary producers | Seaweeds, seagrasses, and phytoplankton. | 123 |
|  | Sessile invertebrates | Mussels, oysters, barnacles, and other encrusting epifauna. | 263 |
|  | Vertebrates | Limited to birds and fish. | 13 |

| | | | |
|---|---|---|---|
| Experimental design | Natural field experiments | No species controlled experimentally (including crab). Without- and with-crab “treatments” are a result of spatial or temporal changes in crab presence (e.g. before/after an introduction or spatially different abundances of crab). | 22 |
| | Unstocked enclosures | Field enclosures or exclosures where only the crab species was manipulated experimentally while the remainder of the community was left undisturbed. | 256 |
| | Stocked enclosures | Field enclosures or exclosures where densities of one or multiple responding species were manipulated along with crab presence, while remainder of the community was left undisturbed. | 152 |
| | Laboratory mesocosm | A closed or mostly closed laboratory-based mesocosm requiring a minimum of two trophic levels and three species. Densities of all species, including crab, were controlled by the original authors. | 193 |
| | Predation experiment | Only one crab predator and one prey species or type (e.g. two species of mussel) in a closed laboratory system. This setup excluded indirect interactions as they tested direct predation only. | 211 |

**Table A.4** **Average carapace widths of all crab species included in the meta-analysis.**

| Crab species | Carapace width (mm) | Source |
|---|---|---|
| *Acanthocyclus gayi* | 24.0 | Garth (1957) |
| *Acanthocyclus hassleri* | 25.0 | Rathbun (1930) |
| *Achelous spinimanus* | 110.0 | Williams (1984) |
| *Callinectes sapidus* | 168.0 | Williams (1984) |
| *Cancer antennarius* | 118.0 | Rathbun (1930) |
| *Cancer borealis* | 143.0 | Williams (1984) |
| *Cancer irroratus* | 119.0 | Williams (1984 |
| *Cancer pagurus* | 130.0 | Ingle (1997) |
| *Cancer productus* | 157.5 | Rathbun (1930) |
| *Caphyra rotundifrons* | 13.0 | Jenkins (2012) |
| *Carcinus aestuarii* | 65.0 | sealifebase.org |
| *Carcinus maenas* | 79.4 | Rathbun (1930) |
| *Cyclograpsus lavauxi* | 28.0 | McLay (1988) |
| *Dotilla fenestrata* | 12.0 | Hartnoll (1973) |
| *Dyspanopeus sayi* | 29.7 | Williams (1984) |
| *Dyspanopeus texanus* | 27.0 | Rathbun (1930) |
| *Eurypanopeus depressus* | 25.0 | Williams (1984) |
| *Eurytium limosum* | 43.0 | Williams (1984) |
| *Grapsus grapsus* | 80.0 | eol.org |
| *Hemigrapsus sanguineus* | 42.0 | Richerson (2017) |

| | | |
|---|---|---|
| *Heterozius rotundifrons* | 23.0 | McLay (1988) |
| *Hyas araneus* | 76.5 | Miller & O'Keefe (1981) |
| *Liocarcinus depurator* | 51.0 | Hayward & Ryland (1995) |
| *Macrocoeloma diplacanthum* | 12.8 | Rathbun (1925) |
| *Menippe adina* | 10.0 | tpwd.texas.gov |
| *Menippe mercenaria* | 129.0 | Williams (1984) |
| *Mennipe nodifrons* | 72.0 | Rathbun (1930) |
| *Metacarcinus gracilis* | 91.0 | Rathbun (1930) |
| *Metacarcinus magister* | 198.0 | Rathbun (1930) |
| *Micropanope* sp. | 6.5 | Williams (1984) |
| *Mictyris longicarpus* | 25.0 | ala.org.au |
| *Mithraculus forceps* | 38.0 | Williams (1984) |
| *Mithraculus sculptus* | 26.4 | Rathbun (1925) |
| *Necora puber* | 109.0 | Hearn (2002) |
| *Neohelice granulata* | 32.0 | Angeletti & Cervellini (2015) |
| *Ovalipes catharus* | 150.0 | McLay (1988) |
| *Ovalipes ocellatus* | 87.0 | Williams (1984) |
| *Pachygrapsus crassipes* | 48.0 | eol.org.au |
| *Pachygrapsus transversus* | 26.4 | Williams (1984) |
| *Panopeus herbstii* | 62.0 | Williams (1984) |
| *Paragrapsus gaimardii* | 48.0 | Campbell & Griffin (1966) |
| *Percnon gibbesi* | 28.0 | Williams (1984) |
| *Petrolisthes armatus* | 14.0 | Masterson (2007) |
| *Pilumnus caribaeus* | 21.6 | Rathbun (1930) |
| *Rhithropanopeus harrisii* | 21.3 | Williams (1984) |
| *Sesarma reticulatum* | 28.0 | Williams (1984) |
| *Trapezia rufopunctata* | 28.0 | Poupin & Juncker (2010) |
| *Uca annulipes* | 18.5 | Crane (1975) |
| *Uca polita* | 25.0 | Crane (1975) |
| *Uca pugilator* | 26.0 | Williams (1984) |
| *Uca pugnax* | 23.0 | Williams (1984) |
| *Uca vocans* | 22.5 | Crane (1975) |
| *Uca vomeris* | 27.0 | Crane (1975) |

See Table A.2 for the native/non-native status of crab species.

**Table A.5 Comparison of the main results from analyses of the full and large-studies-only datasets.**

| Results of the full dataset | Remains true with large-studies-only data? |
|---|---|
| Direct and indirect effects were significant in opposing directions | Yes |
| **Direct effects dataset** | |
| No significant difference between the direct effects of non-native and native crabs | Yes |
| Significant differences in effect size among different experimental designs | Yes |
| All experimental designs have a significantly negative effect on prey abundance | Yes |
| Experimental designs with the strongest effects are laboratory mesocosms and single-species predation experiments | **Natural experiments now have the strongest effect** |
| Non-native crabs reduced prey abundance significantly more than native crabs in laboratory mesocosms | Yes |
| Significant differences in effect size among prey functional groups | Yes |
| All prey functional groups were significantly negatively affected by crab predation | Yes, except for vertebrates (now **NS** because of small sample size) |
| Non-native crabs reduced abundance of primary producers significantly more than predation by native crabs | Trend same but **NS** |
| Native crabs reduced abundance of mobile epifauna significantly more than predation by non-native crabs | Yes |
| **Indirect effects dataset** | |
| No significant difference between the indirect effects of non-native and native crabs | Yes |
| No significant difference in effect size among different experimental designs | Yes |
| Mesocosm experiments had the only significant effect on responding species abundance | Stocked enclosures and mesocosms now **both significant** |
| Non-native crabs increased basal prey abundance significantly more in unstocked field enclosures than did native crabs | Yes |
| Significant differences in effect size among prey functional groups | Yes |
| Effect sizes for sessile invertebrates and primary producers were both significantly positive | Yes |
| Non-native crabs increased abundance of primary producers significantly more than native crabs | Yes |

Differences are highlighted in bold.

**Table A.6** **Comparison of the main results from analyses with and without studies of European green crab (*Carcinus maenas*) included.**

| Results of the full dataset | Remains true when green crab studies removed? |
|---|---|
| Direct and indirect effects were significant in opposing directions | Yes |
| **Direct effects dataset** | |
| No significant difference between the direct effects of non-native and native crabs | Yes |
| Significant differences in effect size among different experimental designs | Yes |
| All experimental designs have a significantly negative effect on prey abundance | Yes |
| Experimental designs with the strongest effects are laboratory mesocosms and single-species predation experiments | Yes |
| Non-native crabs reduced prey abundance significantly more than native crabs in laboratory mesocosms | Yes |
| Significant differences in effect size among prey functional groups | Yes |
| All prey functional groups were significantly negatively affected by crab predation | Yes |
| Non-native crabs reduced abundance of primary producers significantly more than predation by native crabs | Trend same but **NS** |
| Native crabs reduced abundance of mobile epifauna significantly more than predation by non-native crabs | Yes |
| **Indirect effects dataset** | |
| No significant difference between the indirect effects of non-native and native crabs | **No** |
| No significant differences in effect size among different experimental designs | **No** |
| Mesocosm experiments had the only significant effect on responding species abundance | Yes |
| Non-native crabs increased basal prey abundance significantly more in unstocked field enclosures than did native crabs | Insufficient sample size to test for this difference |
| Significant differences in effect size among prey functional groups | Yes |
| Effect sizes for sessile invertebrates and primary producers were both significantly positive | Yes |
| Non-native crabs increased abundance of primary producers significantly more than native crabs | Trend same but **NS** |

Differences are highlighted in bold.

# Supplementary figures

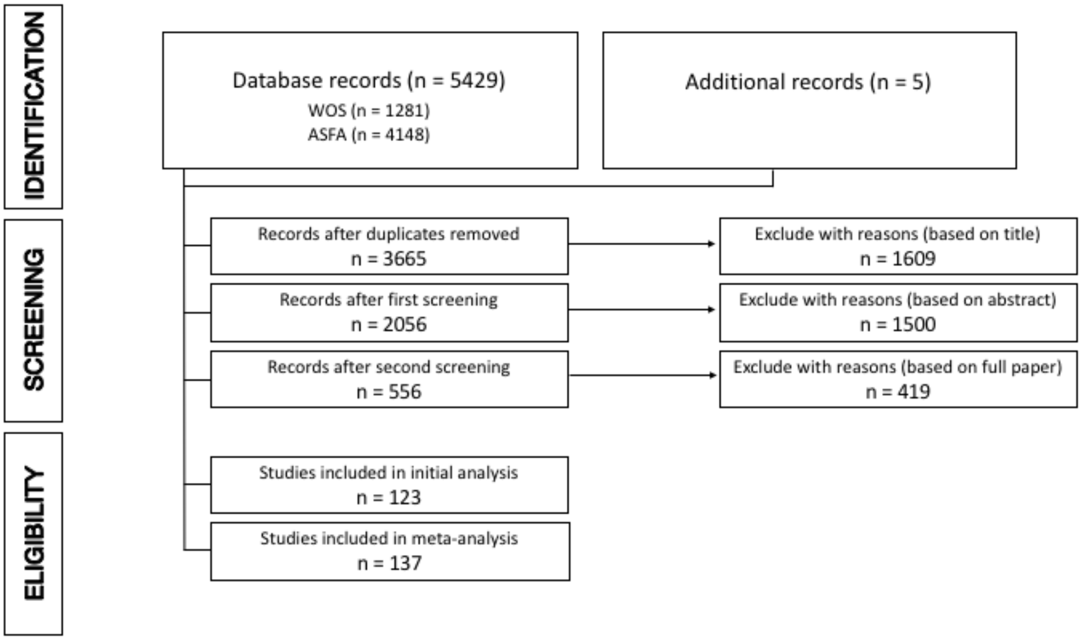

**Figure A.1 Summary of literature selection process and results.**
6.1.1. Sample sizes (n) are shown for each step of the systematic search. WOS: Web of Science; ASFA: Aquatic Science and Fisheries Abstracts. Literature selection was done following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (http://prisma-statement.org/).

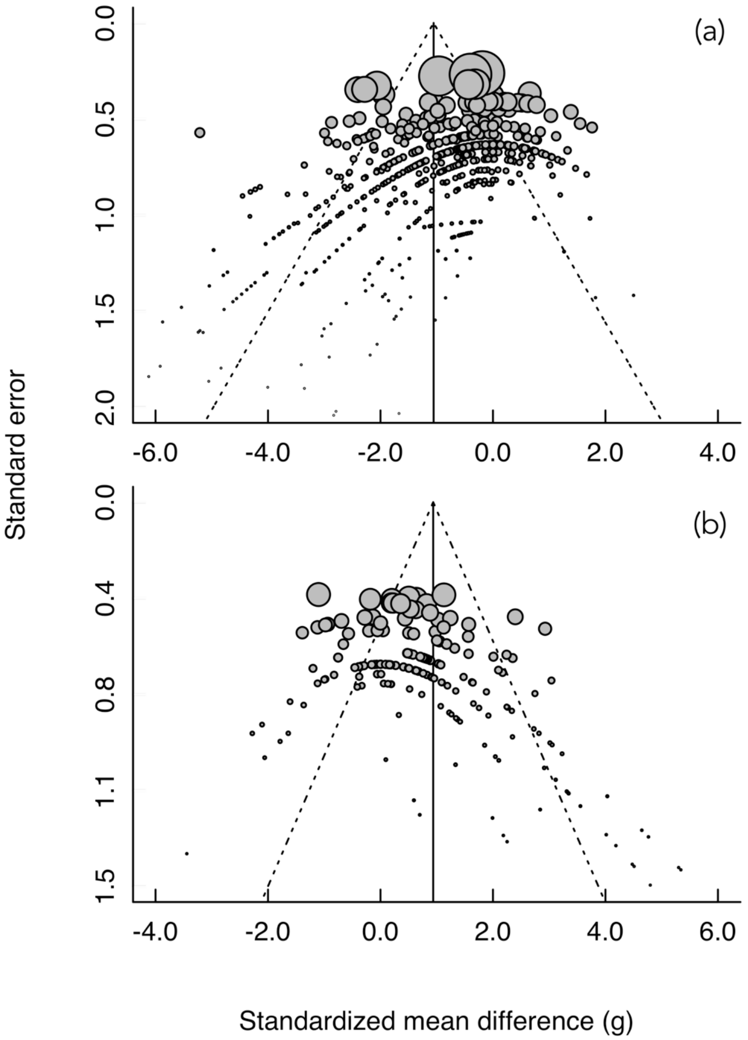

**Figure A.2 Funnel plots relating standard error to effect size for experiments included in the meta-analyses.**

Effect size for **(a)** direct effects and **(b)** indirect effects of crabs on responding species. Point size represents the weight of the experiment, calculated as the inverse of the sample variance (Viechtbauer 2010). Dashed lines represent the 95% CI. The asymmetric shape of the funnels suggests publication bias against small, non-significant experiments.

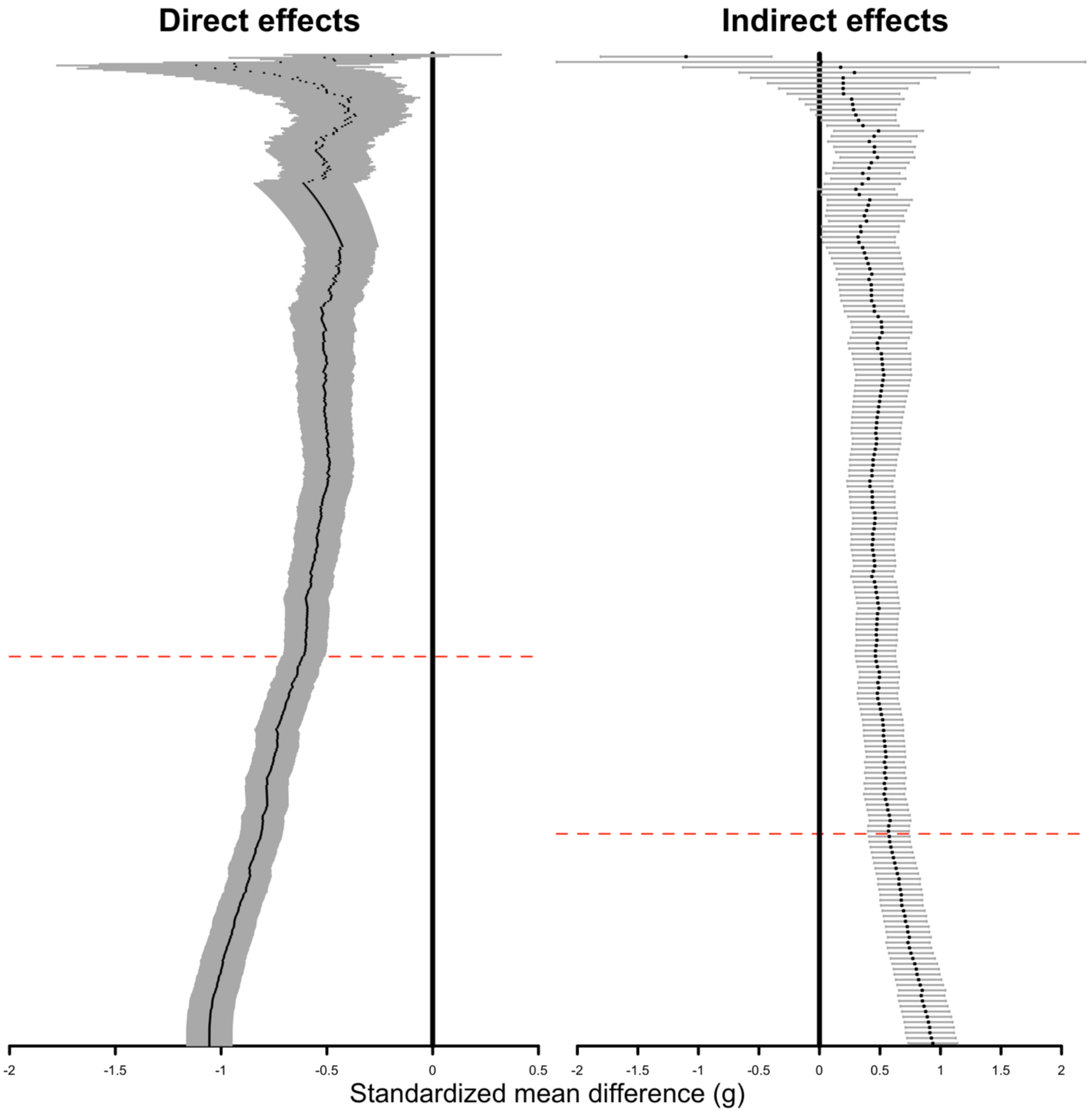

**Figure A.3 Cumulative forest plots for experiments on the direct and indirect interactions between crabs and prey.**

Experiments were added in order of smallest (top) to largest (bottom) variance. Horizontal red lines indicate approximate variance values at which small studies start to shift the overall effect size. These thresholds were estimated visually at values of 0.73 for studies of direct effects of crabs and 1.02 for studies of indirect effects. Studies with variances smaller than these thresholds were included in “large-studies-only” datasets.

## Supplementary references

ala.org.au (2017) *Mictyris longicarpus* Latreille, 1806 (n.d.) Retrieved from https://www.ala.org.au/

Angeletti S, Cervellini P (2015) Population structure of the burrowing crab *Neohelice granulata* (Brachyura, Varunidae) in a southwestern Atlantic salt marsh. Lat Am J Aquat Res 43:539–547

Campbell BM, Griffin DJG (1966) The Australian Sesarminae (Crustacea: Brachyura): Genera *Helice*, *Helograpsus* nov., *Cyclograpus*, and *Paragrapsus*. Memoirs of the Queensland Museum 14:127–174

Crane J (1975) Fiddler crabs of the world (Ocypodidae: genus *Uca*). Princeton University Press, Princeton, NJ

eol.org (2017) Sally Lightfoot Crab (n.d.) Retrieved from http://eol.org/pages/1021865/details

eol.org (2017) Lined Shore Crab (n.d.) Retrieved from http://eol.org/pages/317367/details

Garth JS (1957) The Crustacea Decapoda Brachyura of Chile. Reports of the Lund University Chile expedition 1948-1949. Lunds Universitets Arsskrift, Lund, Sweden

Hartnoll RG (1973) Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. Estuar Coast Mar Sci 1:137–152

Hayward PJ, Ryland JS (1995) Handbook of the marine fauna of north-west Europe. Oxford University Press, Oxford, UK

Hearn AR (2002) The transport chain of velvet crabs from Orkney, the Western Isles and Northumberland to Spain. Sea Fish Industry Authority, Edinburgh, UK

Ingle RW (1997) Crayfishes, lobsters, and crabs of Europe: An illustrated guide to common and traded species. Chapman & Hall, London, UK

Jenkins P (2012) *Caphyra rotundifrons*: Turtle-weed crab. Retrieved from http://www.gbri.org.au/Classes/2012/Caphyrarotundifrons|PhilippaJenkins.aspx

McLay CL (1988) Brachyura and crab-like anomura of New Zealand. University of Auckland, Auckland, NZ

Miller RJ, O'Keefe P (1981) Seasonal and depth distribution, size, and molt cycle of the Spider Crabs, *Chionoecetes opilio, Hyas araneus*, and *Hyas coarctatus* in a Newfoundland Bay. Can. Fish. Aquat. Sci. Tech. Rep. 1003.

Rathbun MJ (1925) The spider crabs of America. Bulletin of the United States National Museum 129, Washington DC, USA

Rathbun MJ (1930) The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. Bulletin of the United States National Museum 152, Washington DC, USA

Richerson MM (2017) *Hemigrapsus sanguineus*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Retrieved from https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=183

Sealifebase.org (2017) *Carcinus aestuarii* Nardo, 1847 Mediterranean shore crab (n.d.). Retrieved from http://www.sealifebase.org/summary/Carcinus-aestuarii.html

Masterson J (2007) Green Porcelain Crab. Retrieved from http://www.sms.si.edu/irlspec/Petrolisthes_armatus.htm

Poupin J, Juncker M (2010) A guide to the decapod crustaceans of the South Pacific. CRISP and SPC, Noumea, New Caledonia.

tpwd.texas.gov (2017) Gulf Stone Crab (*Menippe adina*) (n.d.) Retrieved from http://tpwd.texas.gov/huntwild/wild/species/stonecrab/

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36:1–48

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington DC, USA

# Appendix B.

# Supporting Information for Chapter 3

## Supplementary tables

**Table B.1 Additional information on European green crab collection sites and methods of collection.**

| Region | Site | Lat/Long | Description | Collection method | Collection date |
|---|---|---|---|---|---|
| BC | Barkley Sound (BS) | 49.033583, -125.318135 | Shell/cobble beach, intertidal | Baited Fukui fish traps | July 2014 |
| BC | Quatsino Sound (QT) | 50.523696, -128.022879 | Mudflat, intertidal | Baited Fukui fish traps | August 2014 |
| NS | Bedford Basin (BIO) | 44.681659, -63.612537 | City harbour, rocky subtidal | Baited Fukui fish traps | September 2014 |
| NS | Kejimkujik National Park Seaside (KJ) | 43.872674, -64.821507 | Saltmarsh, intertidal | Baited Russel shrimp traps | September 2014 |
| SA | Table Bay (TB) | 33.919692, 18.443147 | City harbour, silty subtidal | Baited crab traps | August 2014 |
| SA | Hout Bay (HT) | 34.049622, 18.348022 | City harbour, silty subtidal | Baited crab traps | August 2014 |
| NI | Strangford Lough (SF) | 54.392125, -5.5740744 | Subtidal, silty | Hand collected | July 2014 |
| NI | Carlingford Lough (CF) | 54.027458, -6.0701758 | Subtidal, sandy | Hand collected | July 2014 |
| NI | Belfast Lough (BF) | 54.679709, -5.6140715 | Subtidal, silty harbour | Hand collected | July 2014 |

British Columbia, Canada (BC); Nova Scotia, Canada (NS); South Africa (SA); and Northern Ireland, UK (NI).

**Table B.2 Select statistical comparisons of bootstrapped regional parameter estimates.**

| | Lower 2.5% quantile | Upper 2.5% quantile |
|---|---|---|
| Attack rate (*a*) | | |
| **BC v. NI** | 0.78 | 9.39 |
| **NS v. NI** | 0.07 | 2.59 |
| SA v. NI | -0.11 | 5.59 |
| Handling time (*h*) | | |
| BC v. NS | -0.03 | 0.02 |
| SA v. NI | -0.01 | 0.19 |
| **NS v. NI** | 0.02 | 0.12 |

Attack rate *a* and handling time *h* estimates, for pairs of regions (see Fig. 3.3). For every bootstrap iteration (n = 2000) we compared the difference between the parameter estimates to the resulting distribution. If the likelihood of the difference being zero fell between the upper and lower 2.5% quantiles, we concluded that the parameter estimates for those two regions were not significantly different. Significant comparisons are indicated in bold. BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK).

## Supplementary figures

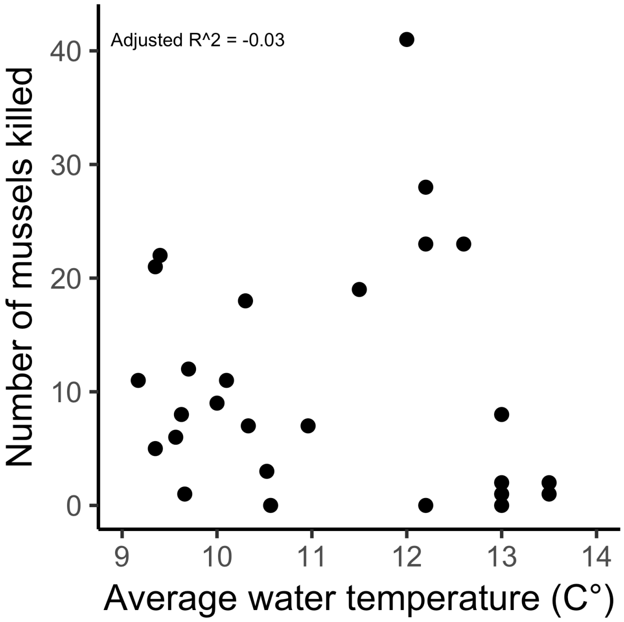

**Figure B.1 Relationship between water temperature and number of prey killed by European green crabs.**
Average water temperature was calculated for each trial (start temperature + end temperature/2), for the highest mussel density only (n = 64 mussels).

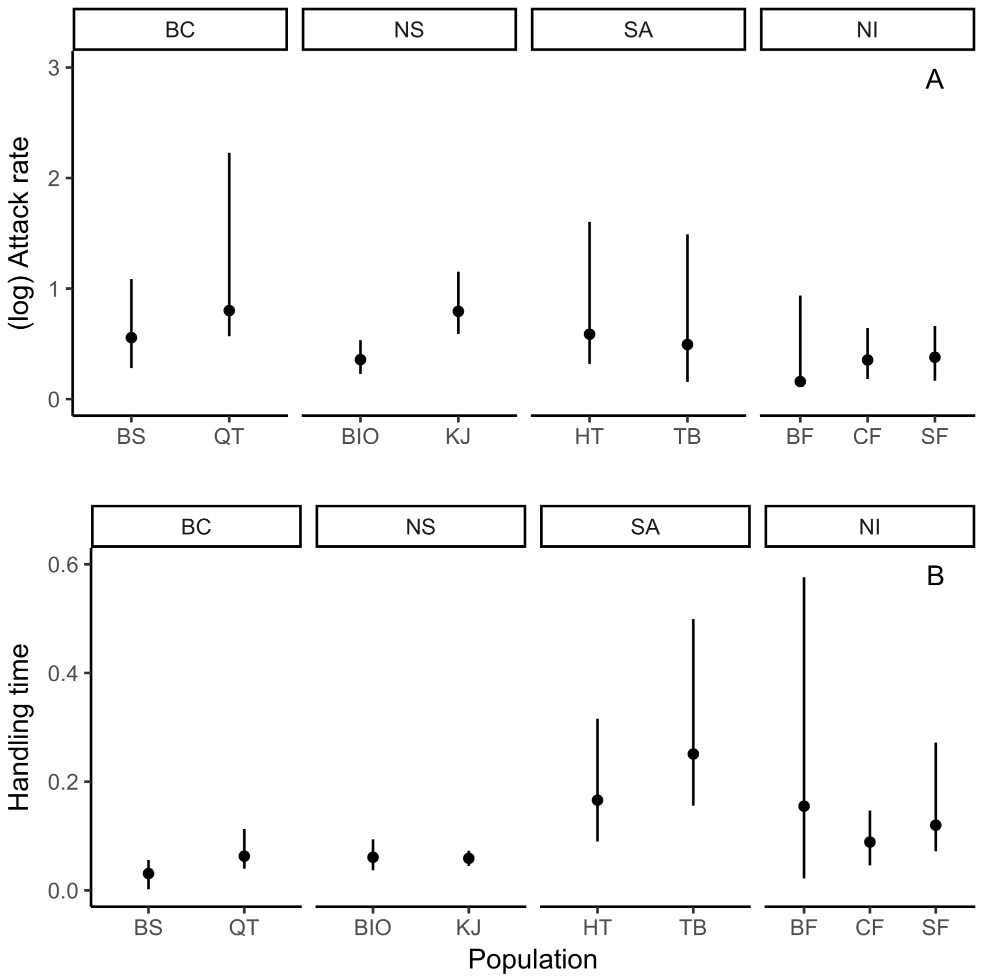

**Figure B.2 Parameter estimates of attack rate and handling time for European green crabs from nine populations, feeding on mussels.**

Parameter estimates (±95% CI) of (A) attack rate *a*, and (B) handling time *h* for bootstrapped (n = 2000) Type II functional response curves of European green crab, from nine populations within four regions, preying on varying densities of mussels. Regions are: BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK); see Table B.1 for additional information on the individual populations within each region. For each pair of populations within a region, differences were formally compared by calculating the difference between the parameter estimates for every iteration of the bootstrap and examining the resulting distribution. If the likelihood of the difference being zero fell between the upper and lower 2.5% quantiles of that distribution, we concluded that the parameter estimates for those two regions were not significantly different. Based on the resulting distributions, the only significant difference detected was for attack rates within Nova Scotia (BIO v. KJ).

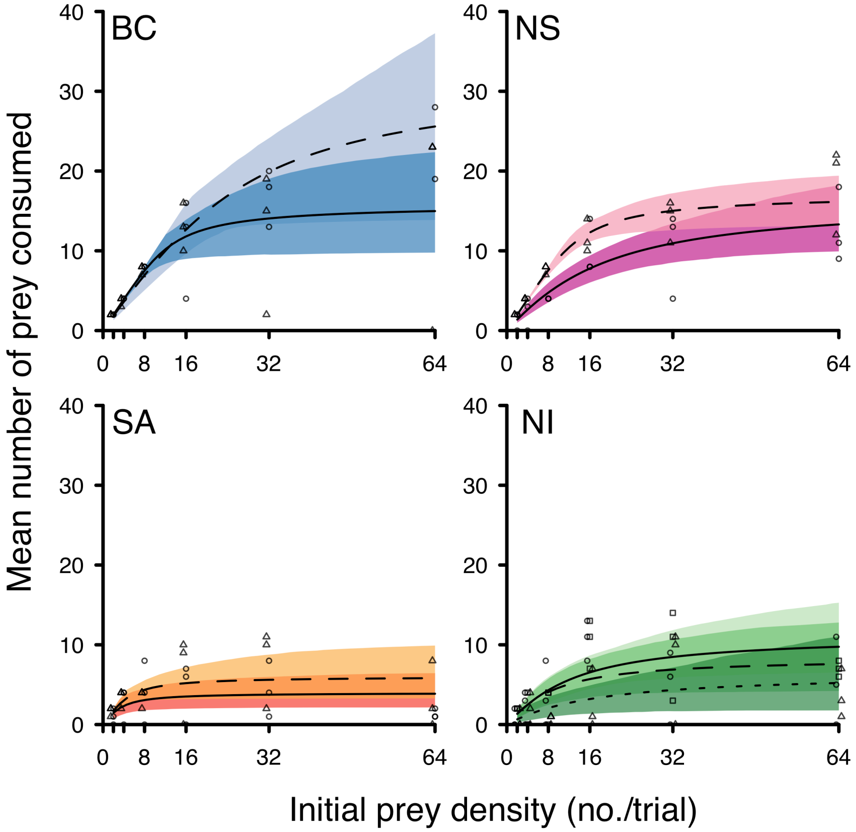

**Figure B.3 Functional response curves for European green crabs preying on mussels (*Mytilus* spp.) from nine populations sampled in four regions.**

Functional response curves, modeled from the raw data (open symbols) with a Type II Rogers random predator equation without prey replacement, for nine populations of European green crabs preying on mussels (*Mytilus* spp.) in four regions: BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK). Populations include: Barkley Sound (dashed; open triangle) and Quatsino Sound (solid; open circle) in BC, Bedford Basin (solid; open triangle) and Kejimkujik National Park (dashed; open circle) in NS, Table Bay (solid; open triangle) and Hout Bay (dashed; open circle) in SA, Carlingford Lough (solid; open square), Strangford Lough (dashed; open triangle), and Belfast Lough (dotted; open circle) in NI. Shaded areas represent the 95% bootstrapped confidence intervals.

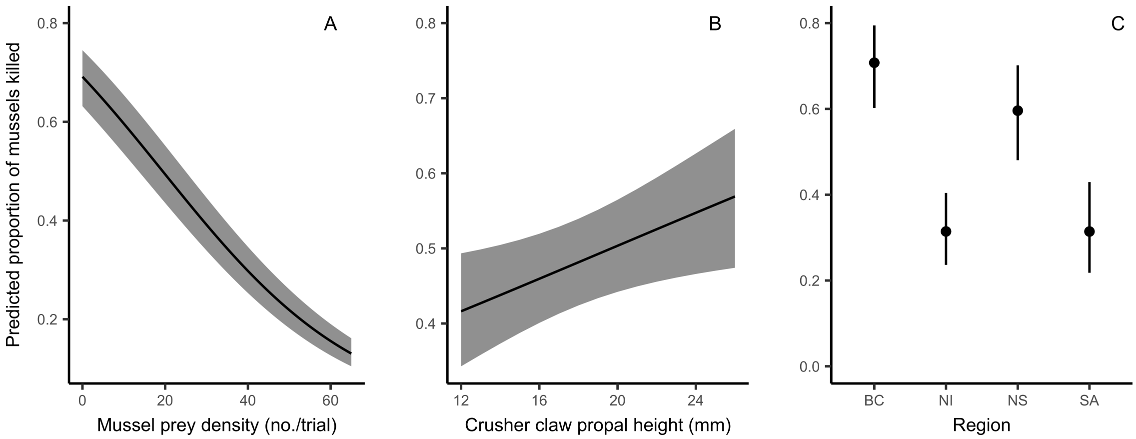

**Figure B.4 Predicted proportion of mussels killed by European green crabs in relation to prey density, claw size (mm), and the region of origin, derived from a modified version of the top generalized linear mixed-effects model.**

The predicted proportion of mussels killed by European green crabs (with 95% confidence intervals) in relation to (A) prey density, (B) claw size (mm), (C) and the region from which crabs were collected: BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK). Predictions are derived from a generalized linear mixed-effects model that is a modified version of our top model (Table 3.1) where all four regions are used, rather than combining BC and NS, and are shown for each factor when the other factors are fixed at their mean or proportional values.

# Appendix C.

# Supporting Information for Chapter 4

## Methods for green crab gut content analysis

Genetic methods developed and performed by the Canadian Centre for DNA Barcoding (University of Guelph, Ontario).

Gut content samples were treated with Lysis was performed with 45uL of insect lysis buffer/ 5uL ProK per sample and an overnight incubation for approximately 16 hours at 56°C following Ivanova (2006). The resulting lysate had 100uL of Binding Mix added to each sample and passed through a 3um PALL filter plate by centrifugation; followed by the addition of 180uL pf protein wash buffer and 700uL of wash buffer with subsequent spins between washes. DNA was eluted in 40uL of elution buffer.

The target genetic marker was amplified using the Polymerase Chain Reaction (PCR) with *rbcLa-F-t1 / MrbcL163-R1-t1* tailed with M13 primers for PCR round 1 (Ivanova et al 2016). Thermocycling conditions, 94C for 2 min; followed by 40 cycles of 94C for 30 seconds, 55C for 30 sec, and 72C for 30sec; with a 5 min 72C extension. PCR round 1 recipe: 6.25uL 10% Trehalose (Sigma); 2uL double distilled water (HyClone); 1.25uL 10X Platinum buffer (Invitrogen); 0.625uL 50mM MgCl2 (Invitrogen); 0.125uL 10uM *rbcLa-F-t1* primer; 0.125uL 10uM *MrbcL163-R1-t1* primer; 0.0625uL 10 mM dNTP mix (Kapa Biosystems); 0.06uL Platinum Taq (Invitrogen); 2uL DNA per sample, for a total of 12.5uL reaction.

For PCR round 2 the PCR1 products were amplified with M13F labelled with IonExpress tags ion01 to ion39 and M13R-TRP1 for the 39 crab gut samples. Thermocycling conditions for PCR 2 is as follows 94C for 2 min; followed by 40 cycles of 94C for 30 seconds, 51C for 30 sec, and 72C for 60sec; with a 5 min 72C extension. PCR round 2 recipe: 6.125uL 10% Trehalose (Sigma); 1.25uL 10X Platinum buffer (Invitrogen); 0.625uL 50mM MgCl2 (Invitrogen); 1.25uL 1uM M13F-ion tagged primer (added individually in separate wells); 1.25uL 1uM M13R-TRP1 primer; 0.0625uL 10 mM dNTP mix (Kapa Biosystems); 0.06uL Platinum Taq (Invitrogen); 2uL of PCR round 1 product (diluted 1:1 with double distilled HyClone water), for a total of 12.5uL reaction.

Sequencing was performed on an Ion Torrent PGM high-throughput sequencer using Ion PGM Template Hi-Q View 400 kit, 314 chip. The resulting sequence reads were associated to their source sample using unique molecular identifier tags, filtered to remove low quality reads (minimum quality of QV20 and minimum length of 100 bp), and trimmed to remove primer and adapter sequences (reads lacking a forward primer were excluded from analysis while reads lacking a reverse primer were allowed to proceed to the next step). Only high quality reads assigned to correct Ion Express MID tags were used in NGS data analysis. Negative PCR and negative extraction controls did not produce any sequencing data.

# Supplementary tables

**Table C.1 Counts of benthic fauna identified in sediment cores, separated by functional group and relative size classifications.**

| block | treatment | clam.lg | clam.md | clam.sm | crab.lg | crab.md | crab.sm | gastropod.md | gastropod.sm | nematode.md | nematode.sm | polychaete.md | polychaete.sm | shrimp.md | shrimp.sm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | exclosure | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 9 | 0 | 0 |
| A | low density | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 9 | 0 | 8 | 0 | 0 |
| A | high density | 0 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 6 | 1 | 6 | 0 | 2 |
| A | no cage | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 5 | 0 | 6 | 0 | 2 |
| B | exclosure | 0 | 1 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 10 | 0 | 4 | 0 | 2 |
| B | low density | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 0 | 4 | 1 | 0 |
| B | high density | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 6 | 0 | 2 |
| B | no cage | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 5 | 0 | 3 | 0 | 0 |
| C | exclosure | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 2 | 0 | 0 |
| C | low density | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 1 | 3 | 0 | 1 |
| C | high density | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 11 | 0 | 0 |
| C | no cage | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 2 | 0 | 2 |
| D | exclosure | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 6 | 1 | 4 | 0 | 0 |
| D | low density | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 14 | 0 | 6 | 0 | 0 |
| D | high density | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 |
| D | no cage | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 1 | 0 | 0 |
| E | exclosure | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 14 | 0 | 4 | 0 | 0 |
| E | low density | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 5 | 0 | 2 |
| E | high density | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 0 | 7 | 0 | 2 |
| E | no cage | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 1 | 2 | 0 | 5 |
| F | exclosure | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 7 | 0 | 1 |
| F | low density | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 1 |
| F | high density | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 54 | 0 | 5 | 0 | 0 |
| F | no cage | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 |
| **Total** | | **3** | **13** | **27** | **1** | **2** | **1** | **4** | **11** | **1** | **222** | **4** | **115** | **1** | **24** |

Functional groups were determined based on the assumption that an organism's mobility and burial depth (i.e., epifaunal or infaunal) would significantly affect risk of predation risk by European green crab. Relative size classes were based on wet weight, indicated by the following: sm (small < 0.1 g); md (medium < 2.0 g); lg (large ≥ 2.0 g). Sediment cores came from plots with different densities of European green crabs (n = 6 plots per treatment). In addition to low and high green crab density treatments (1.4 and 4.2 green crabs $m^{-2}$, respectively), there was an exclosure treatment (0 crabs $m^{-2}$), and an unenclosed (no cage) treatment, which experienced the ambient density of green crabs present at the field site.

## Supplementary references

Ivanova NV, deWaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6:998–1002

Ivanova NV, Kuzmina ML, Braukmann TWA, Borisenko AV, Zakharov EV (2016) Authentication of herbal supplements using next-generation sequencing. PLoS ONE 11:e0156426.

# Appendix D.

# Supporting Information for Chapter 5

## Supplementary tables

**Table D.1 Relative variable importance (RVI) of site-level characteristics used in a boosted regression tree (BRT) model predicting the probability of invasive green crab occurring at a site.**

| Site-level characteristic | Average relative importance | SE |
|---|---|---|
| CPUE *M. magister* | 33.46 | 0.04 |
| Intertidal area (km$^2$) | 9.99 | 0.12 |
| Sediment type | 8.22 | 0.11 |
| Freshwater outflow magnitude | 8.20 | 0.09 |
| Eelgrass (presence) | 7.62 | 0.18 |
| Aspect (SW) | 6.82 | 0.11 |
| Oyster aquaculture (presence) | 4.30 | 0.05 |
| CPUE *C. productus* | 4.03 | 0.08 |
| Aspect (W) | 3.94 | 0.06 |
| Year | 3.51 | 0.05 |
| Inlet length (km) | 3.44 | 0.06 |
| CPUE *M. gracilis* | 2.93 | 0.07 |
| Aspect (SE) | 1.10 | 0.04 |
| Aspect (E) | 0.75 | 0.03 |
| Aspect (N) | 0.65 | 0.02 |
| Aspect (NW) | 0.43 | 0.03 |
| Aspect (NE) | 0.41 | 0.03 |
| Aspect (S) | 0.19 | 0.02 |
| Eelgrass absence (absence) | 0.00 | 0.00 |
| Oyster aquaculture (absence) | 0.00 | 0.00 |

Average and standard error are calculated from RVI values from five BRT model runs.

**Table D.2** **Relative variable importance (RVI) of site-level characteristics used in a boosted regression tree (BRT) model predicting adjusted green crab CPUE occurring at a site.**

| Site-level characteristic | Average relative importance | SE |
|---|---|---|
| Freshwater outflow magnitude | 20.02 | 0.31 |
| Year | 16.92 | 0.26 |
| CPUE *M. gracilis* | 16.18 | 0.16 |
| CPUE C*. productus* | 13.51 | 0.16 |
| Intertidal area ($km^2$) | 10.48 | 0.37 |
| CPUE *M. magister* | 9.60 | 0.13 |
| Sediment type | 6.13 | 0.24 |
| Inlet length (km) | 4.32 | 0.17 |
| Aspect (SW) | 0.89 | 0.07 |
| Oyster aquaculture (presence) | 0.60 | 0.08 |
| Aspect (NW) | 0.47 | 0.03 |
| Oyster aquaculture (absence) | 0.35 | 0.02 |
| Aspect (SE) | 0.29 | 0.03 |
| Aspect (W) | 0.10 | 0.02 |
| Eelgrass (absence) | 0.08 | 0.02 |
| Eelgrass (presence) | 0.05 | 0.01 |
| Aspect (S) | 0.01 | 0.01 |
| Aspect (N) | 0.00 | 0.00 |

Average and standard error are calculated from RVI values from five BRT model runs.