UNIVERSITY OF CALIFORNIA

SANTA CRUZ

BIOGEOGRAPHIC VARIATION IN ABUNDANCE, HABITAT, AND BEHAVIOR OF THE EUROPEAN GREEN CRAB, *CARCINUS MAENAS*

A dissertation submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

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June 2010

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ABSTRACT

BIOGEOGRAPHIC VARIATION IN ABUNDANCE, HABITAT, AND BEHAVIOR OF THE EUROPEAN GREEN CRAB, *CARCINUS MAENAS*

by

RIKKE KVIST PREISLER

Biological invasions provide an opportunity to study one species in different contexts and allow us to investigate factors that control the distribution and abundance of species. Studying invaders in both the native and introduced ranges can inform us about invader traits, communities, and the interaction between an invader and the community that all determine whether an invader succeeds or fails. I used three different approaches to assess invasion success of an invasive invertebrate in a California estuary. First, I used long-term monitoring data, and small scale spatial experiments at a local level. Second, I conducted a short-term, broad scale biogeographic study, to assess an invader in both its native and introduced ranges. Third, I conducted laboratory experiments to assess inter- and intra specific aggression levels in an invader to assess whether there was a relationship between aggression and invasion success. In the local study, using long-term monitoring data I found that abundance of the European green crab, *Carcinus maenas*, in Elkhorn Slough estuary is temporally variable. High temporal variation is likely driven by

recruitment limitation. I detected a negative relationship between abundance of green crab and species of small and large native crabs. These results suggest that control or eradication efforts would be most effective in years where recruitment, and adult abundance, is low, and that efforts should occur across all habitat types in the estuary.

The biogeographic study revealed that green crab abundance was an order of magnitude higher in the native range in Europe and on the US Atlantic Coast, than in the most recently invaded range, the US Pacific Coast. I found that proxies for invasion success, e.g. abundance, size, or ratio of invasive to native crabs, may lead to different conclusions of where the green crab is most successful. Finally, aggressive behavior was highly variable and I found a positive relationship between inter- and intraspecific aggression, which was not correlated to invasion success. Despite many examples of invaders that succeed in the introduced range, this species seem to face novel challenges rather than novel opportunity in the most recently introduced range, the US Pacific Coast.

ACKNOWLEDGEMENTS

I would like to thank my dissertation committee members, Kerstin Wasson, Pete Raimondi, Ted Grosholz, Ingrid Parker and Dan Doak for their continued support and advice in developing and conducting this research. Kerstin has been an incredible inspiration and role model of how to balance a career in science and having a family without compromising either. She has continuously provided advice and direction whether I was developing new ideas, writing grant proposals, or analyzing data. Her rigorous scientific approach in addition to being extremely supportive during difficult times made her an ideal advisor and mentor. Pete's help in experimental design and statistical analysis has been invaluable as well. His ability to make one explain the hypotheses that generated various research questions has been extremely helpful for defining the framework of my research. Ted has been the overall expert during this research. Not only is he an excellent general ecologist, but also a leading expert on green crab invasion ecology, and an excellent statistician. He has been very instrumental in revising the drafts of this dissertation and an invaluable help in preparation for publication. His humor has been refreshing. I feel incredibly fortunate to have had Ted on my committee as the non-UCSC member. Ingrid substituted Dan in the last few years of my research, and despite being added far along into this project, she has invested much time and many resources in helping with revision of the chapters. Her comments have been very insightful, and getting a slightly different perspective has been refreshing. Dan was very helpful early in the process of helping me develop ideas and I found his quantitative perspective very

useful. Further, I would like to thank the undergraduate UCSC volunteers, ESNERR docents, and field assistants who have spent endless hours with me in the field, hauling heavy traps, cutting up stinky bait, and keeping me focused and entertained. Without their help this work would never have been completed. In particular I would like to thank Betsy Davidson, Shirley Murphy, Thomas Preisler, and Tine Buch Rasmussen who all helped me in different parts of the world. Their company and help has been very much appreciated. I have also been fortunate to have been part of two labs during graduate school. I have received continuous support and feedback from the RC-lab and Wasson lab, in particular from Nina d'Amore who has listened to countless presentations for various fora and been very supportive in general. This research could not have been completed with out lab support from Long Marine Lab, Bodega Bay Marine Lab, San Francisco Bay NERR, Waquoit Bay NERR, Great Bay NERR, Jackson Estuarine Lab, Narragansett Bay NERR, Woods Hole Oceanographic Institution, Rønbjerg Marin Station, NIOO-KNAW, and Roscoff Marine Biological Station. Funding has been provided by Elkhorn Slough National Estuarine Research Reserve, Estuarine Research Federation, University of California, Santa Cruz, National Oceanic and Atmospheric Administration/Sea Grant, PISCO, Earl and Ethel M. Myers Oceanographic and Marine Biology Trust, STEPS Institute for Innovation in Environmental Research, and Friends of Long Marine Lab. Last, I would like to express my greatest appreciation of my incredible husband, Thomas Preisler, for his continued love, support, and encouragement. Without him, I would not have been where I am today.

INTRODUCTION

Biological invasions provide an opportunity to study variation in species' traits and population structure and the factors that affect abundance and distribution of a species (Sax et al. 2007). Many hypotheses in invasion biology are aimed at explaining differences between the native and invaded range of introduced species, in terms of abundance of the introduced species, or in terms of its impact on other species or ecological processes (Hierro et al. 2005). There are several theoretical reasons why one would expect an introduced species to fare particularly well in the introduced range. The three most commonly invoked mechanisms are: the Enemy Release Hypothesis (Gillett 1962), which considers a reduced selection pressure from competitors, predators, or parasites, the Novel Niche Hypothesis (Elton 1958, MacArthur and Wilson 1967) which hypothesizes that there are unexploited available resources denoted as empty niches in the introduced range, and the Novel Weapons Hypothesis (Callaway and Aschehoug 2000) which considers that introduced species have competitively superior traits against which native species have no co-evolved defenses. Because of support for the above hypotheses in the plant literature and terrestrial invertebrates we often perceive introduced species to be highly successful in the introduced ranges. However, studies rarely quantify and compare abundances, species' traits or niche breadth in the native and introduced ranges to verify the assumption that the introduced species is in fact highly abundant or otherwise successful in its invaded range relative to its native range (Hierro et al. 2005).

An invasive species can be defined as a non-native species that threatens the diversity or abundance of native species (EPA 2000) or as species, native or non-native, whose population has undergone a stage of exponential growth and rapid range expansion (Occhipinti-Ambrogi and Galil 2004). Invasions are common across taxonomic groups and geographic areas (Vermeij 1991, Lodge 1993) and non-native species have been found in every marine habitat where surveys have been conducted for non-native species (Preisler et al. 2009). Non-native and invasive species are of increasing concern world-wide because of their potential ecological and economical impacts on native species and communities. Invasive species have the potential to greatly alter existing ecosystem structure and function (Elton 1958, Nichols et al. 1990, Ruiz et al. 1997, Grosholz et al. 2000). Invasive species can also be an economical burden to state and federal agencies. Some examples are mussels which clog up aqueducts, marine invertebrates which foul ship hulls, and agricultural pests which can damage crops. Invaded communities are ideal study systems to examine factors that regulate populations under different selection pressures because one can compare the same species in different biotic and abiotic contexts in the native and introduced ranges of the species. Invaders can also be examined early or late in the process of colonizing new areas.

The European green crab provides an ideal opportunity to study the same species in different contexts. More specifically, we can investigate how species traits or population structure may differ among regions with various selective pressures. The native range of the green crab spans from Northern Norway to North Africa

(Yamada 2001) and the green crab has is currently established on six of the seven continents of the world. The green crab invaded the US Atlantic Coast two centuries ago (Say 1817), South Africa in 1983, (Le Roux et al. 1990), Japan in 1984 (Darling et al. 2008), the US Pacific Coast around 1989 (Grosholz and Ruiz 1995), Tasmania in 1993 (Thresher et al. 2003), and most recently Patagonia in 2000 (Hidalgo at al. 2005). The green crab is considered a nuisance species in most of the introduced ranges, because green crab has been shown to affect single species as well as community structure (Vermeij 1982, Grosholz et al. 2000, Freeman and Byers 2006). Green crabs can have multi-trophic level effects on local communities (Grosholz et al. 2000) and can facilitate invasions of other species (Grosholz 2005).

This dissertation research examines spatial and temporal variability in green crab physical and behavioral characteristics and their invasion dynamics. The goals are to quantify and compare the green crab invasions in native as well as introduced ranges. I investigated how green crab abundance, traits and population structure varied in response to differences in factors that can limit distributions, such as habitat types, and factors that can regulate population growth, such as recruitment, competition, and predation. Invasion biology theory involves hypotheses that explain why species become particularly abundant in introduced ranges, including exponential growth and rapid range expansion due to initial low invader density and later lack of invader population regulation due to escape from enemies or decreased intraspecific competition. In different ways, each of my dissertation chapters addresses whether the assumptions of invasion success in the introduced ranges are met, and whether some of the factors that have been postulated to be correlated with invasion success are also correlated with invasion success in the areas of focus in this study.

In my first chapter I investigated the temporal and spatial patterns in the early stages of the European green crab invasion in Elkhorn Slough, an estuary in Central California. The early stages of invasions are rarely studied, because the non-native species may be inconspicuous or found in very low abundances. However, long-term monitoring data, such as the crab monitoring data from Elkhorn Slough can be a useful tool aiding in the characterization of temporal and spatial trends early in the invasion of a non-native species. In this part of my study the goals were to: 1) Investigate temporal variation in one or a few regularly sampled locations in Elkhorn Slough 2) Investigate whether there was a relationship between non-native and native crab species in terms of inversely correlated abundances and 3) Investigate spatial trends of the green crab invasion in order to see whether certain habitats were more vulnerable to green crabs than other habitats. The data for this part of my dissertation span about ten years. In the first chapter, I found that abundance of green crab in Elkhorn Slough is temporally highly variable and the final outcome of the invasions remains uncertain. In the first five years after initial detection of the green crab, abundance was very low. The following five years the population was growing rapidly, and in the last four years green crab abundance has drastically declined and remained low. Size distribution data suggest the cause of low abundance was lack of recruitment. Although there was a relationship between low green crab and high larger native crab abundance there were no clear spatial trends of the invasion. Habitats that differed in terms of marine influence, depth, and tidal exchange all harbored green crabs. Eradication or control efforts should thus be directed at all estuarine habitat types, and would be most likely to succeed in years of low abundance such as the current period. However, the probability of recruitment from San Francisco and other northern bays seems high, making permanent eradication unlikely.

The second chapter of my dissertation is a broad-scale study in which I investigate biogeographic variation in green crab abundance, population structure, and habitat use. I assessed population and individual parameters in two different habitats in two regions of the invaded range and one region of the native range. Many studies of invasions are limited to a single region, partially due to logistical and monetary constraints of researchers who work in a limited geographic area. Yet there are valuable lessons to be learned about invasion success and its predictors by examining the same species in various habitats in multiple geographic regions. Before we can begin to discuss invasion success, or variation in populations in different regions we need tools to consistently quantify invasions among these regions, and only once we are able to quantify invasions can we discuss biogeographic variation in invasions. The goals for this second part of my study were therefore to: 1) Quantify and compare the green crab invasion in two regions to which the green crab was introduced, and compare those two regions to a region in the native range of the European Green Crab; 2) Quantify and compare green crab invasion between two different habitats: estuaries and the open coast because in the native range, and ranges invaded centuries ago, both habitats are utilized by green crabs whereas in more recently invaded ranges, the green crab is only found in estuaries and protected bays, and not on the open coast. The data for the last two chapters were collected on the most recently invaded US Pacific coast, the US Atlantic coast, invaded two centuries ago, and in the native range from Denmark to France, in the period from 2006 to 2008. I found that the biogeographic patterns varied by parameter, for instance with size and abundance showing different trends. Hence, it is important to measure several and carefully chosen parameters when quantifying invasions on a broad scale. Contrary to expectation, I found the green crab to be much less abundant in the most recently invaded range, relative to the native and long-ago invaded ranges. Furthermore, green crab populations in the non-native range which was invaded several centuries ago more closely resembled populations in the native range, than the population in the most recently invaded range. This study provides a framework for future studies in which researchers wish to quantify and compare the severity of a non-native species' invasion across various regions to which a species is non-native.

In addition to abiotic factors such as water temperature, wave intensity, and salinity biotic factors such as food availability, interspecific competition, possible release from natural enemies such as predators and parasites, and life history traits of an invader can all contribute to or impede the invasion success or failure of a non-native species. In the literature there are examples of how increased aggression in a non-native species can enhance invasion success, such as in Africanized honeybees

(Winston 1992). Release from natural enemies or low intraspecific densities can lead introduced species to invest fewer resources in intraspecific aggressive behavior which can lead to increased invasion success as in the example of Argentine ants (Suarez et al. 1999) as opposed to maintaining suites of aggressive behaviors which can be correlated to invasion success of introduced species (Sih et al. 2004). Although it is understood how water temperature, salinity, and high fecundity can facilitate growth in green crab populations, currently, there are no complete explanations as to why green crab invasions are highly variable among biogeographic regions. Because it has been suggested that species' behavior can influence invasion success, the third chapter of my dissertation is an investigation of variation in behavior in individuals of the same species across a large geographic region. Due to anecdotal evidence of variation in aggression levels in green crabs on the US Pacific and Atlantic coasts my research focused on regional behavioral differences in green crabs. More specifically, the goal of this study was to quantify differences in inter- and intraspecific aggression levels of green crabs among three regions of which two were non-native and the third was the native range. In the third chapter, I investigated whether behavioral difference in green crab among the three biogeographic regions was variable and if behavioral differences could possibly explain part of the variation in green crab invasions among the three regions. I found that despite using consistent field and laboratory methods, inter- and intra-specific aggression was temporally and spatially highly variable, with no consistent trends among regions or between years. This leads to the conclusion that one must be cautious when generalizing about aggression levels from behavioral experiments, unless there is extensive replication that yields temporally and spatially consistent results. This finding emphasizes the great challenge of determining whether behavior in this species can enhance or impede invasion success, since behavior was extremely variable.

One common theme in all of the above studies is high variability, whether measuring abundance, individual size, habitat preference, or behavior. In this study I analyzed ten years of data on temporal variation in green crab abundance at one location and I analyzed extensive data sets on spatial variation among biogeographic regions, because I surveyed 53 sites on three different continents within the same year. Additionally, I analyzed extensive behavioral data sets. The most common conclusion I reached whether looking at abundance, size, habitat preference or behavior was that variation at the small scale was higher than variation at larger scales, and therefore it was hard to detect trends in variation across larger scales whether I investigated long term trends of green crab invasion at Elkhorn Slough, abundance differences among biogeographic regions or habitats, or behavioral differences between regions, years or between transported and non-transported crabs. My study strongly suggests that great caution should be applied when generalizing about behavior or abundance of invaders from sampling that is more limited in time or space.

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CHAPTER 1

Investigating temporal and spatial patterns in the early stages of the European green crab invasion in a California estuary

Introduction

Invasive, non-native species are of increasing concern world-wide (Elton 1958; Ruiz et al. 1997; Underwood et al. 2006; Johnson et al. 2008) and have the potential to greatly alter existing ecosystem structure and function (Elton 1958; Nichols et al. 1990; D'Antonio and Vitousek 1992; Grosholz et al. 2000). Numerous non-natives are introduced to new ranges, but not all non-natives become established and not all established non-native species become invasive (Williamson and Fitter 1996; Cohen and Carlton 1998). The National Invasive Species Council defines invasive species as "…an alien (or non-native) species whose introduction does, or is likely to cause economic or environmental harm or harm to human health" (EO 13112 1999). Additionally, invasive species can be defined as species that threaten the diversity or abundance of native species (EPA 2000) or as species, native or non-native, whose population has undergone a stage of exponential growth and rapid range expansion (Occhipinti-Ambrogi and Galil 2004). Population dynamics of early invasion phases in marine systems have rarely been investigated because most non-native species become invasive before they draw any attention (Lodge 1993; Crooks and Rilov 2009). Therefore, the critical stages between introduction, establishment, and invasion are rarely studied unless an existing monitoring program of other species coincidentally detects the early stages of an invasion (Caraco et al. 1997; Smith et al. 1998) or unless the species is a notorious invader or an agricultural pest elsewhere and therefore is being closely watched. Once a non-native species has been introduced and become established, the population can follow various trajectories determined by abiotic or biotic conditions that may limit or facilitate the spread of the invader. First, the established population can crash and the invader goes locally extinct. Second, the population can persist at low to medium densities or abundances, or third, the population can grow rapidly reach high densities. Long-term monitoring data can characterize the trajectory of a newly introduced non-native population and is helpful for determining whether a species will go extinct, become established or invasive in the new region.

Long-term monitoring data can, in addition to tracking temporal trends, facilitate detecting spatial trends in invasions. Habitat heterogeneity in the newly invaded range of a non-native species may lead to spatial variation in species invasions, since certain habitats may be more invasible than other habitats (Williamson and Fitter 1996; Shea and Chesson 2002; Wasson et al. 2005). For example, species-poor habitats may have more empty niches or lower biotic resistance of natives, and can be prone to species invasions (MacArthur 1955; Elton 1958; Hutchinson 1959; MacArthur and Wilson 1967; Stachowicz et al. 1999). Also, anthropogenically altered habitats may favor non-natives that are better adapted to the changed conditions than are the native species that evolved under the historic conditions (Byers 2002). Investigating spatial trends in invasions is important to inform managers whether certain areas are more vulnerable to invasion than other areas. Consequently, management resources can be focused on invasion prevention or eradication in vulnerable habitats.

There are many examples of invaders attaining high densities, abundances, large ranges or simply becoming extremely conspicuous in the invaded range (Nichols et al. 1990; Grosholz 1996; Grosholz and Ruiz 1996; Albins and Hixon 2008). One species with such a potential is the global invader, the European green crab, *Carcinus maenas* (hereafter referred to as green crab). The green crab has been characterized as invasive in many of the regions to which it has been introduced. The native range of the green crab spans from Northern Norway to North Africa (Yamada 2001). The green crab invaded the US Atlantic Coast two centuries ago (Say 1817), South Africa in 1983, (Le Roux et al. 1990), Japan in 1984 (Darling et al. 2008), the US Pacific Coast around 1989 (Grosholz and Ruiz 1995), Tasmania in 1993 (Thresher et al. 2003), and most recently Patagonia in 2000 (Hidalgo at al. 2005). The green crab can affect single species such as soft shell clam *Mya arenaria* (Welch 1968, Whitlow et al. 2003), the whelk *Nucella lapillus* (Vermeij 1982), the marine mussel *Mytilus edulis* (Freeman and Byers 2006) and native crab species, such as *Hemigrapsus oregonensis* (hereafter referred to as mud crab) or juvenile *Cancer productus* which can affect the green crab as well (Grosholz et al. 2000; Hunt and Yamada 2003). (For simplicity, all *Cancer spp.* in this study will be referred to as rock crabs.) Additionally, green crab can have multi-trophic level effects on local communities (Grosholz et al. 2000) and can facilitate invasions of other species (Grosholz 2005).

One goal of our study was to examine early invasion stages by characterizing temporal trends in abundance and population structure in a recent invasion. We investigated the early invasion stages of the European green crab using a long-term monitoring dataset in Elkhorn Slough, a major estuary in Central California, on the Pacific coast of North America. The green crab has successfully invaded nearby San Francisco Bay (Cohen et al. 1995) as well as Bolinas Lagoon, Drake's Estero, Tomales Bay and Bodega Harbor (Grosholz and Ruiz 1995) in California in addition to bays and estuaries in Washington and Oregon (Yamada et al. 2005). Therefore, we expected the population of green crab in Elkhorn Slough to rapidly increase in abundance over time with a population structure reflecting that of a growing population.

A second goal of our study was to assess whether there was a relationship between green crab abundance and native crab abundance. Larger native crabs may provide biotic resistance against the invader (Hunt and Yamada 2003) while the invader may prey upon smaller native crabs (Grosholz et al. 2000; Jensen et al. 2002; Preisler 2010). Hence, this study system possibly contains intra-guild trophic interactions in form of a negative relationship between abundance of native rock crab and green crab, and a negative relationship between green crab abundance and native mud crab abundance. We expected to find a negative correlation between larger native rock crab abundance and green crab abundance, and a negative correlation between green crab abundance and abundance of smaller native mud crabs.

The third goal of our study was to examine spatial patterns of green crab abundance and sizes within the estuary in order to determine whether some habitat types were more vulnerable to invasion than others. Other studies have found green crabs to be larger (Rewitz et al. 2004; Silva et al. 2006) and less abundant (Hunt and Yamada 2003; Yamada and Gillespie 2005) closer to the mouth of estuaries as opposed to closer to the head of an estuary. Due to presence of heterospecific larger crabs near the mouth of Elkhorn Slough we expected green crab to be less abundant near the mouth of the estuary. Additionally, tidal restriction can have an effect on community composition of various vertebrates and invertebrates. For example, Ritter et al. (2008) found that many marine species were more frequently found at sites with unrestricted (fully tidal) vs. restricted tidal exchange. Therefore we investigated whether green crabs abundance was related to tidal exchange. We expected green crabs to be less abundant in fully tidal vs. artificially restricted habitats, because we found abundance of large predatory rock crabs to be higher in the more marine conditions of fully tidal habitats. Last, depth (or tidal elevation) can have an effect on green crab distribution in terms of size and abundance. Larger crab species can displace green crabs from deeper to more shallow habitat in estuaries (Hunt and Yamada 2003) and smaller crab species can be subject to predation from larger crab species (deRivera et al. 2005; Jensen et al. 2007). Green crabs may be more abundant, and smaller in the intertidal than in the subtidal (Breen and Metaxas 2009), possibly due to predation and behavioral changes in green crab due to the presence of cancrid crabs which can displace green crab from the subtidal to the intertidal (Hunt and Yamada 2003; Jensen et al. 2007; League-Pike & Shulman 2009). Therefore, we investigated patterns of variation in green crab abundance and size at two tidal depths, and we expected to find fewer and larger green crabs at deeper depths due to the presence of cancrid crabs in Elkhorn Slough.

Methods and materials

Study system

Elkhorn Slough is an estuary in Central California. The slough is about 8 km long and consists of a main channel with many tidal creeks and a few larger channels branching off the main channel (Fig. 1). The green crab was first detected in Elkhorn Slough in 1994 (Grosholz 1996) and in the following years green crab was detected at very low abundance in the estuary (Grosholz unpubl. data). In 2000-2001 Flores and Miller (2001) deployed a total of 86 traps at four sites (1, 6, 11, 15) (Fig. 1) yet only five green crab individuals were found. In 2001, we established a long-term volunteer crab monitoring program at the estuary, involving limited but consistent annual sampling at three sites. To complement this monitoring program, we conducted targeted sampling at additional sites using additional trap types in order to examine abundance and distribution of green crabs and other crab species in various spatial comparisons. Thus, different subsets of our crab monitoring data were used to address different questions (temporal and various spatial comparisons) in order to ensure that consistent sampling effort was represented in all treatments.

Study species

The European green crab is a crustacean decapod with a bipartite life history and a life span of 3-6 years (Yamada 2001). The green crab is omnivorous and is found across a broad range of salinities (4 to 54 ppt for short-term survival and at least 11 ppt for long-term survival) and temperatures ranging from 0° to 33°C for short-term survival and 10° to 26°C for long-term survival and growth (Yamada 2001). Green crabs typically mate in spring but in areas where the water temperature is above 10°C in other seasons than spring, green crabs may be able to mate almost year round (Preisler personal observation). The female carries the brood for several months, depending on the water temperature (Yamada 2001) and release the newly hatched larvae temporally close to a high spring tide. The pelagic larval duration also depends on water temperature, but lasts 32 to 62 days (Dawirs 1985), during which green crabs undergo four zoeal stages. After the 4th zoeal stage green crab molts into a megalopal stage during which the larva travels via currents back to the near-shore environment. Here, the larvae settle and undergo the last metamorphosis into the first crab stage. On the US Pacific Coast female green crabs are sexually mature at about 35 mm in carapace width (CW) (Mohamedeen and Hartnall 1989, Yamada 2001). CW of adult females is 35-79 mm on the US Pacific Coast and maximum CW for males is 96 mm (Yamada 2001). Native crab species encountered in this study included: *Hemigrapsus oregonensis* hereafter referred to as mud crab, *Cancer antennarius*, *Cancer gracilis*, and *Cancer productus* were at times difficult to distinguish and are therefore grouped in the analyses and hereafter referred to as rock crabs. We also found *Pachygrapsus crassipes* in our traps but these individuals were not included in the analysis, because trapability of this species can be highly variable.

Field methods

To provide a comprehensive characterization of both small and large crabs in the community we used three different trap types: 1) minnow traps (hereafter referred to as standard minnow traps), which are conically shaped plastic traps 42 cm long x 22.5 cm center diameter and 15.5 cm end diameter with a 2.5 cm opening, 2) modified minnow traps (hereafter referred to as modified minnow traps) where the opening in one end was increased to 5 cm in diameter in order to allow larger crabs to enter the traps, and 3) Fukui fish traps, of dimensions 20 x 45 x 60 cm and mesh size 1 x 1 cm. All traps were tethered to a PVC stake and deployed on muddy or sandy substrate by pushing the stake into the substrate. All traps were baited with raw anchovy or sardine placed in a closed bait container made from a 35mm film canister drilled with 18-21 holes of 5 mm in diameter. Finally, to ensure that we could adequately characterize crab species that do not readily enter traps we used pitfall traps made from 3-gallon plastic buckets with an opening of 24 cm in diameter. Pitfall traps were buried with the opening of the bucket flush with the substrate. Traps were deployed at Mean Lower Low Water (MLLW) for all surveys. Additional traps were deployed at 60 cm below MLLW for the spatial pattern study of effect of depth on green crab abundance. All traps at a site were at least 10 m apart, and left in the field approximately 24 hrs. All crabs sampled by traps or pitfall traps were identified, counted and measured. We used analog calipers to measure crab carapace width to the nearest 0.1 mm. Green crabs were also sexed.

Temporal trends: Green crab abundance and population structure

In order to track long-term trends in the green crab invasion at Elkhorn Slough we chose site 6 (Fig. 1) which is easily accessible for our volunteer teams, in the mid-estuary where the highest number of green crabs had initially been found. In spring, between 2001 and 2009 we deployed 3 – 10 modified minnow traps at this site per field day (Table 2). To asses annual differences in green crab abundance (green crabs per trap) we used Analysis of Variance (ANOVA) with crabs per traps as the dependent variable, year as a factor and day as a replicate. In addition to examining long-term trends with this limited dataset from one site and season, we also used a broader dataset which increased sample size but was somewhat less consistent across year. For this broader dataset, we included, in addition to site 6, two other sites, 7 and 12 that were sampled fairly consistently, and used data from both spring and fall (Table 3). For analysis of temporal trends in abundance using both the more limited and broader datasets, we averaged all the data from modified minnow traps set at a single site on a single day, and used this average value (“site day”) as the replicate for analysis of interannual trends using ANOVA. Despite annual variation in site days, each site was sampled approximately the same number of days as any other site, within one year. Thus, there are no artifacts from differing sampling effort across sites in different years. During the course of our monitoring program, we realized that juveniles more commonly encountered in fall than spring, so the original spring sampling program did not suffice for detecting interannual differences in recruitment. Therefore, we used only the broader dataset to examine size distribution of green crabs over time.

Relationship between green crab and native crab abundance

We used non-linear regression determine whether: 1) there was a relationship between green crab abundance and abundance of the smaller native mud crab, *Hemigrapsus oregonensis* and 2) there was a relationship between green crab abundance and abundance of three large rock crab species, *Cancer productus, Cancer antennarius, Cancer gracilis*. Due to difficulty correctly identifying rock crab to species, all rock crabs were pooled and treated as *Cancer spp.*

While only modified minnow traps were used for the temporal analysis for consistency with early periods, here we also used data from later years where both modified minnow traps and Fukui traps were deployed at the same site on the same day. The combination of both trap types allows more comprehensive sampling of a range of sizes of crabs. For the green crab/mud crab correlation, each replicate was one site in one day where either green crab or mud crab was found. For the green crab/rock crab correlation, each replicate was one site in one day where either green crab or rock crab was found. To illustrate: a day at a site where only mud crab was found was used as a replicate for the green crab/mud crab correlation, but not for the green crab/rock crab correlation. Hence we started with one comprehensive dataset for the two analyses, but consequently had to exclude different site days for the two different analyses (Table 4). We used non-linear regression to test whether there was a relationship between green crab and mud crab abundance, and whether there was a relationship between green crab and rock crab abundance. The equation with the best fit was $f(x) = a * e^{(-b * x)}$.

Spatial trends

In order to investigate whether green crabs were more successful in certain habitat types than others, we examined green crab abundance and size (average carapace width) as a function of three aspects of habitat structure in Elkhorn Slough: estuarine location, marine vs. estuarine sites; tidal exchange, restricted vs. non restricted sites; and depth, shallow vs. deep sites.

Location: Estuarine vs. marine influenced sites

To determine whether green crabs or native crabs differed in abundance or size in the more estuarine vs. more marine portions of the estuary, we compared sites in the upper vs. lower estuary in 2008. Estuarine sites were in the mid- to upper estuary about 6 – 8 km from the mouth (sites 5-6, 11 Fig. 1) and marine sites were 0.5

– 1.2 km from the mouth (sites 14-16) (Fig. 1). All sites were at least 400 m apart and had unrestricted tidal exchange. Examination of Elkhorn Slough National Estuarine Research Reserve water quality monitoring data revealed greater seasonal variation in key water quality parameters at the estuarine vs. marine sites. For instance, marine influenced sites vary little in salinity throughout the year; salinity remains at approximately 33 ppt. Estuarine influenced sites vary more in salinity during the year. In winter and spring, salinity is typically 20-24 ppt, in summer and fall 34-36 ppt. Water temperature at marine sites are 10-20ºC throughout the year, whereas estuarine sites attain higher temperatures in summer (up to 26ºC) and lower temperatures in winter (8ºC).

At all sites, on each sampling day, we used three traps of each type, standard minnow, modified minnow, Fukui, and pitfall. Pitfall traps were added to the sampling design for this assessment because we wanted to characterize average size for native mud- and rock crabs in addition to the sizes of and green crabs. We sampled each site twice and used site day as replicate for this analysis (n = 6 for marine sites, n = 6 for estuarine sites). Abundance data were transformed using a fourth root transformation. We used ANOVA to analyze differences in abundance of green crab, mud crab, and rock crab at estuarine vs. marine sites using transformed abundance as the dependent variable and estuarine location (estuarine vs. marine) as a factor. We used ANOVA to analyze differences in sizes of green crab, mud crab, and rock crab at estuarine vs. marine sites using carapace width as the dependent variable and estuarine location as a factor. We used Pearson Chi-Square test to asses differences in distribution of green- , mud- , and rock crab abundance at estuarine vs. marine sites.

Tidal exchange: fully tidal vs. artificially restricted sites

Tidally restricted sites are sites that have a decreased tidal range compared to the main channel due to human alteration such as additions of dikes, berms, culverts or tide gates. The tidally restricted sites sampled here have maximum tidal ranges of approximately 15-100 cm (vs. 250 cm in the main channel) and have higher fluctuations in salinity and temperature both within a day and within a year, due to the decreased tidal exchange of the water (Elkhorn Slough Reserve water monitoring data). In order to investigate the effect of tidal exchange on green crab abundance and size, we sampled three pairs of adjacent fully tidal and tidally restricted sites using Fukui traps in spring 2004. We deployed one trap per site and sampled each site three times. We used site day as a replicate (1 trap x 3 sites x 3 days), n = 9 for restricted sites and n = 9 for fully tidal sites. To explore whether tidal restriction influenced green crab abundance, we used ANOVA with abundance as the dependent variable and site and tidal exchange as factors. Abundance data were natural log transformed. To assess whether tidal restriction influenced green crab size, we used a two-way ANOVA with carapace width as the dependent variable and depth, site, and the interaction of depth and site as factors. Due to sex differences in carapace width, where males are larger than females, only green crab males were used for the size analysis.

Depth: intertidal vs. subtidal elevations

In order to determine whether depth affects green crab abundance or size we trapped at two different depths, subtidal, 60 cm below MLLW and intertidal at a tidal height of MLLW. We trapped at sites 3, 7, and 12 in summer 2004, using Fukui traps. At each site we deployed one subtidal and one intertidal Fukui trap per day. We sampled each site three times and thus had 9 traps per treatment, or 18 total traps (3 sites x 3 dates x 2 depths). Each trap day was used as a replicate. To determine whether depth had an effect on green crab abundance we used ANOVA with abundance as the dependent variable and site and depth as factors. Abundance data were natural log transformed. To determine whether depth had an effect on male green crab size we used a two-way ANOVA with carapace width as the dependent variable and depth, site, and the interaction of depth and site as factors.

Results

Temporal trends: green crab abundance and population structure

We detected temporal variation in the relative abundance and population structure, of green crab in Elkhorn Slough (Fig. 2, Fig. 3). Green crab abundance varied significantly among years (ANOVA, df = 95, 6; F = 7.545; $p < 0.0001$). Tukey post-hoc analysis showed that abundance in 2006 was significantly higher than all other years ($p < 0.01$), except 2009. No other significant differences between years in abundance were detected by this analysis (Fig. 2a). This analysis was conducted using the limited dataset, with data only from site 6, in spring, using modified minnow traps. If we conduct the same analysis, using the more extensive, but less consistent sampling (Table 3) we get very similar results (Fig. 2b). Green crab abundance varied significantly among years (ANOVA, df = 434, 8; F = 5.285; $p < 0.0001$). Tukey post-hoc analysis showed that abundance in 2006 was significantly higher than all other years ($p < 0.01$), except 2003 and 2004 (Fig. 2b). Therefore, the more comprehensive dataset was used to examine the population size distributions from 2001 to 2009 (Fig. 3).

In the early years of the invasion, 2001 to 2002, we caught no individuals > 60 mm while in later years, 2005-9, an increasing proportion of the population consisted of individuals > 60 mm, and in 2009, only individuals > 55 mm were found. The size distribution provides evidence of recruitment in 2003-2005 and 2007 (higher proportion of individuals < 45 mm). Since 2008 no recruits have been observed (Fig. 3).

Relationships between green crabs and native crabs

We found a highly significant negative relationship between green crab and mud crab abundance (non-linear regression, $f(x) = a * e^{(-b * x)}$, df = 237, 1; $p < 0.0001$). We also found a highly significant negative relationship between rock crab and green crab abundance (non-linear regression, $f(x) = a * e^{(-b * x)}$, df = 185, 1; $p < 0.0001$).

Spatial Trends

Estuarine vs. marine influenced sites

Green crabs were significantly more abundant at estuarine sites (0.60 crabs per trap, sd = 1.358) than at marine sites (0.02 crabs per trap, sd = 0.086). (ANOVA, $p < 0.001$). Mud crabs were significantly more abundant at estuarine sites (10.90 crabs per trap, sd = 8.146) than at marine sites (4.46 crabs per trap, sd = 4.343) (ANOVA, $p = 0.042$) and rock crabs were significantly more abundant at marine sites (0.11 crabs per trap, sd = 0.231) than at estuarine sites (1.02 crab per trap, sd = 0.895) (ANOVA, $p = 0.002$) (Table 5, Fig. 4).

Mud crab size was significantly larger at marine (23.7 mm, sd = 3.63 mm) than at estuarine sites (19.5 mm, sd = 3.89 mm) (t-test, $t = -12.575$, df = 554, $p < 0.0001$). We found no significant differences in green-, or rock crab size at estuarine vs. marine sites. There was a significant difference in the proportion of different crab species found at estuarine vs. marine sites (Pearson Chi-square = 86.040; df = 2; $p < 0.001$). The total numbers of individuals of the different species were: Estuarine: Green crab = 38, Mud crab = 360, Rock crab = 4; Marine: Green crab = 1, Mud crab = 204, Rock crab = 48 individuals (Fig. 4). Mud crabs contribute the largest proportion of individuals in both areas, but the ratio of green crabs to rock crabs is inverted between estuarine and marine sites: the green crab to rock crab ratio at the estuarine sites is high, and the green crab to rock crab ratio at the marine sites is low. There was no significant effect of trap type on abundance of any of the crab species, when comparing pitfall traps to the two types of minnow traps and Fukui traps.

Tidal exchange: fully tidal vs. restricted sites

Tidal exchange did not influence abundance of green crab (ANOVA, df = 30,1, F = 0.001, p = 0.975). Tidal exchange did have an effect on male green crab size (Table 6, Fig. 5). Green crabs were significantly larger in tidally restricted sites, except for at sites 12/13 (t-test, t = 0.962, df = 22, p = 0.347). At sites 3/4 male green crab carapace width was larger at the restricted site (64.7 mm, sd = 14.43) than at the fully tidal site (53.0 mm, sd = 19.50). At sites 7/8 carapace width at the restricted site (74.5 mm, sd = 7.02) was significantly larger than at the fully tidal site (63.3 mm, sd = 9.71) (t-test, t = 3.666, df = 31, p = 0.001).

Depth: intertidal vs. subtidal elevations

We found no effect of depth on green crab abundance (ANOVA, df = 30, 1, F = 0.082, p = 0.777). We found an effect of depth on male green crab size (Table 6, Fig. 6). Male green crab average carapace width was significantly larger at subtidal (53.0 mm, sd = 11.7), than at intertidal (40.6 mm, sd = 10.2) depths (t-test; df = 43; t = 2.777; p = 0.008), at site 3. No other significant effects of depth were found. At site 7 there was no significant difference (t-test, t = 1.294, df = 16, p = 0.214) in carapace widths between deep (63.3 mm, sd = 9.10) and shallow (53.4 mm, sd = 20.91) depths. Likewise at site 12, carapace widths at deep (56.1 mm, sd = 16.92) vs. shallow (55.6 mm, sd = 14.94) depths were not significantly different (t-test, t = 0.097, df = 32, p = 0.923).

Discussion

Monitoring early invasion phase and tracking invasion trends

The early phases of invasions are rarely studied, but it is clear that any number of outcomes are theoretically possible after introduction and early establishment, ranging from local extinction (e.g., nudibranch *Tritonia plebeia,* Allmon and Sebens 1988; e.g. , snail *Achatina fulica*, Simberloff and Gibbons 2004) to exponential population growth and local invasion, (e.g., clam *Potamocorbula amurensis*, Carlton et al. 1990; e.g., alga, *Sargassum muticum*, Engelen and Santos 2009). Very rarely have the early phases of invasions been documented for marine systems, hence the frequency of different trajectories is not well characterized, for different species or for the same species in different regions. For species which have become invasive in many bioregions, such as the European green crab (Cohen et al. 1995; Grosholz and Ruiz 1995, Yamada 2001), the assumption is often made that population growth will be rapid following introduction to a new site with appropriate physical conditions. Such assumptions underlie management and prevention guidelines of many agencies which prioritize species with a track record of invasion success, and certainly are warranted as a precautionary principle. We expected population growth of the green crab at Elkhorn Slough would be rapid following early introduction and establishment, because conditions are within the documented physical tolerances of the species (Yamada 2001). In the first years of our monitoring program, from 2001 to 2006 we documented rapid increase in abundance. Had we ended our study then, we would have concluded that the green crab was successfully established in the estuary. However, in subsequent years, the population has dramatically declined. More recently, green crabs at Elkhorn Slough have persisted but at very low abundance. Despite abundance being low from 2007-2009 it is still higher than in 2001 after which the population dramatically increased.

Invasions are often studied retrospectively. In contrast, we aimed to predict success early in the invasion of green crabs at this estuary, using demographic data. However, we determined that temporal variation in green crab abundance is very high and the long-term trajectory of the green crab invasion at Elkhorn Slough is thus difficult to predict. Similarly, the long-term pattern of the population dynamics is highly variable for the Chinese mitten crab, *Eriocheir sinensis* in Europe, yet the mitten crab continues to persist in the invaded range. It is possible that the green crab population at Elkhorn Slough will continue to go through boom-and-bust cycles as known from other invasive species (Simberloff and Gibbons 2004). Continued monitoring is necessary to monitor if the population continues to alternate between high and low abundance, or whether it stabilizes.

Role of recruitment limitation

The long-term monitoring data from Elkhorn Slough indicate that the green crab is highly abundant some years, while not abundant at all during other years. One plausible explanation for the high variation is that abundance is driven by variable recruitment, whether from interannual differences in local retention or in replenishment from San Francisco Bay or other estuaries to the north where green crabs are established. Green crabs spend 32 to 62 days as pelagic larvae before settling to the near-shore environment and metamorphosing into the adult stage of their life cycle. In 2003-2005 we found evidence of recruitment at Elkhorn Slough, based on higher abundance of the juvenile size classes, but since 2006 hardly any individuals < 45 mm have been found. This is fairly strong evidence for recruitment limitation, although we cannot rule out early post-settlement or juvenile mortality. Size data from the long-term monitoring program were essential in order to detect recruitment and lack thereof. Similar recruitment patterns have been observed for other regions, for example Yaquina Bay in Oregon which has been extensively surveyed. Recruitment was good in 2003 and 2005 and has been limited since (Yamada and Gillespie 2008). This similarity in patterns suggests that broad oceanographic or climatic effects are strong influences on recruitment perhaps in addition to local effects within an estuary. In order to better understand the dynamics of green crab populations within and among estuaries, it would be useful to investigate larval supply in future studies, and to determine whether recruitment patterns are synchronous between regional estuaries (suggesting a strong role for regional oceanographic or climatic factors) or asynchronous (indicating the importance of local within-estuary drivers of recruitment).

Interactions with native crab species and habitat differences

Not all habitats are equally invasible (Cohen and Carlton 1998). Numerous factors may correlate with invasibility, including number or identity of native species present, degree to which the habitat has been anthropogenically altered, or physical matching of conditions (Grosholz and Ruiz 1995, Stachowicz et al. 1999, Byers 2000). Other studies have found that green crabs may be displaced from certain habitats by some large native crab species (Jensen et al. 2002; Hunt and Yamada 2003; Jensen et al. 2007; deRivera et al 2007) and that green crabs can displace smaller crab species (Grosholz et al. 2000). Hence, habitats with abundant larger crab species may be resistant to green crab invasions whereas habitats with smaller crab species may be more vulnerable, because in competitive interactions between crabs the largest individual typically wins (Jivoff 1997; Hunt and Yamada 2003). These hypotheses are consistent with the significant negative correlations we found between abundance of green crab and of mud crab and rock crab.

We expected that green crabs might be less abundant in the more marine influenced portions of the estuary, where larger coastal crab species are more abundant. The green crab on the US Pacific Coast is not found on the open, more wave-exposed coast (Preisler et al. 2009). Our results revealed that the abundance of green crabs is lower at more marine sites. This is in accordance with the findings of Wasson et al. (2005) who found the estuarine portion of the Elkhorn Slough estuary to be more invaded overall by non-native benthic invertebrates than the marine portion of the estuary. Experimental manipulations could determine whether the lower abundance in the marine portions of the estuary is due to predation by cancrid crabs or other factors, such as physical conditions.

Anthropogenically altered habitats may be especially vulnerable to invasion (Byers 2002; Wolff 2005). In this study one major human alteration, tidal restriction resulting in restricted tidal exchange, did not appear to have strong effects on green crab invasion in the estuary. Abundance did not significantly differ in sites with full vs. restricted tidal exchange but green crab sizes were larger in the tidally restricted sites at two of the three sites surveyed. We had suspected that native rock crabs might be less abundant in the more variable physical conditions resulting from water control structures, and that release from this predator might have resulted in higher green crab abundance. This mechanism did not appear to affect abundance. However, it is possible that green crabs are subject to predation from the larger rock crabs in the fully tidal sites, causing only green crabs in restricted sites to survive long enough to attain larger sizes.

We also found no strong differences in green crab abundance between the low intertidal and shallow subtidal zone of the estuary, but size was greater in the subtidal at one site. In various crab species including green crab, juvenile life stages are more abundant at shallow depth (Breen and Metaxas 2009) which could explain why we found green crab size to be smaller at shallow depth. It is possible that juvenile green crabs prefer this habitat because there are fewer predators such as fish and predatory hetero- and conspecific crabs. Moksnes (2004) has shown that larger green crabs predate on juvenile conspecifics.

We found the ratios of green-, mud, and rock crab to be very different between the estuarine vs, marine influenced sites. Rock crabs were by far found in the highest ratio to green crab at the marine influenced site. Additionally, green- and mud crabs were significantly more abundant at estuarine influenced sites. The similarity in patterns of high abundance of green crabs and mud crabs at the estuarine sites, where rock crabs are rare suggests that competition between green crab and this native mud crab species is not playing a major role in affecting abundance or habitat use. Native cancrid crabs which might pose a threat to green crabs at the marine sites could have an effect on green crab abundance at marine influenced sites.

Implications for management

Temporal trajectories of invasions can be used to inform management (Ashley et al. 2003). Our monitoring data can be used to inform management at Elkhorn Slough and other Pacific estuaries. Although it may be difficult to predict future population sizes, there is no doubt that the green crab is currently established at Elkhorn Slough. Our data show potential for high abundance and rapid population growth at various locations in the estuary, and in contrasting tidal exchange regimes and depths. Given the current rarity of green crabs at the slough this may be an effective time to attempt control or even eradication. In years where green crabs are highly abundant, trapping efforts would be immense and eradication attempts might be insurmountable. However, if eradication is focused in years coinciding with low green crab abundance it is possible that almost all adult green crabs could be removed from a certain area or the entire estuary. Successful eradication would only be possible if most green crab recruits in the estuary are supplied by local retention of larvae. If Elkhorn Slough receives high numbers of green crab larvae from San Francisco Bay or other estuaries to the north where green crabs are established, local eradication will not be very efficient. Further studies identifying larval origin are vital for informing management planning. However, given that Elkhorn Slough represents the current southern limit of the green crab invasion on this coast, it is possible that larval recruitment from estuaries to the north is rare, and that eradication might be successful. If invasion success is variable across habitat types, this can inform management strategies, so that effort is targeted at areas that are most vulnerable, for instance anthropogenically altered habitats (Byers 2002). We found no striking habitat differences in abundance of green crabs – all portions of the estuary had fairly substantial numbers of green crabs. Hence, our recommendation to managers of Elkhorn and other regional estuaries is not to focus on any particular habitat type when conducting control or eradication efforts, but rather focus on the estuary as a whole, covering a broad range of suitable green crab habitats including estuarine and more marine sites, fully tidal and artificially restricted habitats, and both intertidal and subtidal zones. Long-term monitoring data on native and non-native crab species in Elkhorn Slough thus provide useful insights into the temporal and spatial variation in population structure of the European green crab. Such long-term monitoring data can be used to inform management and to generate hypotheses about mechanisms leading to temporal and spatial variation that can be tested by targeted short term experimental studies.

Table 1. Sites sampled in Elkhorn Slough estuary. Tidal restriction refers to artificially decreased tidal range through culverts, tide gates, or berms. Different subsets of sites were used for different analyses in this study.

Site	Site Name	Full tidal exchange
1	Hudson Landing rail road	yes
2	Hudson Landing Porter	no
3	North Azevedo entrance channel	yes
4	North Azevedo Pond	no
5	Kirby Footbridge	yes
6	Kirby Park	yes
7	North Marsh entrance channel	yes
8	North Marsh restricted	no
9	Hidden Pond entrance channel	yes
10	Hidden Pond	no
11	Hummingbird Island	yes
12	South Marsh	Yes
13	South Marsh: Whistlestop Lagoon	No
14	Upper Vierra	Yes
15	Vierra	Yes
16	Jetty Rd	Yes
17	Bennett Slough	No

Table 2. Sampling effort for survey of temporal variation in green crab abundance at site 6, in spring, Elkhorn Slough 2001 to 2009. Sampling effort was variable in terms of site days sampled per year. Effort in terms of number of traps at site 6 varied from 3 to 10 modified minnow traps per day. Total number of modified minnow traps per year varied from 3 to 38 traps. Although total number of traps per year is variable, all data were collected in spring at the same site, and variation in annual abundance was calculated as crabs per trap. A high number of traps in a year increases the accuracy of the abundance estimate, in terms of crabs per trap, for that year.

Year	Site Days	Modified minnow traps on each site day	Total number of modified minnow traps each year
2001	2	3, 4	7
2002	0	-	0
2003	1	6	6
2004	0	-	0
2005	9	3, 3, 3, 4, 4, 5, 5, 5, 6	38
2006	2	10, 10	20
2007	1	10	10
2008	3	3, 5, 10	18
2009	1	3	3
Total	**19**	**102**	**102**

Table 3. Sampling effort for comprehensive survey of temporal variation in green crab abundance and population structure at sites 6, 7, and 12 in spring and fall, 2001 to 2009. Sampling effort was variable in terms of site days sampled each year but within each year, no site was sampled extensively compared to any other site. Modified minnow traps is the sum of traps across all sites and days within each year.

Year	Sites sampled	Site Days	Modified minnow traps	Average number of modified minnow traps per site day	Timing of trapping
2001	6, 7, 12	13	46	3.5	spring, fall
2002	6, 7, 12	7	27	3.9	spring, fall
2003	6, 7, 12	4	17	4.3	spring
2004	6, 7, 12	8	11	1.4	spring, fall
2005	6, 12	18	77	4.3	spring
2006	6, 7, 12	8	29	3.6	spring, fall
2007	6, 7, 12	4	19	4.8	spring, fall
2008	6, 7, 12	6	29	4.8	spring, fall
2009	6, 7, 12	5	15	3.0	spring, fall
Total		**73**	**270**		

Table 4. Sites sampled and total number of traps each year for analyses of relationships between green crab/mud crab, and green crab/rock crab. We used standard minnow, modified minnow and Fukui traps and samples are from all seasons. A site sampled in one day was used as a replicate if one or the other species of crabs was found at the site. If only rock crab was found, the site day was used in the green crab/rock crab analysis. Likewise if only mud crab was found the site day was used in the green crab/mud crab analysis. If only green crab was found at a site in a day, the site day was used in both correlation analyses. Hence, different sites and different numbers of site days were used for the two different correlations. The column "Total traps" summarizes the total sum of traps used when all site days are added within one year for each type of correlation. While site day was used as replicate, total number of traps for all days and sites is shown in the fourth and seventh columns as a measure of sampling effort.

Correlation	Green crab/Mud crab			Green crab/Rock crab		
Year	Sites	Site days	Total traps	Sites	Site days	Total traps
2001	1, 6-8, 12-13	40	88	1, 6-7, 12-13, 15	13	44
2002	6-8, 12-13	10	32	7, 12	3	11
2003	6-8, 12-13	19	55	6-8, 12-13	14	43
2004	3-4, 6-8, 12-13	49	93	3-4, 6-8, 12-13	48	90
2005	1, 6-9, 11-13, 15-17	45	164	1, 6-9, 11-13, 15-17	43	157
2006	1, 6-9, 11, 13, 15, 17	30	169	1, 6-9, 11, 13, 15, 17	29	159
2007	1, 6-8, 11-13, 15	9	48	6-8, 11-12, 15	7	42
2008	5-8, 11-13, 15-16	36	140	5-8, 11-12, 14-16	30	117
TOTAL		**238**	**789**		**187**	**663**

Table 5. ANOVA table of effect of estuarine location on abundance of green-, mud-, and rock crab. Abundance data were transformed using a fourth root transformation. Green- and mud crabs were more abundant at estuarine sites than at marine sites. Rock crabs were more abundant at marine sites than at estuarine sites.

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
Rock crab	3.630	1	3.630	26.464	<0.0001
Error	3.841	28	0.137		
Green crab	1.094	1	1.094	7.037	0.013
Error	4.352	28	0.155		
Mud crab	2.124	1	2.124	7.175	0.012
Error	8.289	28	0.296		

Table 6. ANOVA table of effects of tidal exchange and depth on male green crab average carapace width. Green crabs were significantly larger at tidally restricted sites 4 and 8, than at the fully tidal sites 3 and 7. Green crabs were significantly larger at subtidal depth than at intertidal depth but only at site 3.

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
Site	1,513.60	2	756.802	3.185	0.046
Tidal exchange	1,603.48	1	1,603.48	6.748	0.011
*Site*Tidal exchange*	73.175	2	36.588	0.154	0.858
Error	20,434.98	86	237.616		
Site	2,263.28	2	1,131.64	4.606	0.012
Depth	1,072.09	1	1,072.09	4.363	0.039
*Site*Depth*	925.706	2	462.853	1.884	0.158
Error	22,605.21	92	245.709		

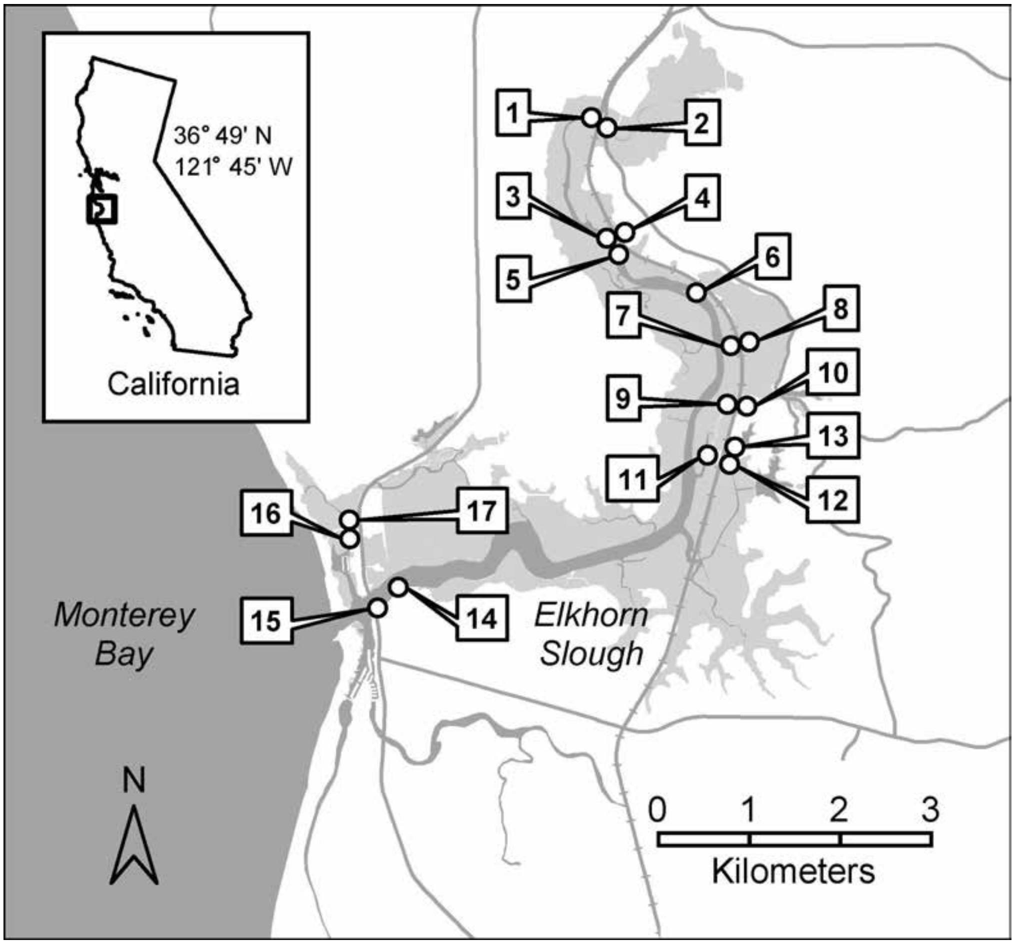

Figure. 1 Map of crab sampling sites at Elkhorn Slough, California. See Table 1 for site names and tidal exchange.

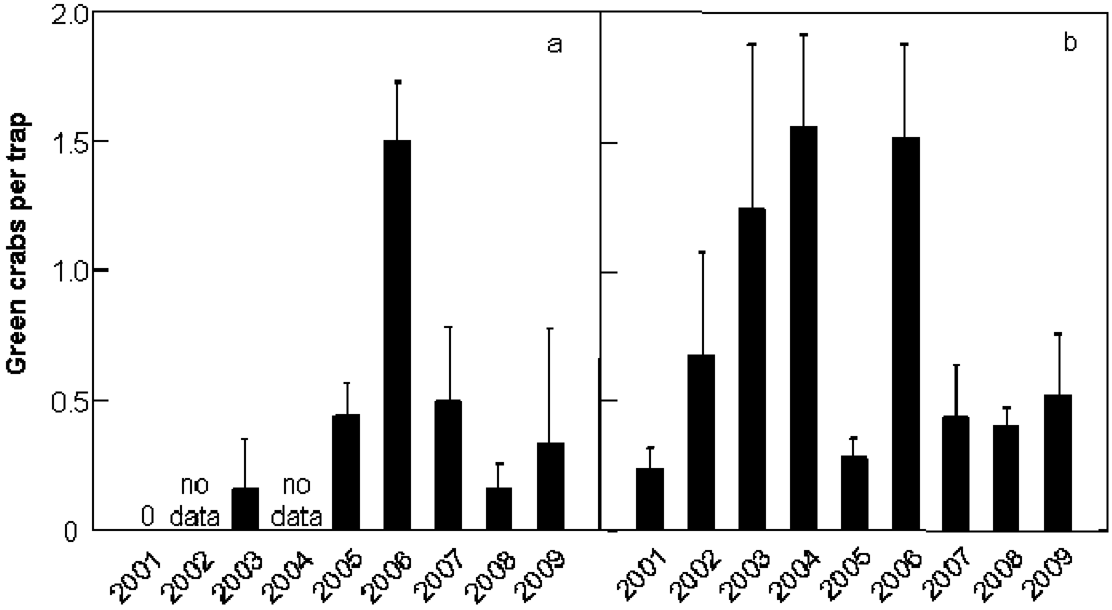

Figure. 2 Relative abundance of green crabs per trap (+/- SE) in Elkhorn Slough over time. a) Relative abundance of green crabs over time using most consistent but limited data (Table 3), only including site 6, in spring, using modified minnow traps. b) Relative abundance using broader dataset (Table 4), including two additional sites, (7 and 12) and one additional season, fall. In both a) and b) only in 2006 is relative abundance significantly different from other years (ANOVA).

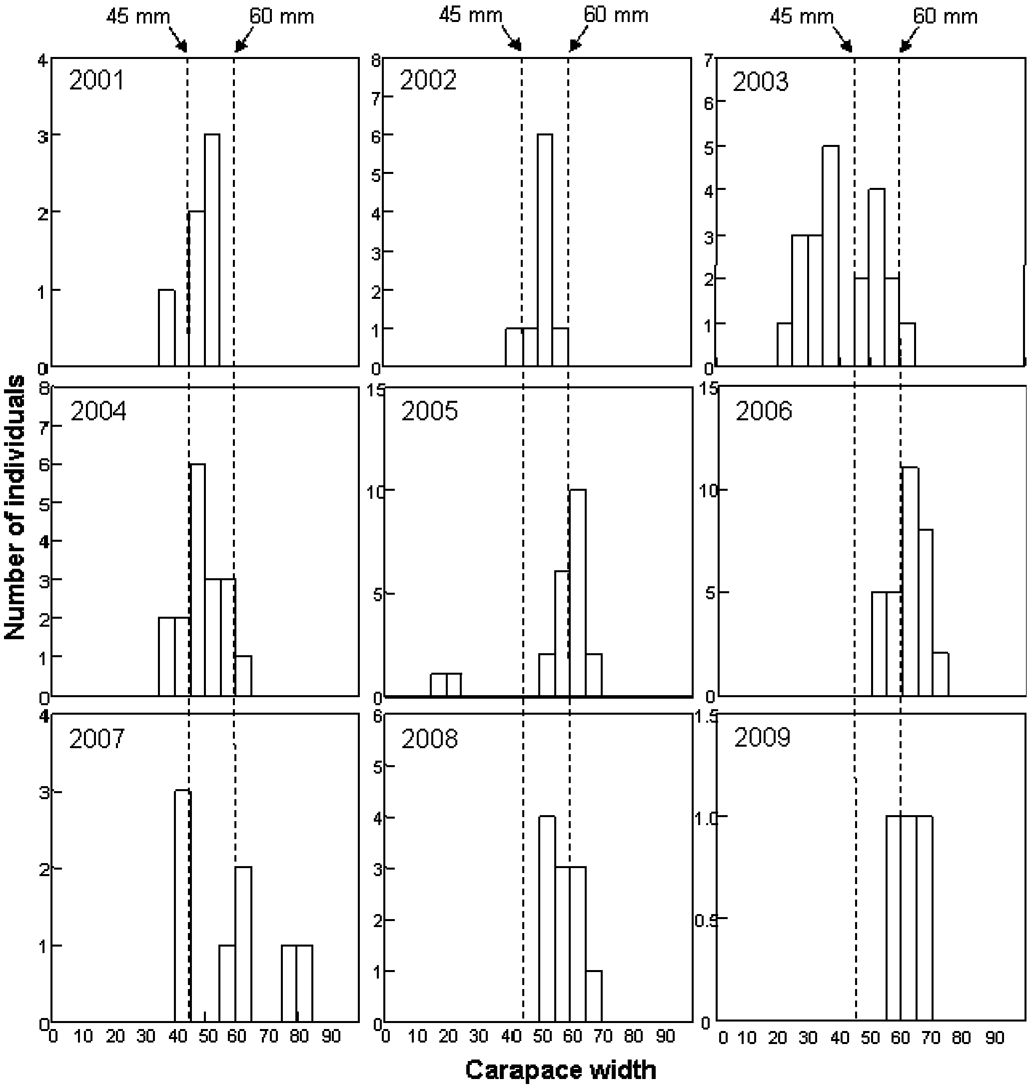

Figure. 3 Size distributions of male green crabs at Elkhorn Slough from 2001-9. Proportion of population consisting of juveniles (< 45 mm) is very low except in 2003-5. Proportion of population consisting of individuals > 60 mm is higher in 2006-9 than in earlier years.

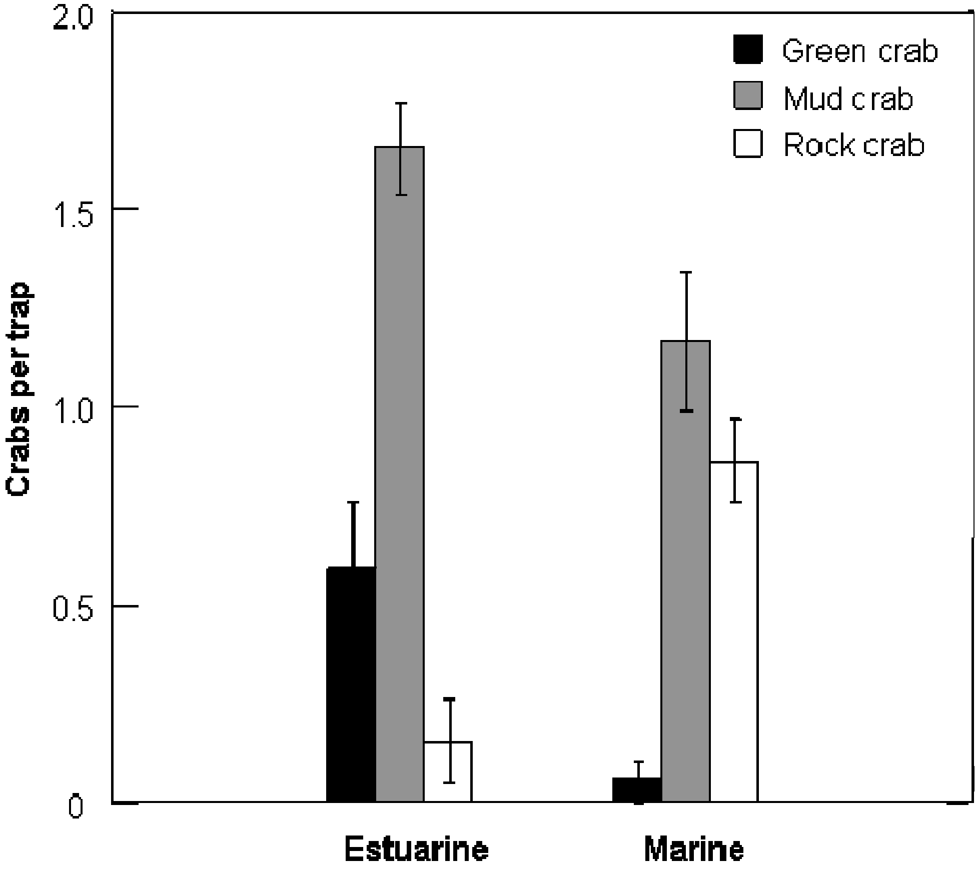

Figure. 4 Average number of individuals per trap (+/- SE) of different crab species at estuarine and marine sites. Abundance data were fourth root transformed. The two distributions "estuarine" and "marine" are significantly different (Pearson Chi-Square). Mud crabs contribute the highest number of individuals in both locations. The ratio of green crabs to rock crabs is high in estuarine influenced habitat and low in marine influenced habitat.

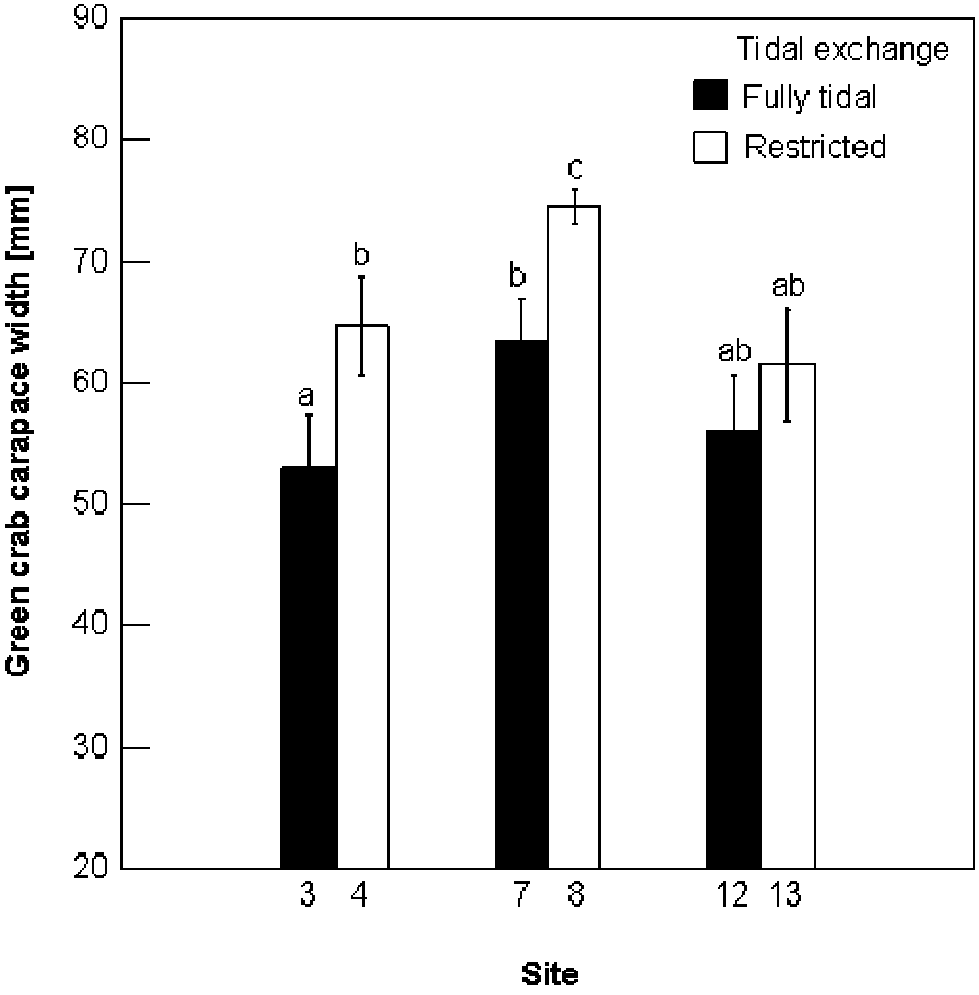

Figure. 5 Effect of tidal exchange on green crab carapace width (+/- SE). Male green crab carapace width was larger at the restricted site than at the fully tidal site at sites 3/4 and 7/8. At site 12/13 the difference in carapace widths was not significant (t-test).

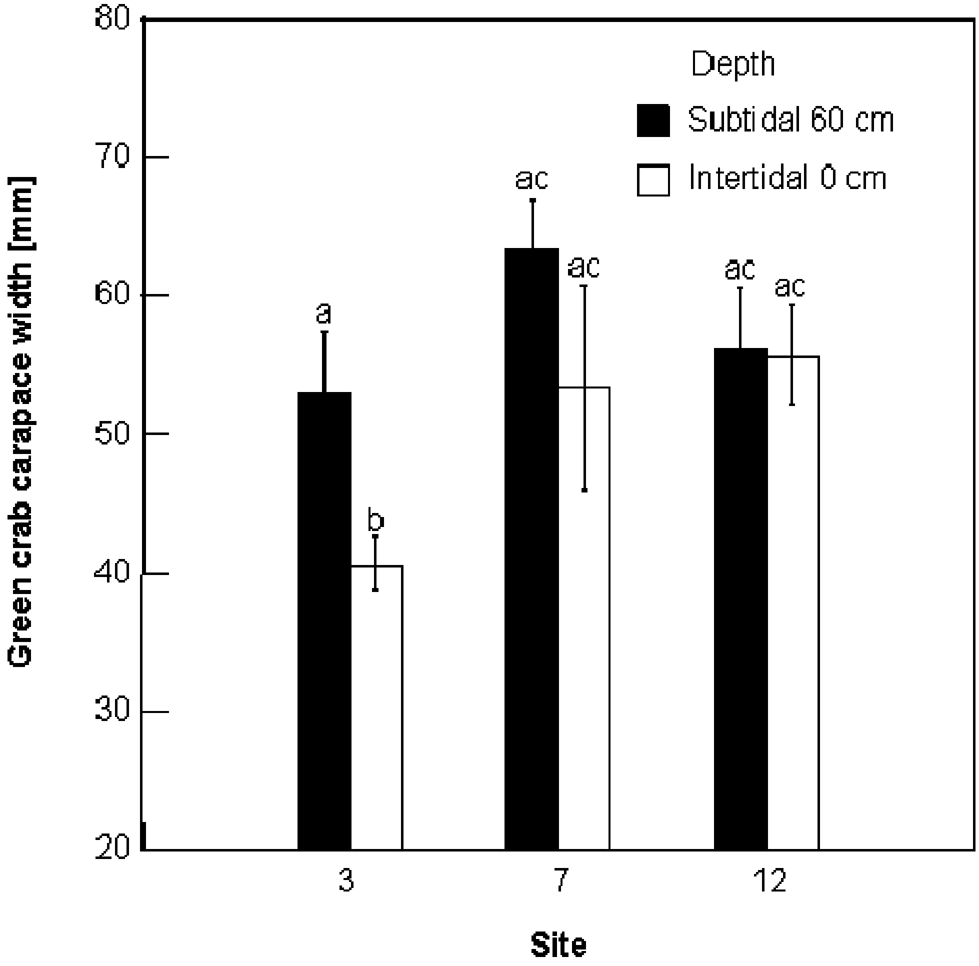

Figure. 6 Effect of depth on male green crab average carapace width (+/- SE). Male green crab carapace width is significantly larger at subtidal, than at intertidal depths at site 3 (t-test).

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CHAPTER 2

A framework to quantify and compare invaders in their native and introduced ranges: Biogeographic variation in European green crab abundance, morphology and habitat

Introduction

The process of invasion occurs as an interaction between the non-native species and the community it is invading: characteristics of both will affect invasion success. In early studies in the field of invasion biology empty niches and lack of competition were identified as factors contributing to invasion success (Elton 1958, MacArthur and Wilson 1967). However, a few early and numerous more recent studies include investigations of how traits of non-native species can influence invasion success (Baker 1965, Suarez et al. 1999, Byers 2000, Sakai et al. 2001, Torchin et al. 2003, Engelen and Santos 2009). Such traits could be behavioral in the form of aggression (Suarez et al. 1999) or physiological in form of converting energy intake to tissue growth (Byers 2000). Yet, in other studies composition of the invaded community has been the focal point of the study (Nichols et al. 1990, Cohen and Carlton 1998, Stachowicz et al 1999, Grosholz et al. 2000). A majority of studies of non-native species have been conducted solely in the introduced range, due to seemingly high abundance of the non-native species. Abundance of the non-native species is rarely quantified and compared in the introduced and in the native range and the assumption that the non-native species is highly successful in the introduced range, is rarely tested (Hierro et al. 2005).

Many studies of invasions are limited to a single region, partially due to logistical constraints of researchers who typically work in a limited geographic area, and partially due to concern about impacts. However, impact studies of a non-native species must focus on the invaded community in the region of interest that is within manageable scope. Hence, many studies examine one or more invaders in a single region. Yet, there are valuable lessons to be learned about invasion success and its predictors by examining the same invasive species in multiple geographic regions (Hierro et al. 2005). Many studies of terrestrial plants have taken this approach (Maron et al. 2004, Okada et al. 2007, Colautti et al. 2009). However, the same approach is rarely employed for marine invaders. Examining the same invasive species across multiple regions offers a great opportunity to study how abundance, population structure and other invader attributes change in different environmental contexts.

In this study, I quantified and compared variation in characteristics of European green crab, *Carcinus maenas* (hereafter referred to as green crab), populations across a range of biogeographic regions and habitat types. The European green crab is a model species for a broad geographic study of an invader in different habitats because of its global distribution. The native range of the green crab spans the European Atlantic Coast (hereafter referred to as EAC) from Northern Norway to

North Africa (Yamada 2001). The green crab invaded the Atlantic coast of the United States (hereafter referred to as USA) two centuries ago (Say 1817), South Africa in 1983 (Le Roux et al. 1990), Japan in 1984 (Carlton and Cohen 2003), the Pacific Coast of the United States (hereafter referred to as USP) around 1989 (Grosholz and Ruiz 1995), Tasmania in 1993 (Thresher et al. 2003), and most recently Patagonia in 2000 (Hidalgo at al. 2005). In this study I focus on three regions in which the green crab is found, the native European Atlantic Coast (EAC), the Atlantic Coast of the United States (USA), and the recently invaded Pacific Coast of the United States (USP).

Successful invaders may become more abundant in the introduced vs. native range due to escape from native predators, competitors, or parasites (Elton 1958, Gillett 1962, Lohrer et al. 2000, Torchin et al. 2003). Such predictions appear to have been validated by rapid population growth, rapid range expansion, and extremely high abundances in the introduced ranges of some non-native species, for example argentine ants, kudzu, zebra mussels, and the marine alga *Caulerpa*. Although uncommon, some evidence points in the opposite direction; for example clover is less abundant in its invaded range (Gilbert and Parker 2010). For the European green crab, comparisons of native vs. introduced range studies have found supporting evidence for some of the above predictions of success. For example Torchin et al. (2003) found support for the enemy release hypothesis by finding lower parasite levels in green crabs in the introduced than in the native range. Additionally, average carapace width of individuals is larger in the introduced vs. native range (Grosholz and Ruiz 2003, Torchin et al. 2003). Finally, deRivera et al. (2005) found that green crab range limits on the US Atlantic Coast may be controlled by species interactions, such as predation by other crab species, e.g. blue crab, *Callinectes sapidus*. Despite a wealth of green crab studies, no studies have yet systematically quantified green crab abundance, population structure, or other indicators of invasion success consistently across these ranges. In this study I develop a framework which allows us to quantify and compare individual and population level characteristics of green crab in order to determine whether green crab is more successful in the introduced range than the native range.

In addition to characterizing and comparing indicators of green crab invasion success across biogeographical regions, I was interested in examining differences in invasions between two coastal habitat types, estuaries vs. open coasts. From the invasion literature it is known that not all habitats are equally invaded. A recent review by Preisler et al. (2009) found that globally, estuaries are more invaded than open coasts, but the strength of this pattern varies dramatically across regions. For example, data from two estuaries in central and southern California on the US Pacific Coast indicated that estuaries had six to ten times as many non-native species as the adjacent open coast. One estuary and adjacent open coastal site in New Hampshire on the US Atlantic Coast were about equally invaded, and in two estuaries and on adjacent open coasts on the European Atlantic Coast the number of non-native species were approximately four to five times higher in estuaries whereas in a third European estuary, the open coast was slightly more invaded than the estuary. Although there is high regional variation in degree of invasion, it is often the case that estuaries are more heavily invaded than the adjacent open coast. Some suggested hypotheses for these patterns are that the propagule pressure is higher in estuaries due to the location of ports and shipping activities in estuaries. Secondly, it is possible that estuarine fauna is more depauperate than that of the open coast and thus more invasible (Cohen and Carlton 1998). A third hypothesis is that estuaries have been heavily impacted by human alteration and thus native species are no longer well adapted to the environment and no longer enjoy a “home court advantage” (Byers 2002). Last, a fourth hypothesis explores the idea that estuaries may experience a high degree of local retention of propagules or larvae, due to limited circulation of water masses within the estuary (Byers and Pringle 2006, Byers 2009). A high degree of local larval retention within an estuary could cause adults in an estuary to continuously replenish the estuarine populations as opposed to exporting propagules or larvae during a pelagic larval stage in the introduced species’ life history.

The goals of this study were 1) To quantify and compare characteristics of a global invader across biogeographical regions, including the native and some introduced ranges and 2) To compare those same characteristics of a non-native species in estuarine vs. open coast habitat. This study of the European green crab is unique because all regions and habitats were sampled with identical protocols within the same field season. As such it is one of the most consistent and comprehensive studies of an invasive species, with respect to sampling across that many sites at such a broad geographic scale.

Methods and materials

Comparing green crab invasions among regions and between habitats

In order to quantify and compare characteristics of the green crab across biogeographical regions and among different habitats, I assessed various individual and population level parameters to evaluate green crab invasion success. I assessed individual characteristics such as carapace width, number of missing limbs per crab and sex. Additionally I recorded the identity of the species, carapace width (CW), sex, and abundance of any crab species found in the traps, other than green crab. For each region and habitat I then calculated the following parameters for green crab: average- and maximum carapace width, sex ratio, ratio of green crabs to other crabs, and size distribution. Last, I compared variation in the parameters mentioned above in the native and introduced range, and in two different habitats within all ranges, estuary and the open coast.

Sampling design

In order to quantify population characteristics of the European green crab among regions I sampled a total of 53 sites distributed over three regions (Table 1). One region in the native range: the European Atlantic Coast (EAC). The first of two regions in the introduced range: the Atlantic Coast of the United States (USA). The second region in the introduced range, invaded two decades ago was the Pacific Coast of the United States (USP) (Fig 1). Within each region I chose three locations. For example, within the region USA, the three locations were: New Hampshire, Massachusetts, and Rhode Island (sites 4, 5, 6 respectively in Fig. 1). Within one location e.g. Massachusetts, I sampled three estuarine sites, and three sites on the adjacent open coast. Hence, I sampled 3 regions x 3 locations x 3 sites x 2 habitats = 54 sites minus one coastal site at Bodega Bay, USP = 53 sites. See Table 1 for dates and locations of all sites. All sites were sampled in 2007 within approximately one month of the peak of the recruitment season in each region in order to catch both adults and recruits.

Field Methods

At each of the 53 sites, I deployed an array of traps to characterize the crab community. At each site, I used three different trap types: 1) minnow traps, which are conically shaped plastic traps 42 cm long x 22.5 cm center diameter and 15.5 cm end diameter with a 2.5 cm opening, 2) modified minnow traps, where the opening in one end was increased to 5 cm in diameter, in order to allow larger crabs to enter the traps, and 3) Fukui fish traps, of dimensions 20 x 45 x 60 cm and mesh size 1 x 1 cm. Fukui traps were individually tethered to a PVC stake or tied to a cinder block and one of each of the two minnow trap types were tethered on one PVC stake or tied to one cinder block, then deployed on muddy or sandy substrate. All PVC stakes or cinder blocks with affixed traps were placed at least 10 meters apart. Each site had a total of 30 individual traps per day consisting of 10 traps x 3 trap types, or 10 trap-sets containing one of each trap type, hereafter referred to as one “trap-set”. All traps were baited with one of the following raw or frozen bait types: anchovy (USP), sardine (USP), mackerel (USA, EAC), menhaden (USA, EAC), and squid (USP, EAC). Bait is listed in order of preference and bait was chosen based on availability. To ensure that traps were baited for the entire time of trap deployment, inside each trap I placed the bait in a closed container made from a 35mm film canister drilled with 18-21 holes of 5 mm in diameter. All crabs sampled by traps were identified, counted and measured. We used analog calipers to measure crab carapace width to the nearest 0.1 mm. Green crabs were also sexed.

Abundance

In order to compare green crab abundance across regions I measured abundance as number of crabs per trap-set per day. Each trap-set was deployed at each site for one day. Crabs per trap-set per day will hereafter be referred to as “crabs per trap” or “abundance”. Abundance data were tested for normality and transformed using a 4^{th} root transformation. I tested whether there were differences in green crab abundance among the three regions, EAC, USA, USP. For each regional analysis “Coastal” and “Estuarine” habitats were analyzed separately. In each habitat I tested for an effect of region on green crab abundance, using a nested ANOVA. Crabs per trap was the dependent variable and the factors were region, location nested within region, and site nested within location nested within region. I also tested whether there were differences in green crab abundance between the two habitats, “Coast” and “Estuary” separately in the three regions EAC, USA and USP. Within one region I tested for the effect of location and habitat on green crab abundance, using ANOVA with crabs per trap as the dependent variable and habitat, location, and site nested within location as factors.

Carapace width

To assess crab body size I measured crab carapace width (CW) across the widest part of the carapace to the nearest 0.1 mm, using analog calipers. Carapace width is strongly correlated with age. Hence, a large individual is older than a small individual, when comparing two individuals of the same sex within the same location in which resource availability is fairly uniform. As a result, individuals of CW smaller than a specific CW defined separately for each region can be considered recruits. The following CWs for males are considered recruits in the three different regions: EAC CW < 20 mm, USA CW < 25 mm, USP CW < 30 mm (extrapolated from Yamada 2001). I compared average and maximum CW of individuals across regions and habitats. Because males are larger than females, males and females were analyzed separately in the analysis of CW difference among regions and habitats. Because CW data were normally distributed data were not transformed. To compare average CW among all regions I used only the habitat “Estuary” because no green crabs were found in the USP “Coast” habitat. Males and females were analyzed separately. I used ANOVA with CW as the dependent factor and region, location nested within region, and site nested within location nested within region as factors. To compare average CW between the regions EAC and USA in “Coastal” and “Estuarine” habitat I analyzed males and females separately. I used ANOVA with

CW as the dependent variable and habitat, location, and site nested within location as factors. To compare average CW within one region between habitats I analyzed each of the regions EAC and USA separately. I also analyzed males and females separately. I use ANOVA with CW as the dependent variable and habitat, location, and site nested within location as factors.

To compare maximum CW among habitats and regions I extracted the 90th percentile of CWs of male and female green crabs in each region and each habitat and then calculated the average carapace width for only that 90th percentile of crabs. Hereafter, this measurement is referred to as maximum carapace width. I used ANOVA to test for regional effects on estuarine maximum carapace widths in all regions. Males and females were analyzed separately. CW was the dependent variable and as factors I used region, location nested within region, and site nested within location nested within region. I used ANOVA to test for regional effect on coastal maximum carapace widths in only EAC and USA because no green crabs were found in coastal habitat in USP. Males and females were analyzed separately. CW was the dependent variable and as factors I used region, location nested within region, and site nested within location nested within region. I used ANOVA to test for habitat effects on maximum carapace widths in all regions. Males and females were analyzed separately. Each region (EAC and USA) was analyzed separately, CW was the dependent variable and as factors I used habitat, location and site nested within location. USP was excluded from this analysis because no green crabs were found in coastal habitat in USP.

Missing limbs

Missing limbs can be an indicator of inter- or intraspecific competition as well as predation (Torchin et al. 2003). Number of missing limbs was used as a proxy for crab condition. A missing limb was quantified as an absent or regenerating leg or chela. A limb was determined to be regenerating if only a limb bud was present, or if the limb was visibly considerably smaller than the corresponding limb on the other side of the crab. Number of missing or regenerating legs or chelae, were counted and added to yield total number of missing limbs per individual green crab. I then calculated the average number of missing limbs per crab for each site. Smaller crabs molt more frequently than larger crabs (Yamada 2001). A missing limb can be regenerated when crabs molt, however, the regenerated limb is smaller than the other limbs. After a certain number of molts, the regenerated limb is difficult to distinguish from the other limbs. Hence, limb loss can be underestimated in younger individuals when compared to older individuals. Therefore, in order to control for crab size, and hence molt frequency, only the upper 50th percentile of size classes was used for the limb loss analysis in both habitats, both sexes, and all regions. For the regional comparison coastal and estuarine crabs were used analyzed separately. Also, males and females were analyzed separately. For the habitat comparison, USP was excluded due to the absence of green crabs on the open coast in this region. Number of missing limbs per crab was a number between 0 and 10. Therefore, missing limbs data were transformed by applying the natural log (ln) to (number of missing limbs + 1). I used ANOVA to test for regional effect on missing limbs. I used transformed missing limb data as the dependent variable and region, location nested within region, and site nested within location nested within region as factors. I used ANOVA to test for habitat effect on missing limbs. I used transformed missing limb data as the dependent variable and habitat, location, and site nested within location as factors.

Sex ratio and interspecific ratio

Sex ratio was calculated as the fraction of male green crabs per trap. The data were transformed using arcsin-square root transformation. Transformed fractions of males were analyzed using ANOVA. For the regional analysis I analyzed coastal and estuarine habitats separately. I used the transformed fraction of males as the dependent variable and region, location nested within region, and site nested within location nested within region as factors. In the habitat analysis I analyzed the regions EAC and USA separately. I used the transformed fraction of males as the dependent variable and habitat, location, and site nested within location as factors.

Interspecific ratios of individuals of different species were assessed in order to characterize the crab community in which the green crab is found. I measured the abundance of green crabs relative to the abundance of other crabs species as the “green crab to native crab ratio”. I calculated the fraction of individuals of other crab species found at a given site out of the total number of individuals of all crabs. “Other crabs” were divided in two groups. The first group was “small native” species which were species with smaller average adult carapace width than green crabs when comparing equal age classes. The second group was “large native” species which were species with larger average carapace width than green crabs when comparing equal age classes. The fraction of “large native crab” and “small native crab” was transformed using arcsin-square root transformation. I used ANOVA to analyze the effect of region on fraction of large and small native crab. I analyzed coast and estuarine habitat separately. I used the transformed fraction as the dependent variable and region, location nested within region, and site nested within location nested within region as factors. I used ANOVA to analyze the effect of habitat on fraction of native crab species. Each region, EAC and USA, were analyzed separately. I used the transformed fraction as the dependent variable and habitat, location, and location nested within region as factors. For a list of all species included in the analysis from the different regions, see Table 2.

Size distribution

I assessed whether the green crab populations in all regions and both habitats consisted of all age and size classes by visually inspecting histograms of green crab CWs. Juveniles likely to have recruited in the past year (hereafter “recruits”) were defined as follows: EAC CW <20 mm, USA CW <25 mm, EAC CW <30 mm (extrapolated from Yamada 2001). I used a non-parametric two-sample KS-test to determine whether the size distributions differed among regions and habitats. Only males were used for this analysis. For the regional comparison, only estuarine green crabs were used in the analysis. For the habitat comparison, USP was excluded from the analysis.

Results

Abundance

Regional variation in abundance: Native vs. introduced range

I found regional variation in green crab abundance between the native and introduced ranges. When I compared only the coastal habitat, green crabs were least abundant in USP, the most recently introduced range (ANOVA $F_{6,2} = 24.821$, $p = 0.001$, Tukey's post-hoc $p < 0.002$) but there was no significant difference in abundance between the native range EAC, and the introduced range, USA (ANOVA $F_{6,2} = 24.821$, $p = 0.001$, Tukey's post-hoc $p = 0.626$) (Fig. 2A). In estuarine habitat, there were also significant differences in abundance among regions (ANOVA $F_{6,2} = 7.540$, $p = 0.023$). Green crabs were significantly less abundant in USP than in EAC (Tukey's post-hoc, $p = 0.022$) but only marginally significantly less abundant in USP than USA (Tukey's post-hoc,$p = 0.063$). A possible explanation, that green crabs were only marginally less abundant USP than in USA is low sample size in USP. There was no significant difference in abundance between EAC and USA (Tukey's post-hoc, $p = 0.641$) (Fig. 2B). In estuarine habitats, there was a strong effect of site, which most likely is the reason for no significant difference in abundance between USA and EAC.

Habitat variation in abundance: coast vs. estuary

In USP green crab abundance was significantly higher in estuarine (0.425 +/- 1.12 crabs per trap) than coastal habitat (0.0 +/- 0.0 crabs per trap) (ANOVA $F_{109, 1} =$

4.320, $p = 0.040$). Green crabs have not yet been observed in open coast habitat in USP, but is frequently found in estuaries. I found no habitat effects in any other regions.

Carapace width: average and maximum sizes

Regional variation in average carapace width: native vs. introduced range

In coastal and estuarine habitat there was no overall effect of any region on male or female average carapace width (Table 3).

Habitat variation in average carapace width: coast vs. estuary

There was no uniform effect of habitat on average carapace width. However, within each region, at different locations there were strong but highly variable effects of habitat on average carapace width (Fig. 3). In EAC the effect of habitat on male crab size was different in all three sampled locations (ANOVA $F_{1120,1} = 4.976$, $p = 0.026$). In Denmark, coastal males were smaller (CW = 29.9 mm, sd = 11.82) than estuarine males (CW = 35.9 mm, sd = 10.63) (ANOVA $F_{463,1} = 30.765$, $p < 0.0001$) whereas the opposite was true for France where coastal male CW (60.2 mm, sd = 10.38) was more than twice the size of the CW of estuarine males (28.9 mm, sd = 11.75) (ANOVA $F_{451,1} = 755.997$, $p < 0.0001$). In the Netherlands, there was no effect of habitat on male size (coast CW = 45.4 mm, sd = 11.17, estuary CW = 47.4 mm, sd = 13.11) (ANOVA $F_{218,1} = 1.381$, $p = 0.241$).

Regional variation in maximum carapace width: native vs. introduced range

I found a stronger effect of region and habitat on green crab size when I analyzed only the 90th percentile of large green crabs, than when I analyzed the entire population. Although there was no effect of region on male and female maximum carapace width in coastal habitat (ANOVA $F_{3,1} = 0.664$, $p = 0.475$) I found some effects of region in estuarine habitat. In estuarine habitat there was a significant effect of region on male and female maximum carapace width (ANOVA, Table 4A). In estuaries males were largest in USP (CW = 83.6 +/- 2.48 mm N = 3), intermediate in USA (CW = 67.5 +/- 4.91 mm N = 67) and smallest in EAC (CW = 60.7 +/- 4.03 mm N = 73) (ANOVA, Table 4B, Fig. 4A). In estuaries females were largest in USP (CW = 65.8 +/- 0.21 mm N = 2), intermediate in USA (CW = 56.0 +/- 3.46 mm N = 39) and smallest in EAC (CW = 52.8 +/- 3.34 mm N = 82) (ANOVA, Table 4C, Fig. 4B).

Habitat variation in maximum carapace width: coast vs. estuary

Similarly to the absence of effect of habitat on average carapace width, I found no uniform habitat effect on maximum carapace width on males or females. However, in EAC, males on the coast (N = 44, CW = 70.5, sd = 2.95) were significantly larger than females in the estuary (N = 73, CW = 60.6, sd = 4.03) (ANOVA, Table 5).

Missing limbs

Regional and habitat variation in missing limbs

I found no overall effect of region on coastal male, coastal females and estuarine males (ANOVA, Table 6). The only marginally significant difference in this analysis was an effect of region on estuarine females (ANOVA $F_{4,2} = 5.612$, $p = 0.069$) Tukey's honestly significant post- hoc analysis revealed that in USA estuaries females are missing significantly more limbs than females in EAC estuaries ($p = 0.043$) (Fig. 5). Similarly, I found no uniform effect of habitat on number of missing limbs in EAC males (ANOVA $F_{543,1} = 2.021$, $p = 0.156$), EAC females (ANOVA $F_{556,1} = 2.659$, $p = 0.104$), USA males (ANOVA $F_{480,1} = 0.301$, $p = 0.584$) or USA females (ANOVA $F_{361,1} = 0.001$, $p = 0.977$).

Ratios

Regional and habitat variation in sex ratio

I found no effect of region on green crab sex ratio in neither coastal nor estuarine habitat In the two regions where green crab is found in both coastal and estuarine habitats, EAC and USA, I found no effect of habitat on green crab sex ratio.

Regional and habitat variation in green crab to native crab ratio

I found a regional effect on fraction of large native crab in coastal habitat (GLM, $F_{6,2} = 70.770$, $p < 0.0001$). The fraction of larger native crabs was larger in USP than in USA (Tukey's post-hoc, $p = 0.0001$) and larger in USP than in EAC

(Tukey's post-hoc, p = 0.0001) (Fig. 6A). I also found a regional effect on fraction of small native crab in coastal habitat (GLM, $F_{4,2}$ = 13.338, p = 0.017). The fraction of small native crabs was smaller in USP than in USA (Tukey's post-hoc, p = 0.016) and larger in USP than in EAC (Tukey's post-hoc, p = 0.025) (Fig. 6B).

In the two regions EAC and USA I found no effect of habitat on fraction of neither large nor small native crab species. In USP I found an effect of habitat on fraction of small native crab species (ANOVA $F_{24,1}$ = 11.336, p = 0.003). Fraction of smaller crabs was higher in the estuary (0.356 +/- 0.770 crabs per trap) than on the open coast (0.132 +/- 0.482 crabs per trap) (Fig. 6B).

Size distribution

Regional variation size distribution: native vs. introduced range

The size distributions of green crab populations in estuaries USA and EAC are graphically similar (Fig. 7B and Fig. 7C whereas the size distribution in USP was strikingly different from the two other regions (Fig. 7A). Due to identical sampling effort absolute number of recruits can be directly compared. In EAC there were 91 recruits (individuals <20mm), in USA there were 154 recruits (individuals <25mm) and in USP there were no recruits (individuals <30 mm). The smallest individual in USP was 63.0 mm. The size distributions were significantly different among regions (KS-test, p < 0.0001) for all pair-wise comparisons.

Habitat variation in size distribution: coast vs. estuary

Within each region, the size distributions of green crab populations between habitats are graphically dissimilar (Fig. 7B vs. Fig. 7D and Fig. 7C vs. Fig 7E) and in EAC and in USA coastal and estuarine distributions are significantly different from each other (KS-test, $p < 0.0001$. There were more green crab recruits in estuaries than on the open coast. In EAC there were 31 recruits on the coast vs. 60 recruits in the estuary. In USA there were 30 recruits on the coast vs. 124 recruits in the estuary.

Discussion

High abundance of introduced species in the invaded vs. native range can be explained by the enemy release hypothesis (ERH) coined by Gillett (1962), the novel weapons hypothesis (Callaway and Aschehoug 2000), or the empty niche hypothesis (Elton 1958). According to the enemy release hypothesis introduced species can attain high abundances in the invaded range due to the absence of or decrease in competition, predation, or parasitism. Competitors, predators and parasites that may have co-evolved with a species in its native range can keep a species in check, preventing this species from exponential population growth and rapidly expanding its ranges. However, once a species is exported from the native range, those natural enemies disappear and the introduced species can exhibit rapid population growth and range expansion in the invaded range. The novel weapons hypothesis explains how a species has evolved certain defenses against native predators and competitors in the native range e.g. allelopathy in plants. Once an allelopathic plant species is exported from the native range, it is possible that the chemicals which used to be an efficient defense is now a very powerful offense or weapon to which the species in the invaded range has evolved no response. Hence an invader can proliferate in the invaded range. Last, the empty niche hypothesis suggests that an introduced species can attain high abundances in the introduced range because no other species utilizes the niche that the invader fills. Green crabs are highly abundant in their native range but green crab invasion success over a biogeographic range is variable and it is not well understood exactly why.

I expected that green crab would be highly abundant and that the ratio of green to native crab species would be high in the most recently introduced range USP. Also, Torchin et al. (2003) found that green crab in USP had lower levels of parasites than green crab in the native range which could cause green crab in the introduced range to be more successful. Contrary to expectation, I found that the green crab is more successful in terms of abundance, presence of recruits, green crab to native crab ratio, and habitat utilization in the native range relative to the introduced range. Relatively low abundance in estuaries and absence of green crab from the open coast on the US Pacific Coast may be partially due to the rich native crab community (Hunt and Yamada 2003, deRivera et al. 2005, Jensen et al. 2007). Cancrid crabs can, in addition to preying on green crabs, compete with green crabs for food and shelter (Hunt and Yamada 2003). Additionally, green crabs found in proximity of the rock crab, *Cancer productus*, have a higher number of missing limbs (Jensen et al. 2007) than green crabs in areas without *Cancer productus*. However, in this study, we found no consistent effects of region or habitat on number of missing limbs in green crab, which is slightly surprising given the fact that the ratio of cancrid crabs to green crabs is highest on the US Pacific Coast, and higher on the open coast, where the green crab is not found, than in estuaries where the green crab is found. It is possible that there is increased competition and/or predation from other crabs in the invaded range, which is consistent with the enemy release hypotheses albeit the fewest enemies seem to be found in the native range. Although parasites might be few or absent, other enemies such as predators and competitors may keep the green crab abundance low in the introduced range.

The green crab is not yet found on the open coast in USP. However, over time, the green crab may be able to inhabit the open coast. There can be a time lag from the time of introduction to the time of very high abundance and sustained populations (Kowarik 1995, Crooks and Soule 1996, Simberloff and Gibbons 2004). The current population structure on the US Pacific Coast strongly suggests that recruitment limitation exists; There are good recruitment years (e.g. 2003 and 2005) (Chapter 1, this dissertation) but certainly there are several years where recruits are virtually absent from the population. It is possible that the US Pacific Coast green crab invasion can still spread and exhibit rapid and sustained population growth if at least one season of excellent conditions occurs and consequently the green crab populations on the US Pacific Coast could be larger in the future. This possibility is supported by the fact that I found an invasion gradient when progressing from East to West. The US Atlantic Coast had intermediate results in terms of abundance, carapace widths, numbers of recruits, and green crab to native crab ratios. This suggests that green crab anbundance on the US Pacific Coast may currently be low but the green crab may still have the potential to become very abundant once the invasion is a century or two old.

One interesting pattern revealed by this study is that green crab size, in terms of maximum carapace width, shows the opposite pattern of all other parameters measured in this study. Carapace width is largest on the US Pacific Coast which is what Grosholz and Ruiz (2003) found as well. One possible explanation could be that the lower abundances in USP may indicate less intraspecific competition for resources, or higher resource availability and thus individual green crabs have more available resources such as food and shelter which can increase survival and individuals can attain larger sizes. Another possible explanation is the temperature range in USP and on the open coast elsewhere is limited. Very cold winter temperatures occur less frequently here. It is possible that open coast green crabs in EAC and USA, or green crabs on the US Pacific Coast can feed for a greater part of the year, than green crabs in estuaries, where the water temperatures may get too low in the winter, in order for the green crabs to be metabolically efficient. Or, higher average water temperature over the course of a year could facilitate faster growth. On the US Pacific Coast the estuarine winter temperature does not get as low as the estuarine winter temperature in Northern Europe.

Coast vs. estuary

In addition to assessing green crabs in native and introduced ranges, I examined the patterns found by Preisler et al. (2009) that estuaries are more invaded than the open coast. In the native range EAC and the introduced range USA, I did not find strong or consistent effects of habitat on green crab abundance, average or maximum carapace width, number of missing limbs, and green crab to native crab ratio. This is largely due to the fact that variation at the level of site was very high, and that any consistent effect of habitat was swamped by the extremely high variation at the site level. One interesting pattern to notice is that in EAC recruits are found in relatively high abundance on the open coast. This is not the case for any of the other regions. However, recruits are more abundant in estuaries than on the open coast in general. In USP green crab are not, at least yet, found on the open coast and the green crab in this region can be deemed more successful in estuaries than on the open coast. Hence, the regional patterns indicate that green crabs are more successful in estuaries than on the open coast.

Preisler et al. (2009) suggests different hypotheses to explain this pattern but here I discuss only hypotheses that seem to be supported by the green crab pattern. First, it is possible that species associated with estuaries are more likely to be introduced to new ranges, due to the fact that ports and harbors are often located in estuaries and protected bays. Second, estuarine species diversity may be more depauperate and hence more invasible than that on the open coast. Third, larval retention in estuaries may enhance estuarine invasions (Byers and Pringle 2006). The first hypothesis is likely to be supported since the green crab is well adapted to estuarine conditions, with its broad tolerance levels of salinities and temperatures (Yamada 2001). The second hypothesis of depauperate estuarine fauna is likely to be supported strongly on the US Pacific Coast where there are only two native crab species that are common in estuaries (*Hemigrapsus oregonensis* and *Pachygrapsus crassipes*). Both species are smaller than green crab. There are several native rock crab species which are common on the open coast and which are all larger than the green crab. There is possibly less predation on estuarine green crab from other larger crab species allowing green crabs to be more successful in estuaries. This hypothesis also seems weakly supported for USA where the native crab community is more species rich on the open coast than in the estuaries. However, the native blue crab, *Callinectes sapidus* which is a predator on green crabs is common in estuaries, which weakens the support for this hypothesis on the US Atlantic Coast. The third hypothesis of higher degree of larval retention in the estuary is possibly supported. If, during El Niño years, green crabs spread to adjacent estuaries, the increase in current strength may facilitate the spread of larvae that otherwise would not travel as far. Hence it is possible that a high number of larvae are always present, but only in years of a particularly strong current are the larvae dispersed far. Consequently, the hypothesis of larval retention is partially supported. However, this may not be universally true across estuaries. For example, in Bodega Bay, green crabs have been extremely abundant over a long period of time suggesting some degree of larval retention. Also, Cohen and Carlton (1998) have suggested the potential for larval retention in San Francisco Bay. In Elkhorn Slough, green crab abundance peaked about ten years after the initial introduction and has been declining since (Chapter 1, this dissertation). Hence, if there was a high degree of local larval retention of green crabs in Elkhorn Slough, this population should have been able to sustain itself as opposed to dramatically declining and then persisting at extremely low abundance. However, the mouth of Elkhorn Slough has been artificially enlarged by the placement of Moss Landing Harbor in 1947. Hence, the lower estuary has very short residence time and Elkhorn Slough may have less larval retention than is typical for estuaries.

Conclusion

This study shows that different parameters used to quantify invasion success may lead to different conclusions as to whether an invasive species is successful in a given area or not. If I had measured only abundance, I would conclude that the green crab is least successful on the US Pacific Coast and in open coast habitat, where as if I had only measured carapace width I would have reached the opposite conclusion, that green crabs are most successful on the US Pacific Coast. Ecologically, abundance and species ratios seem more important parameters to measure if one wants to assess invasion success. In this study, body size does not seem like a good indicator of invasion success even though larger crabs are less vulnerable to predation and better competitors when obtaining food, shelter or mates. Hence, one can use different parameters to assess invasion success but it is critical to remember that each parameter has its own implications. From this study, I conclude that European green crab is more successful in estuaries than on the open coast, and more successful in the native and long ago invaded ranges compared to the most recently invaded range. In addition, the magnitude of that effect increases from the native range to the long-ago invaded to the recently invaded range. It should be noted that at the small scale spatial variation in abundance of this species is extremely high, which poses a great challenge in consistently assessing and comparing individual and population level parameters of this species across a broad geographic range.

Surprisingly, for a global invader ranked 18 out of 100 of the world's worst invaders, in the global invasive species database, there is no place like home: it is not more successful in the invaded ranges, according to most parameters measured in this study. This statement can not be extrapolated to ranges outside this study. In other invaded ranges, such as Tasmania and on Vancouver Island, Bristish Columbia, extremely high green crab densities have been found (Gillespie et al. 2007). However, I conclude that even globally invasive species are not equally successful everywhere. Being a successful invader does not necessitate extremely high abundance everywhere. The reason that green crab is considered a successful global invader is that this species has invaded five of six continents to which it was not native and green crab has become highly abundant in at least a few of these introduced regions at different points in time. Once a species has been deemed a global invader, this particular species is often expected to be a successful invader everywhere if no actions are taken to prevent the spread of the invader. However, this is not the case for the European green crab on the US Pacific Coast.

Finally, this study provides an essential framework that is currently missing in studies of invasive species. It allows us to quantify and compare species invasions across ranges and habitats, which consequently allows us to identify vulnerable regions or habitats that have not yet been invaded by the European green crab. The approach and sampling design of this study could be applied to other global species invasions of concern, for example the lion fish invasion in the Caribbean.

Table 1. Location of all 53 study sites and timing of sampling in 2007. Regional abbreviations are EAC for the European Atlantic Coast, USA for the US Atlantic Coast and USP for the US Pacific Coast. Habitat abbreviations are “E” for estuarine site and “C” for coastal site.

Region	Location	Site number	Location	Habitat	Site	Latitude	Longitude	Sample dates
EAC	1	1	Denmark	E	Sebbersund	56.962252	9.571145	July
EAC	1	2	Denmark	E	Bjornsholm	56.852473	9.207888	July
EAC	1	3	Denmark	E	Risgaarde	56.756515	9.238443	July
EAC	1	4	Denmark	C	Thyboron	56.724601	8.220148	July
EAC	1	5	Denmark	C	Thorsminde	56.367266	8.121631	July
EAC	1	6	Denmark	C	Hvide Sande	55.999704	8.119537	July
EAC	2	7	The Netherlands	E	Kanal	51.636913	3.900740	August
EAC	2	8	The Netherlands	E	Kats	51.541028	3.867720	August
EAC	2	9	The Netherlands	E	NIOO-KNAW	51.490724	4.054448	August
EAC	2	10	The Netherlands	C	Nordzee strand	51.778903	3.864083	July
EAC	2	11	The Netherlands	C	Neeltje Jans	51.639877	3.699460	August
EAC	2	12	The Netherlands	C	Roompot	51.623860	3.679383	August
EAC	3	13	France	E	Guillec	48.687768	4.063833	August
EAC	3	14	France	E	La Penze	48.653722	3.952333	August
EAC	3	15	France	E	Kernic	48.651500	3.952333	August
EAC	3	16	France	C	Roscoff Lab	48.727128	3.983942	August
EAC	3	17	France	C	Santec	48.718732	4.013886	August
EAC	3	18	France	C	Tevenn	48.705358	4.047911	August
USA	4	19	New Hampshire	E	Backyard	43.132757	70.885899	June
USA	4	20	New Hampshire	E	Cedar pt	43.127370	70.857446	June
USA	4	21	New Hampshire	E	Adams Pt boat launch	43.095723	70.867528	June
USA	4	22	New Hampshire	C	So Odiorne	43.040935	70.714202	June
USA	4	23	New Hampshire	C	In between	43.028912	70.722778	June
USA	4	24	New Hampshire	C	Rye Harbor	42.999534	70.749466	June
USA	5	25	Massachusetts	E	Boat House	41.580088	70.525017	May
USA	5	26	Massachusetts	E	Washburn Bay	41.571811	70.527079	June
USA	5	27	Massachusetts	E	Meadowneck	41.568121	70.515321	June
USA	5	28	Massachusetts	C	Island sound	41.552568	70.547426	May
USA	5	29	Massachusetts	C	78 Waterside	41.541788	70.617267	June
USA	5	30	Massachusetts	C	Shorelab	41.528727	70.646576	June
USA	6	31	Rhode Island	E	Bristol	41.693690	71.244757	June
USA	6	32	Rhode Island	E	Providence Island 1	41.628470	71.330926	June
USA	6	33	Rhode Island	E	Providence Island 2	41.597526	71.307732	June
USA	6	34	Rhode Island	C	Pt Judith	41.374398	71.515721	June
USA	6	35	Rhode Island	C	Noyes Neck	41.326722	71.755611	June
USA	6	36	Rhode Island	C	Coastguard	41.306235	71.857799	June
USP	7	37	Bodega Bay	E	Miller	38.202185	122.922706	May
USP	7	38	Bodega Bay	E	Marshall	38.159895	122.894661	May
USP	7	39	Bodega Bay	E	Tomasini	38.139013	122.872227	May
USP	7	40	Bodega Bay	C	Doran	38.306108	123.052608	May
USP	7	41	Bodega Bay	C	Pt Reyes	37.995590	122.977279	May
USP	8	42	San Francisco Bay	E	Buckeye	38.006617	122.473530	May
USP	8	43	San Francisco Bay	E	China Camp	38.000243	122.460612	May
USP	8	44	San Francisco Bay	E	Road	37.982103	122.471945	May
USP	8	45	San Francisco Bay	C	Golden Gate North	37.833611	122.477219	May
USP	8	46	San Francisco Bay	C	Golden Gate South	37.809319	122.474563	May
USP	8	47	San Francisco Bay	C	Pacifica	37.596487	122.508236	May
USP	9	48	Elkhorn Slough	E	Kirby Park	36.840196	121.743892	April
USP	9	49	Elkhorn Slough	E	Hummingbird Island	36.823960	121.742740	April
USP	9	50	Elkhorn Slough	E	Vierra	36.809098	121.783449	April
USP	9	51	Elkhorn Slough	C	Half Moon Bay	37.502603	122.478017	April
USP	9	52	Elkhorn Slough	C	Santa Cruz Harbor	36.963534	122.002714	April
USP	9	53	Elkhorn Slough	C	Monterey Harbor	36.606232	121.894130	April

Table 2. Crab species, other than green crab, found in the different regions. Size designation denotes whether a species was classified as small or large native crab in the analysis of ratios of green crab to other crab species.

Region	Species	Size designation
EAC	*Hyas arenaria*	Small
EAC	*Hemigrapsus sanguineus*	Small
EAC	*Liocarcinus puber*	Large
USA	*Hemigrapsus sanguineus*	Small
USA	*Panopeus herbstii*	Small
USA	*Dyspanopeus sayi*	Small
USA	*Callinectes sapidus*	Large
USA	*Cancer irroratus*	Large
USA	*Cancer borealis*	Large
USA	*Ovalipes ocellatus*	Large
USA	*Libinia emarginata*	Small
USA	*Libinia dubia*	Small
USP	*Pachygrapsus crassipes*	Small
USP	*Hemigrapsus oregonensis*	Small
USP	*Cancer antennarius*	Large
USP	*Cancer productus*	Large
USP	*Cancer gracilis*	Large

Table 3. ANOVA table of regional effects on green crab average caracapace widths. Each habitat, coast and estuary, and each sex, male and female, were analysed separately. I found no regional effect on average size in either sex or habitat.

Source	SS	df	Mean Squares	F-Ratio	p-Value
Estuarine Males	23,572.19	2	11,786.09	0.853	0.491
Error	55,259.99	4	13,815.00		
Estuarine Females	3,251.21	1	3,251.21	0.296	0.610
Error	54,864.44	5	10,972.89		
Coast Males	525.016	1	525.016	0.03	0.872
Error	70,998.65	4	17,749.66		
Coast Females	2,342.70	1	2,342.70	0.181	0.692
Error	51,724.57	4	12,931.14		

Table 4. ANOVA table with Tukey's post-hoc analysis of regional effect, in estuarine habitat, on male and female maximum carapace width. A) There were significant effects of region on estuarine male and female maximum carapace widths. B) Tukey's post hoc analysis for estuarine males. C) Tukey's post hoc analysis for estuarine females. For both males and females maximum carapace width is largest in USP, intermediate in USA and smallest in EAC.

A

Source	SS	df	Mean Squares	F-Ratio	p-Value
Estuarine males	2,355.46	2	1,177.73	17.941	0.005
Error	328.215	5	65.643		
Estuarine females	397.275	2	198.637	10.375	0.026
Error	76.582	4	19.145		

B

Males, Tukey's post hoc

Region	Region	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
EAC	USA	-7.414	0.014	-11.874	-2.953
EAC	USP	-23.4	0.013	-38.928	-7.865
USA	USP	-15.98	0.057	-31.541	-0.424

C

Females, Tukey's post hoc

Region	Region	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
EAC	USA	-3.492	0.093	-6.525	-0.458
EAC	USP	-13.2	0.032	-24.365	-2.043
USA	USP	-9.712	0.080	-21.019	1.595

Table 5. ANOVA table of habitat effect on male and female maximum carapace width. There were no uniform effects of habitat on carapace width. Yet, in EAC, males on the coast were significantly larger (70.5 mm, sd = 2.95) than males in estuaries (60.7 mm, sd = 4.03).

Source	**SS**	**df**	**Mean Squares**	**F-Ratio**	**p-Value**
EAC males	157.033	1	157.033	13.111	<0.0001
Error	1,269.56	106	11.977		
EAC females	8.592	1	8.592	0.948	0.332
Error	996.991	110	9.064		
USA males	2.976	1	2.976	0.171	0.681
Error	1,569.68	90	17.441		
USA females	34.525	1	34.525	3.139	0.081
Error	670.861	61	10.998		

Table 6. ANOVA table of regional effect on number of missing limbs per crab. There was no overall regional effect on male, female, coastal and estuarine green crabs.

Source	SS	df	Mean Squares	F-Ratio	p-Value
Coastal males	0.001	1	0.001	0.001	0.973
Error	3.744	4	0.936		
Coastal females	0.458	1	0.458	0.309	0.617
Error	4.45	3	1.483		
Estuarine males	1.371	1	1.371	2.473	0.177
Error	2.772	5	0.554		
Estuarine females	3.061	2	1.531	5.612	0.069
Error	1.091	4	0.273		

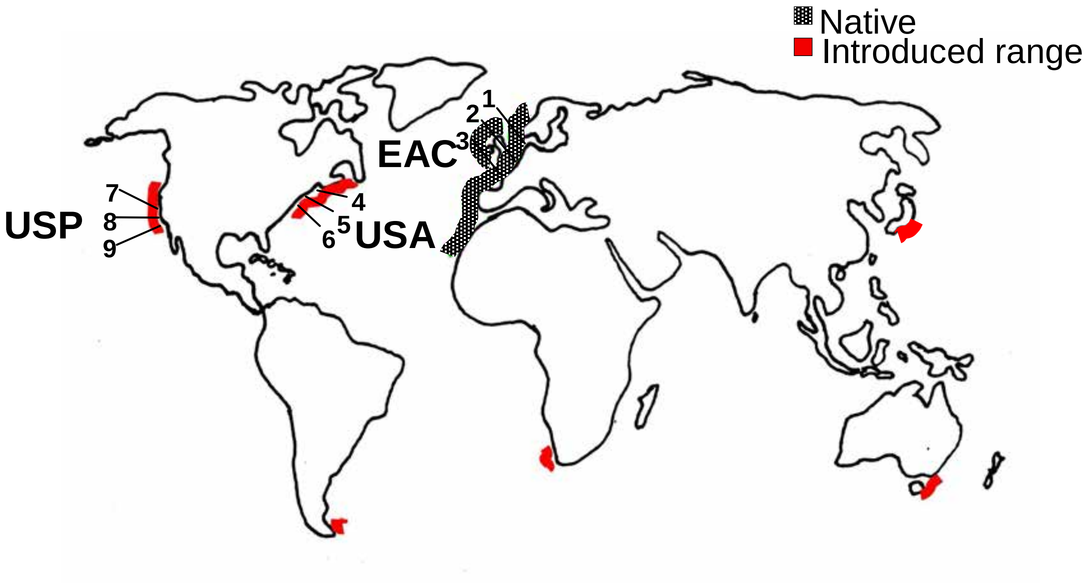

Figure 1. Map of green crab distribution and study locations. Green crab is native from Northern Norway to Northern Africa, and introduced in Japan, Tasmania, South Africa, Argentina, and North America. In 2007, I sampled three locations in the native region, EAC, locations 1, 2, and 3. In the introduced regions, in USA, locations 4, 5, and 6 were sampled, and in USP, location 7, 8, and 9 were sampled. At each location, there were three estuarine and three open coast sites (See Table 1). All sites were sampled in within approximately one month from the time of peak recruitment.

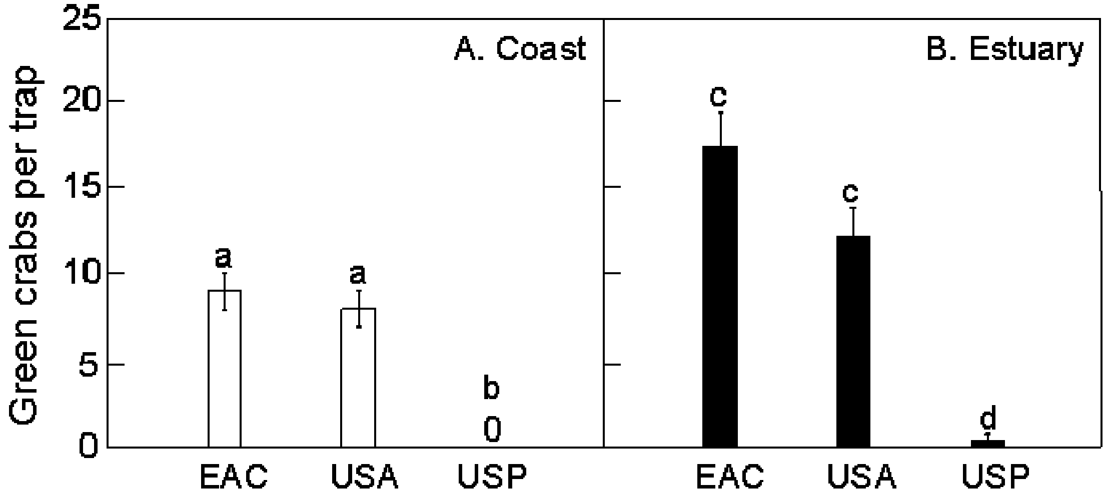

Figure 2. Regional and habitat differences in green crab abundance (+/- SE). A) Coastal habitat, regional abundance of green crab is lowest in USP. B) Estuarine habitat, regional abundance of green crab is lowest in USP. The fact that USP green crab abundance is only marginally significantly different from USA is most likely due to high variation at the site level. The same letter above two bars indicates that the two abundances are not significantly different from each other.

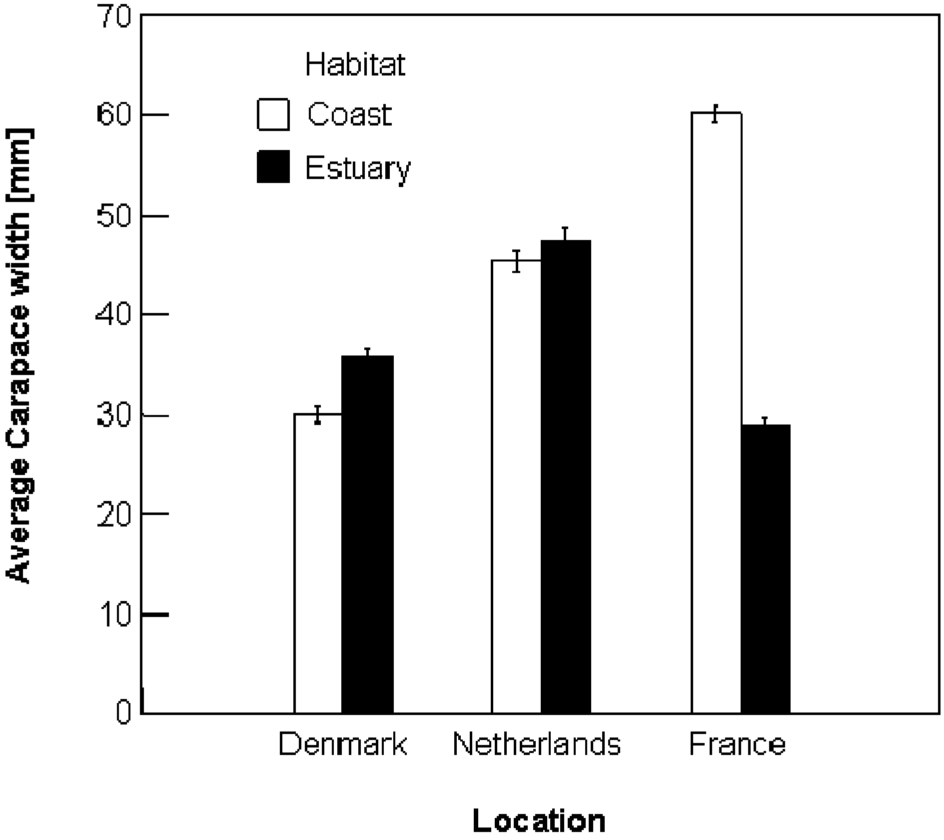

Figure 3. Variable effect of habitat on male average carapace width (+/- SE). In EAC, the effect of habitat on male green crab carapace width was different in each of the three locations.

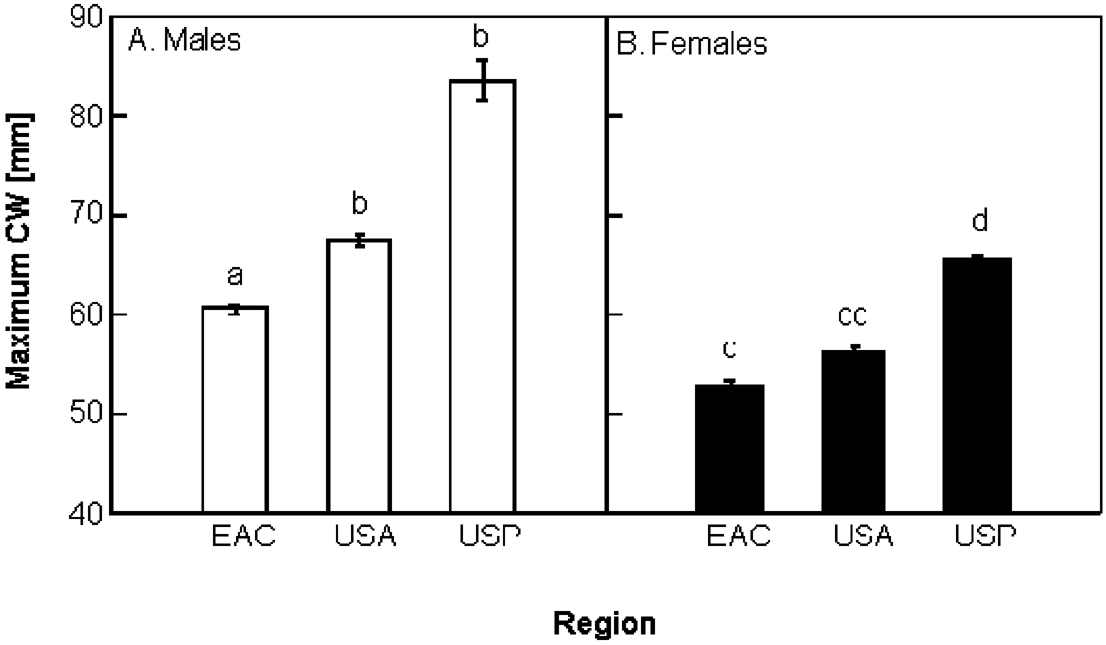

Figure 4. Regional effects on estuarine male and female maximum carapace widths. Maximum carapace width is the average carapace width of the 90th percentile of each sex in each region in each habitat. A) Estuarine male maximum carapace width was smallest in EAC. B) Estuarine female maximum carapace width was significantly smaller in EAC than in USP. The same letter above two bars indicates that the two abundances are not significantly different from each other.

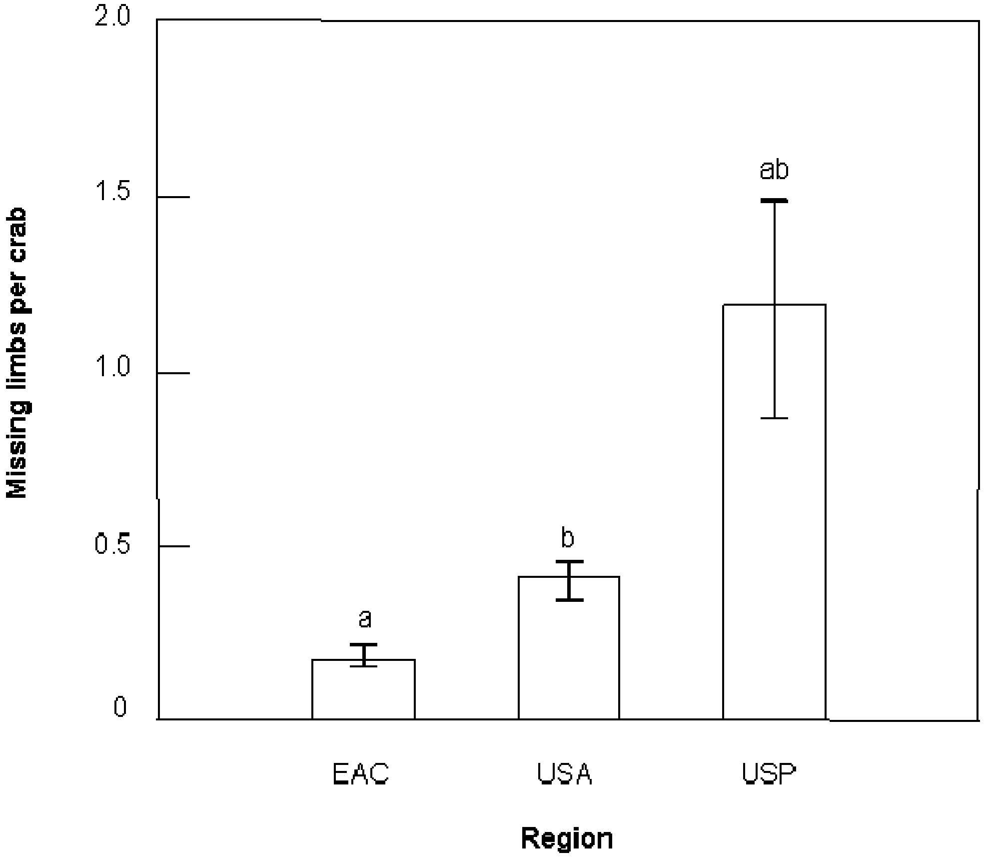

Figure 5. Regional effect on number of missing limbs per crab on estuarine females (+/- SE). Female estuarine crabs in USA are missing significantly more limbs than estuarine females crabs in EAC.

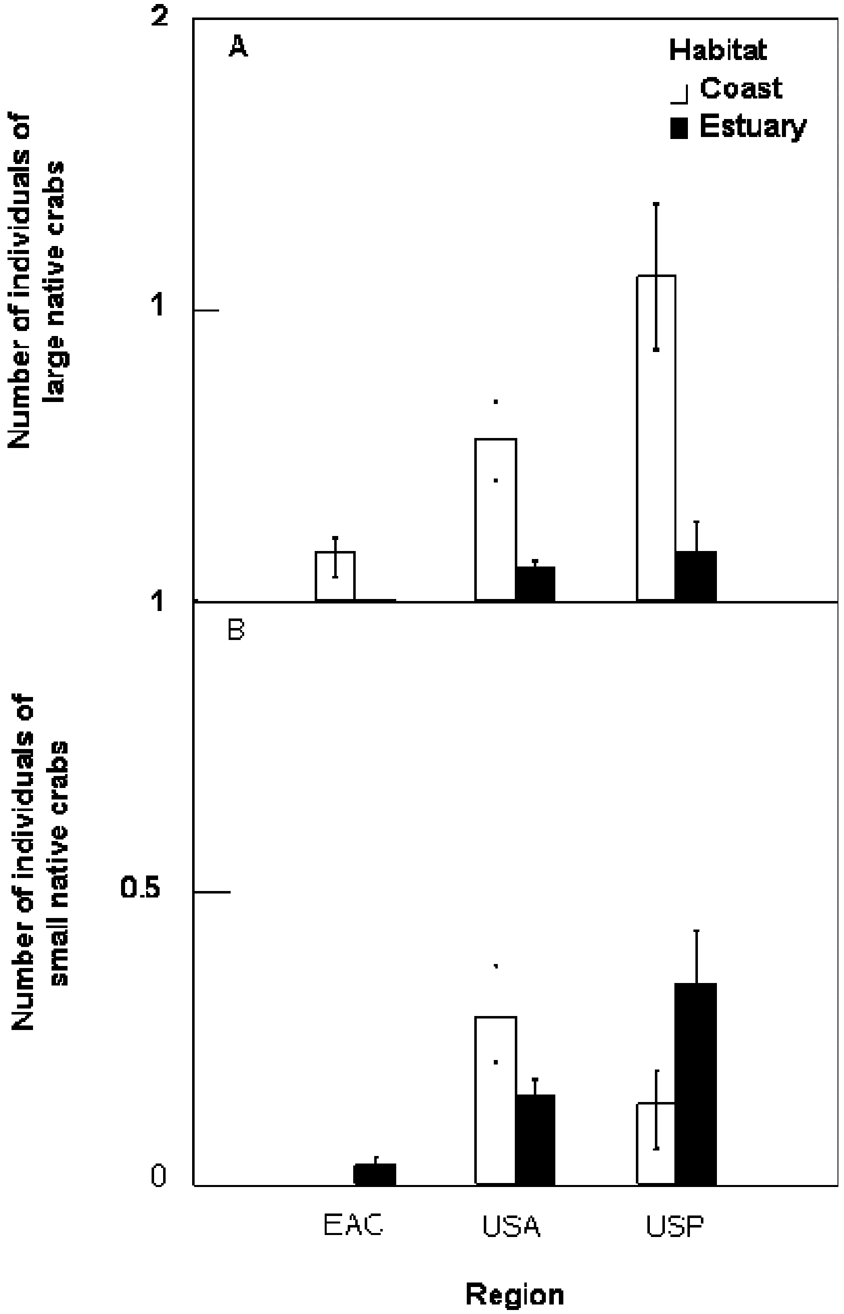

Figure 6. Regional and habitat differences in fraction of large and small native crab species (+/- SE). A) Number of individuals of large native crabs per trap, by region, in coastal and estuarine habitat. B) Number of individuals of small native crabs per trap, by region, in coastal and estuarine habitat.

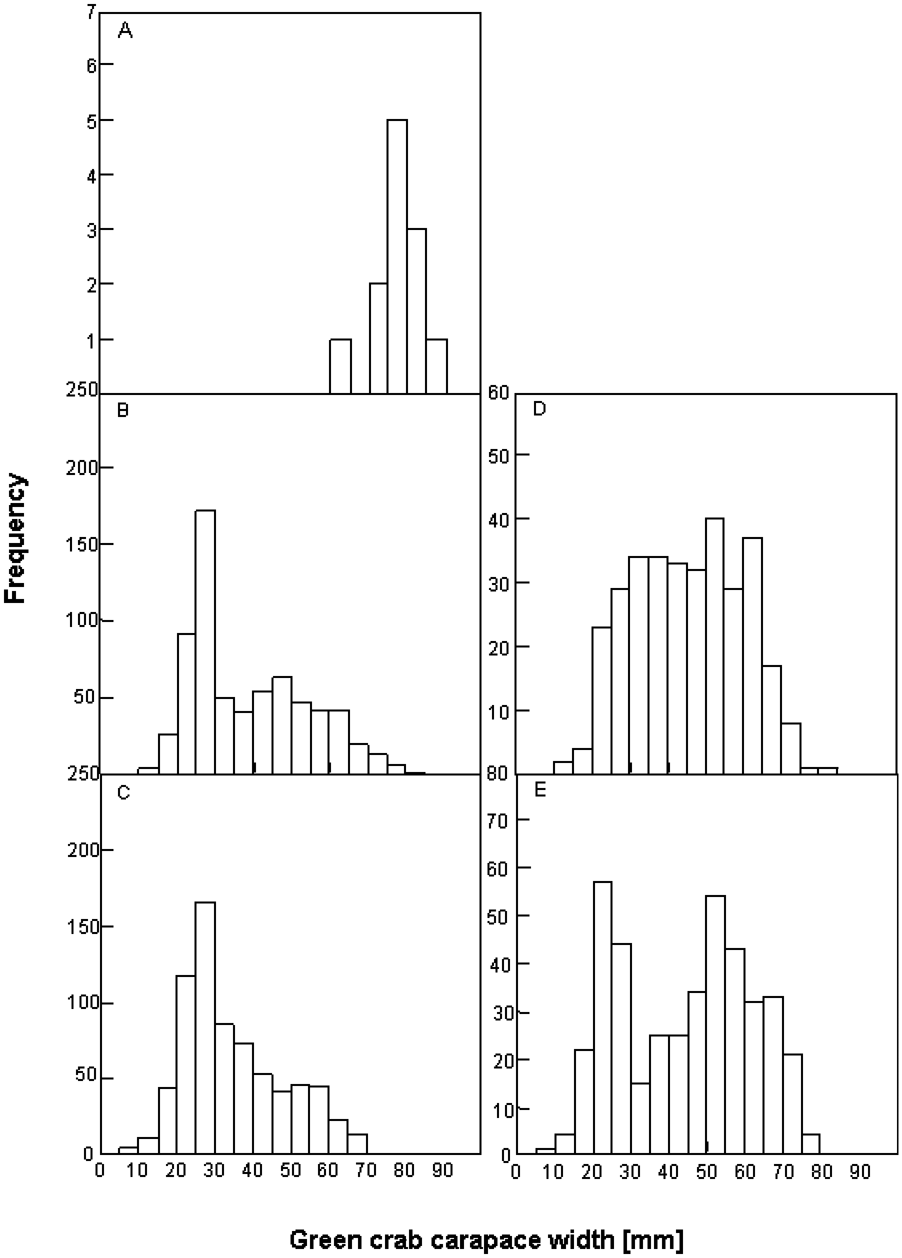

Figure 7. Size distributions of male green crabs by region and habitat. Green crab male size distribution in A) USP, Estuary; B) USA, Estuary; C) EAC, Estuary; D) USA, Coast; E) EAC, Coast. In USP, no recruits (individuals <30 mm) were found.

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CHAPTER 3

Inter- and intraspecific aggression levels of a global invader, the European green crab, *Carcinus maenas*

Introduction

Role of behavior in invasions

Many factors can influence invasive species' success, such as species diversity or species interactions in the recipient community (Elton 1958, MacArthur and Wilson 1967, Lodge 1993, Cohen and Carlton 1998, Stachowicz et al 1999, Grosholz et al. 2000, Lohrer and Whitlatch 2002). Characteristics or life history traits of invaders can also influence invasion success, such as rapid growth, high fecundity, high dispersal ability and short life span (Elton 1958, Baker 1965, Erlich 1989, Hayes and Barry 2008). Furthermore, behavioral characteristics can contribute to invasion success or failure (Winston 1992, Holway and Suarez 1999, Suarez et al. 1999, Sih et al. 2004). One such characteristic is aggressive behavior. Both theory and empirical studies have linked behaviors such as inter- and intraspecific interactions to invasion success. Interspecific aggression is a commonly invoked mechanism to explain invader success (Holway and Suarez 1999, Barbaresi et al. 2004, Sih et al. 2004) and there are many examples of interspecifically aggressive species that are successful in the invaded range, such as Africanized bees (Winston 1992) Argentine ants (Suarez et al. 1999), crayfish (Hill and Lodge 1999, Barbaresi et al. 2004), and grapsid crabs (Jensen et al. 2002).

Interspecific and intraspecific aggression

Interspecifically aggressive species can be intraspecifically aggressive as well (Pintor et al. 2009). The relationship between interspecific and intraspecific aggression has been studied in crayfish (Barbaresi et al. 2004) and *Anolis* lizards (Ortiz and Jenssen 1982, Hess and Losos 1991, Bolger and Case 1992), and increased interspecific and intraspecific aggression has been suggested to contribute to invasion success (Pintor et al. 2009). A suite of correlated aggressive behaviors that lead to inter- and intraspecific aggression can be described as “behavioral syndromes”, a term coined by Sih et al. (2004). Aggressive behavior can be advantageous during invasions due to increased foraging efficiency and high attack rates on heterospecifics (Barbaresi et al. 2004, Sih et al. 2004, Pintor et al. 2009). While interspecific aggression can facilitate establishment in early invasions, intraspecific aggression can be disadvantageous during population growth of an invader. For example, agonistic encounters in green crab can increase response time to food and mate cues (Fletcher and Hardege 2009) which may inhibit invasion success. Thus, interspecific aggression can be advantageous when species’ are first establishing due to superior interspecific competitive ability (Bolger and Case 1992) but once established, high levels of aggression may affect conspecifics and can limit population growth (Lankau et al. 2009). Conversely, in some invaders interspecific aggression is negatively correlated to intraspecific aggression, which is the case for some *Anolis* lizards in the Caribbean (Bolger and Case 1992) and for argentine ants in North America. Decreased intraspecific aggression in argentine ants is primarily due to low genetic diversity in the invaded range (Suarez et al. 1999). This negative relationship between inter- and intraspecific aggression seems potentially highly beneficial for the invader, which can then out compete or predate on potential competitors, without using resources on intraspecifically aggressive interactions, which in turn can allow rapid population growth and range expansion of the invader. Hence, one factor potentially contributing to invasion success is behavioral traits. Additionally, flexibility in behavioral traits may likewise be contributing factor. Barbaresi et al. (2004) discussed how variation among invaded locations, in behavioral flexibility such as plasticity in ranging behavior in crayfish *Procambarus clarkii* could contribute to invasion success. The contribution of high competitive ability to invasion success has been studied in plants and the contribution of high aggression levels has been studied in colonial organisms such as bees and ants. Variation in aggression levels in invertebrate invasions has been investigated in crayfish (Hill and Lodge 1999), but not in crabs.

Invader behavior in its native and invaded ranges

There are different pathways to becoming a successful invader due to increased or decreased aggression in the invaded range. Some successful invaders are highly aggressive in both native and introduced ranges and in other invaders behavior varies from the native to the introduced range. One example of the former, where a species is highly competitive and dominant in the native range as well as the introduced range, and thus consistently superior, is garlic mustard. Part of the explanation to its success is the competitors' the lack of defenses against allelopathy in the introduced range. In the native range, defenses against allelopathy have evolved in competitors of garlic mustard (Lankau et al. 2009). Another example where behavior is not particularly different between the native and introduced range is the Asian shore crab, *Hemigrapsus sanguineus*. Lohrer et al. (2000) found that the invasive shore crab did not greatly differ in resource utilization between native and introduced ranges. In contrast, there are examples of introduced species which are not particularly dominant or aggressive in the native range, but became highly aggressive in the newly invaded range such as Africanized honeybees (Winston 1992). Invasive species provide an opportunity to study how aggressive behavior of a species may or may not change from the native to the introduced range. Intraspecific interactions may respond differently from interspecific interactions. The relationship between inter- and intraspecific aggression can be positively, negatively, or not at all correlated in the native range, but this relationship may change once a species is introduced to a new range. While there are studies on invasive species and variation in traits in native vs. invaded ranges (Hierro et al. 2005) and while there are studies comparing how a similar native and an invasive species exhibit different behaviors in the same range (Roudez et al. 2008) there are very few studies of how the behavior of one species varies between the native and introduced ranges. Therefore, the goal of this study was to investigate variation in interspecific predation and intraspecific aggression levels in different regions where a global invader has become established and compare those levels of aggression to that of the native range. Because the native species assemblage in the invaded community is different from the native species assemblage in the native community, it was necessary to transplant species and conduct laboratory trials with the same invasive species encountering a suite of unfamiliar native species from the region where the invader had recently invaded, the US Pacific Coast, and the invasive species encountering a suite of familiar native species from a region which was invaded long ago, the US Atlantic Coast.

Green crab aggression in native and invaded regions

I investigated inter- and intraspecific aggression levels of the global invader, the European green crab, *Carcinus maenas*. I assessed whether there was a relationship between interspecific and intraspecific aggression levels and whether behavior was flexible, or in other words if behavior varied between native and introduced ranges, and if green crab were more or less intraspecifically aggressive towards green crabs from their "own" region as opposed to towards green crabs from other regions by answering the following questions: 1) Is there regional variation in inter- and intraspecific aggression? 2) Is there a relationship between inter- and intraspecific aggression? 3) Is behavior flexible?

I expected lower intraspecific aggression levels in the introduced ranges for two reasons. First, relative abundance of green crabs is similar between the European

Atlantic Coast (here after referred to as EAC) and the US Atlantic Coast (here after referred to as USA). Relative abundance of green crab on the US Pacific Coast (hereafter referred to as USP) is about one tenth of relative abundance of EAC and USA (Chapter 2, this dissertation). Lower invader density in USP could cause a relaxation in selection for high intraspecific aggression leading to lower aggression levels when encountering conspecifics. Second, Bagley and Geller (2000) documented that the genetic diversity of the European green crab is lower in the introduced ranges than in the native range. Hence, I might expect lower intraspecific aggression in the introduced range as seen in Argentine ants. Green crabs are highly successful in their native range but green crab invasion success over a biogeographic range is variable (Chapter 2, this dissertation) and it is not well understood exactly why. Because we know that behavior can contribute to invasion success, I investigated whether green crab behavior is variable in the native (EAC) and introduced ranges (USA, USP).

Methods and materials

Lab trials are commonly used to quantify competitive ability and aggression levels as a proxy for field aggressive behavior in decapods. Similar methods have been used for crayfish (Baird et al. 2006) and for green crabs (McDonald et al. 2001, Hunt and Yamada 2003). In order to assess inter- and intraspecific aggression levels I conducted two types of experiments. In order to test whether there was regional variation in interspecific interactions I paired a green crab with a smaller or larger individual crab of a different species and recorded the outcome of the interaction. In order to test whether there was regional variation in intraspecific green crab aggression levels, I paired two similarly sized green crabs (max 15% difference in carapace width) and quantified their interactions. The two types of experiments are described in detail below. The two types of trials were conducted in all three regions during 2006 to 2008 (See Table 1-3 for details on species' identity, locations, and timing of trials). I captured crabs for the trials using three different trap types: 1) minnow traps, which are conically shaped plastic traps 42 cm long x 22.5 cm center diameter and 15.5 cm end diameter with a 2.5 cm opening, 2) modified minnow traps, where the opening in one end was increased to 5 cm in diameter, in order to allow larger crabs to enter the traps, and 3) Fukui fish traps, of dimensions 20 x 45 x 60 cm and mesh size 1 x 1 cm. Fukui traps were individually tethered to a PVC stake or tied to a cinder block and one of each of the two minnow trap types were tethered on one PVC stake or tied to one cinder block, then deployed on muddy or sandy substrate. All traps were baited with one of the following raw or frozen bait types: anchovy (USP), sardine (USP), mackerel (USA, EAC), menhaden (USA, EAC), and squid (USP, EAC). I placed one bait container inside each individual trap. Bait containers were made from a 35mm film canister drilled with 18-21 holes of 5 mm in diameter.

All traps were deployed at Mean Lower Low Water and left in the field approximately 24 hrs. After capture, all crabs were separated by species and kept in 16 – 30 gallon communal holding tanks at the respective marine labs. Green crabs in holding tanks were also separated by sex. Because inter- and intraspecific behavior trials were conducted at different laboratories within USA and EAC, I used ANOVA to test for intra-coastal variation in inter- and intraspecific aggression levels and found no significant effect of laboratory location on aggression levels. Additionally, I found no significant effect of year on inter- or intraspecific aggression levels when comparing trials from 2006 and 2007 and therefore trials from these two years were pooled in the analyses.

Interspecific interaction trials

In order to test whether there was regional variation in interspecific interactions I let green crabs encounter a smaller or larger crab of a different species in controlled lab experiments. If green crabs were harmed by larger crabs in one region, but unharmed by larger crab species in another region, this might partly explain some of the variation in green crab invasion success in the different regions. If there were regional differences in resistance in smaller crabs to green crab attacks, then smaller crabs could provide interspecific competition to green crabs, which might partly explain some of the variation in green crab invasion success in the different regions.

Interspecific trials were divided in two groups: “green crab vs. small native crab” and “green crab vs. large native crab”. The carapace width of the small native crab was at least 10 mm smaller than the green crab. The large native crab was at least 10 mm larger than the green crab in carapace width. The size range of green crab, used in inter and intraspecific trials, for each region was: EAC 50.0 – 73.3 mm;

USA 40.1 – 77.2 mm; USP 51.0 – 93.3 mm. I used both males and females in the interspecific experiments. I transferred one green crab and one crab of a different species to a 14 L aerated plastic tub of dimensions 38 x 25 x 15 cm. The tub was divided into two areas separated by a plastic grid of mesh size 1 x 1 cm, which prevented crabs from interacting before the trial. Crabs were starved for 24 hrs and acclimatized to the tubs for at least 12 hrs. After acclimatization, the dividing grid was removed and the two crabs were allowed to interact for at least 12 hrs. After a 12-hr period, I recorded the outcome of the interaction. Possible outcomes were: both crabs were unharmed, one or both crabs sustained injuries such as losing chelae or legs, or one crab was subject to predation from the other crab. The outcomes were recorded as one of two possibilities: If the green crab injured or consumed part or all of the native crab, the outcome was recorded as “green crab won”. If the green crab did not injure or consume part of all of the native crab the outcome was recorded as “green crab did not win”. For a complete list of which crab species were used in the different locations, see Table 1-2. I calculated the ratio of trials in which the “green crab won” to “green crab did not win”. I used Pearson Chi-Square test analyze whether the ratio of green crab “wins” to green crab “no wins” differed among regions. Trials with “green crab vs. small native crab”, and “green crab vs. large native crab” were analyzed separately and 2008 was analyzed separately. The average sizes of green crabs and smaller and larger native crabs, in addition to the species’ identity of the other crab species were similar among years.

A pilot study in 2006 had indicated that in USA, small native crab species survived very frequently when encountering green crabs. Therefore, in 2008 I tested whether USA small native crabs were more resistant than USP small native crabs when exposed to USA green crabs. If so, I would conclude that USA small native crabs are highly green crab resistant. I also tested whether USA green crabs were less aggressive interspecific predators than USP green crabs by letting USA green and USP green crabs encounter a small native crab to see if survival of the small native crab was higher when encountering a USA green crab than when encountering a USP green crab. If so, I would conclude that USA green crabs are less interspecifically aggressive than USP green crabs (see Table 4-6 for experimental design). In order to control for an effect on crabs of being transported across the country I repeated trial types 1-4 in Table 4 in both USA and USP. If the ratio of green crab wins is lower in trial type 1 than in 2, and if the ratio of green crab wins is lower in trial type 3 than in 4 I would conclude that USA small native crabs are more green crab resistant than USP small native crabs (Table 5A). If the ratio of green crab wins is lower in trial type 1 than in 3 and lower in trial 2 than in 4 then I would conclude that USA green crabs are less interspecifically aggressive than USP green crab (Table 5B). I used Pearson Chi-Square analysis to test differences in all of the above ratios.

Intraspecific interaction trials within and between regions

In order to assess whether there was regional variation in intraspecific aggression levels I conducted the lab trials described below. Only male crabs were used in all intraspecific aggression experiments. I transferred two similar sized green crabs to a 14 L aerated plastic tub of dimensions 38 x 25 x 15 cm. The tub was divided into two areas separated by a plastic grid of mesh size 1 x 1 cm, which prevented crabs from interacting before the trial. Crabs were starved for 24 hrs and acclimatized to the tubs for at least 12 hrs. After acclimatization, the dividing grid was removed and the green crabs were observed for 15 minutes. During these 15 minutes I recorded, in one-minute increments, which agonistic interactions took place. Agonistic behaviors were adapted from Baird et al. 2006 (Table 7). Aggression level was then quantified as the total number of minutes in the 15 minute interval, in which agonistic interaction occurred. Aggressive minutes were tested for normality, and transform using a fourth-root transformation.

I conducted two kinds of intraspecific interaction trails. In the first type, I tested regional variation in intraspecific aggression and green crabs were only paired with green crabs from within their own region. In order to test whether intraspecific aggression varied as a function of region, I used ANOVA with transformed aggression minutes as the dependent variable, and crab origin region as a factor. The intraspecific trials were conducted in 2006, 2007, and 2008 (Table 1, Table 6). All regions were sampled in all years, except that EAC was not sampled in 2008. Therefore, I analyzed temporal effects on aggression separately for each region USP (2006-2008), USA (2006-2008) and EAC (2006-2007). Also, because EAC was not sampled 2008, I analyzed the effect of region separately for each year: 2006 (USP, USA, EAC), 2007 (USP, USA, EAC), 2008 (USP, USA). In each region, I used

ANOVA to test whether intraspecific aggression varied among years. Transformed "aggressive minutes" was the dependent variable and year was the factor. In each year, I used ANOVA to test whether intraspecific aggression varied among regions. Transformed "aggressive minutes" was the dependent variable and region was the factor.

In the second type of intraspecific aggression trials, in 2008, I tested whether regional variation in intraspecific aggression was flexible. In other words, I tested whether green crabs were more or less aggressive when encountering a green crab from their own region as opposed to encountering a green crab from a different region. I conducted three types of trials for this experiment in which I paired one green crab with another green crab from its own or from a different region (Table 6, Trial type 1-3). In order to control for a potential effect of transportation I conducted all three trial types on both the US Atlantic Coast (at WHOI) and the US Pacific Coast (at LML) (Table 3, Table 6). I used ANOVA to test whether there was a difference in transformed aggressive minutes among the three different trial types. Additionally, I conducted another three types of trial in which I paired one green crabs with another green crabs from its own or from a different region. In these trials I controlled for a potential effect of transportation by only using crabs that had been transported (Table 6, Trial type 4-6). Finally, to test whether there was an effect of transporting crabs across the country I used the trials in which crabs encountered a crab from their own region (Table 6, Trial type 1 and Trial type 3). In trial type 1, I used ANOVA to test whether there was a difference in aggressive minutes between

USA green crabs at WHOI and USA green crabs at LML. In trial type 3, I used ANOVA to test whether there was a difference in aggressive minutes between USP green crabs at WHOI and USP green crabs at LML.

Results

Regional variation in interspecific aggression: green crab vs. native crabs

I found some regional variation in interspecific aggression of green crabs vs. small native crab species but not in green crabs vs. large native crab species. When a green crab encountered a larger native crab, in all cases but one, the green crab did not win (Table 8A) which was in USA in 2006 against a blue crab *Callinectes sapidus*. There was no significant difference in ratio of green crab wins to no wins among the three regions USP, USA, and EAC (Pearson Chi-Square = 0.975, df = 2, p = 0.614).

There was regional and temporal variation in interspecific aggression when a green crab encountered an individual small native crab. In 2006-7, USA green crabs were interspecifically the least aggressive (Fig. 1A) but in 2008, USA green crabs were as interspecifically aggressive as USP green crabs (Fig. 1B). In 2006-7, there was a significant difference in ratios of green crab wins to green crab no wins among regions (Pearson Chi-Square = 22.341, df = 2, p < 0.0001) (Fig. 1A, Table 8B). This difference did not persist in 2008, where there was no difference in ratios of green crab wins to no wins between regions (Pearson Chi-Square = 0.096, df = 1, p = 0.757) (Fig. 1B, Table 8C).

Native crab resistance or low green crab aggression

In 2008 I tested whether USA small native crabs were particularly green crab resistant or whether USA green crabs were particularly poor predators on small familiar and unfamiliar native crab species and found no support for either case. I found no difference in ratio of green crab wins to no wins when comparing “USA small native vs. USA/USP green crab” to “USP small native vs. USA/USP green crab” (Pearson Chi-Square = 2.617, df = 1, p = 0.106) (Table 9A). Likewise, I found no difference in ratio of green crab wins to no wins when comparing “USA/USP small native vs. USA green crab” to “USA/USP small native vs. USP green crab” (Pearson Chi-Square = 0.096, df = 1, p = 0.757) (Table 9B). Hence, USA small native crabs were not particularly green crab resistant and USA green crabs were not particularly less aggressive in the year of this experiment, 2008.

Temporal and regional variation in intraspecific aggression

I found some temporal and regional variation in green crab intraspecific aggression levels. There was no temporal variation in aggression levels in USP among the years 2006-2008 (ANOVA $F_{73,2} = 1.902$, $p = 0.157$) (Fig. 1C-D) or in EAC between 2006 and 2007 (ANOVA $F_{118,1} = 0.035$, $p = 0.851$). In USA, there was a significant effect of year (ANOVA $F_{120,2} = 16.284$, $p < 0.0001$). Tukey’s post-hoc revealed that green crabs in USA were more aggressive in 2008 than in any other year ($p < 0.0001$) but there was no difference USA between 2006 and 2007 ($p = 0.303$) (Fig 1C-D).

I found regional variation in aggression level in some years. In 2006, there was regional variation in green crab aggression among the three regions (ANOVA $F_{62,2} = 6.552$, $p = 0.003$). Tukey's post-hoc revealed that USA green crabs were less aggressive than both USP green crabs ($p = 0.044$) and EAC green crabs ($p = 0.002$). In 2007, there was similar regional variation in green crab aggression among the three regions (ANOVA $F_{183,2} = 10.752$, $p < 0.0001$). Tukey's post-hoc revealed that EAC green crabs were more aggressive than USA green crabs ($p < 0.0001$) and EAC green were marginally more aggressive than USP crabs ($p = 0.056$). In 2008, there was no regional variation in green crab aggression between USA and USP (ANOVA $F_{90,1} = 0.153$, $p = 0.697$) (Fig. 1D).

Flexibility in intraspecific aggression: encounters between green crabs from their own region and from a different region

I did not find significant differences in time spent on aggression whether a green crab encountered a green crab from its own region, vs. a green crab from a different region in the reciprocal transplant experiment (ANOVA $F_{95,2} = 0.281$, $p = 0.756$) (Fig. 2A). I also did not find significant differences in time green crabs spent on aggression in the experiment where I only used transported crabs (ANOVA $F_{36,2} = 0.418$, $p = 0.662$) (Fig. 2B). Hence, green crabs were not more or less aggressive when encountering a crab from their own region as opposed to encountering a crab from a different region.

Transport effect

There was an effect of transportation on green crab aggression levels. USA green crabs were less aggressive in trials, when the crabs had been transported (ANOVA $F_{32,1} = 6.965$, $p = 0.013$). USP green crabs were marginally less aggressive in trials where the crabs had been transported (ANOVA $F_{46,1} = 2.998$, $p = 0.090$) (Fig. 3). However, the effort of transportation does not invalidate any of the above results because either reciprocal transplants were performed, or aggression levels were only compared between trials where either all or no crabs had been transported.

Discussion

The goal of this study was to investigate regional differences in green crab inter- and intraspecific aggression, to see if there was a relationship between inter- and intraspecific aggression, and to see if behavior was flexible. Surprisingly, I found that despite using consistent methods, inter- and intra-specific aggression was temporally and spatially highly variable in our laboratory trials, with no consistent trends between regions. However, there was a positive relationship between inter- and intraspecific aggression levels. In two years, both intra- and inter-specific aggression was significantly lower in two years on the US Atlantic Coast than in the other regions. These results leads to the conclusion that one must be cautious when generalizing about aggression levels from behavioral experiments, unless there is large sample size and excellent replication that yields temporally and spatially consistent results.

Interspecific predation, regional and temporal variation

Several studies have investigated interspecific interactions between introduced green crabs and native crabs and other non-native crabs in the same range (McDonald et al. 2001, Jensen et al. 2002, Lohrer and Whitlatch 2002, Hunt and Yamada 2003, deRivera et al. 2005). Other studies have investigated different aspects of green crab behavior. For example, it has been suggested that green crabs are fast learners which could contribute to invasion success (Roudez et al. 2008). In most of these studies of aggressive crab behavior, individuals have been competing for a resource such as food or shelter both for inter- or intraspecifically staged experiments. In this study I hypothesized that agonistic interactions could occur even if no resource was present. The mere presence of a potential competitor can elicit an aggressive response. It has been suggested that aggressive behavior of the European green crab could contribute to its global invasion success (MacDonald et al. 2007) by being able to win agonistic encounters with other species (McDonald 2001).

I expected to find variation in interspecific predation among the three regions. I expected interspecific aggression to be higher in the two introduced regions relative to the native region perhaps with particularly high aggression levels in USP due to high abundance of large native crabs which pose a threat to European green crabs (McDonald et al. 2001, Hunt and Yamada 2003, deRivera et al. 2005). I found no regional or temporal differences in interspecific aggression between green crabs and large native crabs. The only case in which a green crab injured a large native crab was in USA in 2006 again a blue crab, *Callinectes sapidus*. Hence green crabs are not more aggressive toward large other species in the introduced range thus green crabs are no better or worse at defending themselves against large crab predators in the introduced or native range. In contrast, predation by green crab on small native crab species was lowest in USA in 2006 and 2007 and there was no significant difference in predation on small native crab species among regions in 2008 where small native crab species were subject to high levels of green crab predation regardless of region. Hence, contrary to expectation green crab was less interspecifically aggressive in the introduced range USA in two of three years. There was a positively relationship between patterns of inter- and intraspecific aggression within each year. In 2006 and 2007 intraspecific and intraspecific aggression in USA was lower than in the other regions. This can contribute to the green crab successfully establishing in new ranges although high levels of intraspecific aggression could be disadvantageous when population densities become high, and thus hinder continuous rapid population growth, but perhaps aide in range expansion. There was a highly significant effect of year in both inter- and intraspecific aggression levels when comparing 2008 to any other year. I had no a priory expectation that behavior in a region would vary across years. However, if behavior is influenced by density dependent processes (Pintor et al. 2009) then behavior may vary across years. Hence, interspecific predation was both temporally variable and contrary to expectation in both introduced regions.

When I assessed whether small native US Atlantic Coast crabs were particularly green crab resistant or whether USA green crabs were particularly poor predators on small crab species I found no support for either case as the interspecific predation patterns were different in 2008 compared to 2006 and 2007. In 2006 and 2007 I found that when a small native crab in USA encountered a USA green crab, small native crab survival was very high. On the contrary, when a small native crab in USP encountered a USP green crab, small native crab survival was very low. I conducted the experiments to see if there was support for the hypotheses that 1) small native USA crabs were particularly green crab resistant and 2) USA green crabs were particularly less interspecifically aggressive in 2008. Unfortunately, in this year, I found no effect of region on neither inter- nor intraspecific aggression levels. Therefore, it is not surprising that neither did I find support for any of the two above hypotheses. This leads to the conclusion that inter- and intraspecific aggression levels are highly temporally variable, and thus possibly flexible. Within on region, I found no support for consistency in high or low inter- or intraspecific aggression levels. However, I did find a consistent positive relationship between inter- and intraspecific aggression levels across years and regions.

Intraspecific aggression

I expected to find variation in intraspecific aggression among the three regions. In argentine ants, part of the explanation for great invasion success is decreased intraspecific aggression. Despite the differences in population structures between crabs and colonial ants, in both cases the populations in the invaded ranges have lower genetic diversity than populations in the native range, most like due to a founder effect (Suarez et al. 1999, Bagley and Geller 2000). Hence, I hypothesized that green crabs were intraspecifically less aggressive on the US Pacific Coast, where the genetic diversity is lower than on the USP Atlantic Coast and the European Atlantic Coast (Bagley and Geller 2000). However, our findings were again in dissonance with our expectations.

In 2006 and 2007 USA green crabs were the least intraspecifically aggressive but in 2008 there was no significant difference in intraspecific aggression between USA and USP. Hence, there were no consistent differences in intraspecific aggression levels among regions, or across years. Due to the regional differences in intraspecific aggression in 2006 and 2007, and because green crabs from within a region, e.g. USP, are more genetically similar to each other than to green crabs from another region, e.g. USA, I hypothesized that intraspecific trials in which a green crab encountered a green crab from another region would yield higher levels of aggression than in intraspecific trials in which a green crab encountered a green crab from its own region. I found no significant patterns and intraspecific aggression levels did not change whether a green crab encountered a conspecific from its own region or a conspecific from another region. One possible explanation for no discernible variation in intraspecific aggression level in regionally mixed trials could be that I conducted these experiments in 2008, where I also found no regional effect of aggression level. Hence, there is consistency in aggression levels among the different types of experiments within one year.

One interesting observation made in the laboratory was that when kept in holding tanks or buckets, all the green crabs aggregated in one area of the tank. This behavior is very different from the behavior of grapsid and cancrid crabs which, when confined together, usually place themselves as far from other individuals as possible. This type of behavior can be an important mechanism allowing for high intraspecific densities. Overall, in some years, green crabs displayed lower intraspecific aggression levels in one of the introduced regions but this behavioral pattern was not consistent in all years and in the year with the most extensive experiments, intraspecific aggression did not vary between native and introduced ranges. From the interspecific predation trials, and intraspecific aggression trials I can reject that green crabs are consistently more or less inter- and intra-specifically aggressive in the introduced regions, both in terms of interspecific encounters with smaller and larger natives. Preisler (Chapter 2, this dissertation) likewise found that the green crab is not consistently highly abundant in the introduced ranges and the behavioral results in this study complement those abundance results. The green crab is a global invader, but does not seem to have any particular behavioral features making it particularly successful in the invaded regions and in this study I did not find support for the hypothesis that selective pressures have driven a change in interspecific or intraspecific aggression of the European green crab in the invaded regions.

Flexibility in aggressive behavior

Overall, there was high variation in both inter- and intra-specific aggression levels across years. Only, in 2006 and 2007 were USA green crabs the least aggressive. I also found that crabs which had been transported to another coast were significantly less intraspecifically aggressive that non-transported green crabs. The above results show that aggression levels are not fixed among regions or over time, but are highly variable. However, the effect of transportation did not confound the results because either conducted experiments in which crabs were reciprocally transplanted, or I investigated effects on either transported or non-transported crabs.

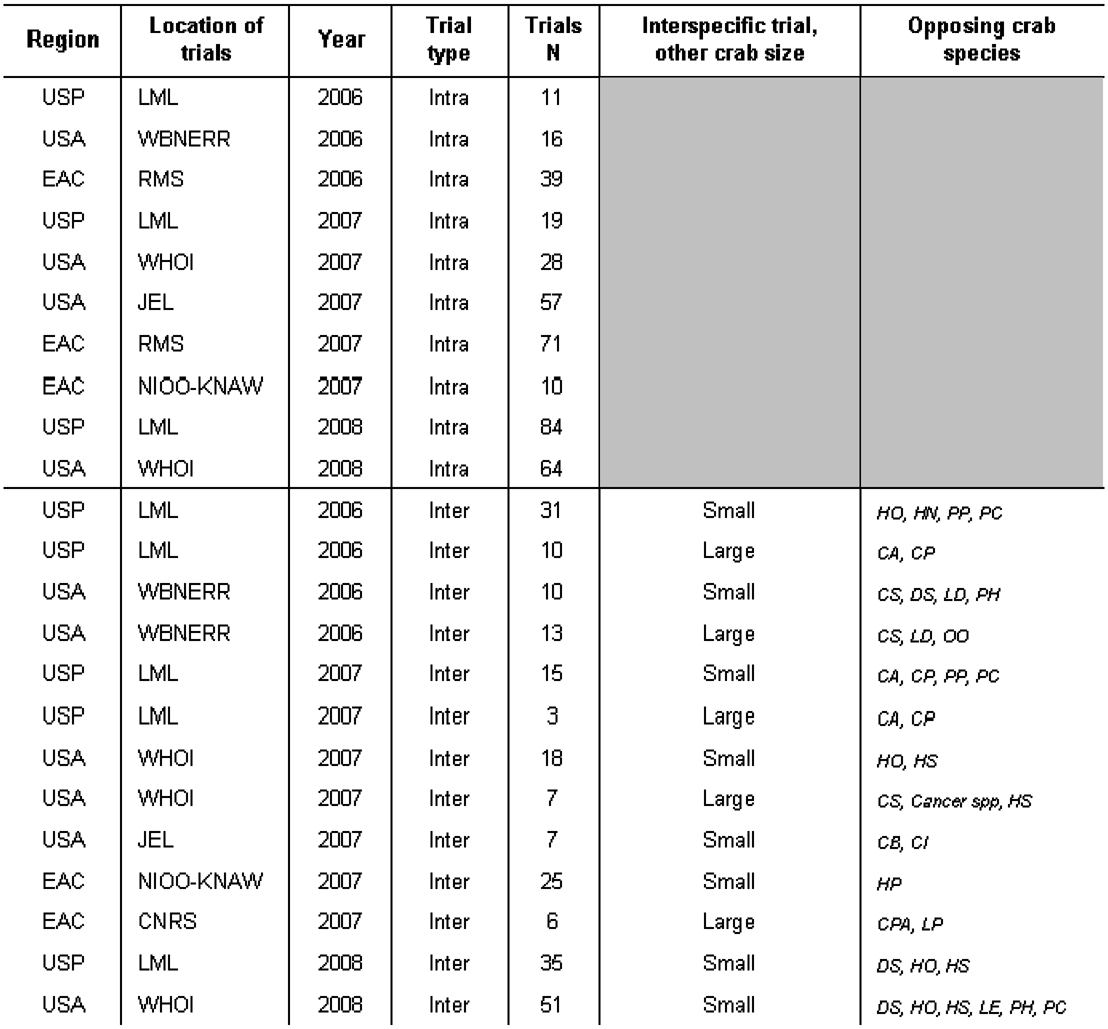
One caveat of this study is that all behavioral trials were conducted in the lab, and I have no direct evidence that the same interactions would occur if green crabs encountered con- and heterospecifics in the field. However, in other behavioral studies results in the field corroborate the results from the lab (Huntingford et al. 1995). Laboratory trials are a commonly used tool for indicating population level aggression for decapods and are usually considered reliable (Jivoff 1997, Jensen et al. 2002, Hunt and Yamada 2003, Baird et al. 2006, Fletcher and Hardege 2009). However, had I only sampled a given region in one year, for example 2006, I might have mistakenly concluded that overall, USA green crabs are less aggressive than USP green crabs, or green crabs in EAC. Since there was temporal variation in aggression levels within one region, one needs to sample all regions that are to be compared within the same year, if the goal is to make a biogeographic comparison. These results illustrate that behavior is dynamic and can respond rapidly to local conditions or experiences of individual crabs, which may vary over short time periods for instance when transported, or from year to year. Therefore, caution is needed when behavior is studied, because I found annual and regional behavioral variation. One can not assess behavior once in a region, and then assume that such behaviors may persist across years. In conclusion it is difficult to say how green crab behavior contributes to, or inhibits invasion success. Among the three regions in this study, green crab is most abundant in the native range (Chapter 2, this dissertation), but green crab is not consistently more or less aggressive in the native range. It is interesting how aggression may be adjusted in response to changing conditions, and additional experiments would be required to determine what the mechanisms for the behavioral variation are.

Potential mechanisms for behavioral variation

Genetic difference can account for behavioral differences between populations of the same species in different regions, as in the case of argentine ants (Suarez et al. 1999). However, given the short temporal scale of this study (three years) it is unlikely that an evolutionary change in green crab behavior occurred between 2007 and 2008. It is more likely that changes in environmental conditions such as water temperature, dissolved oxygen, food availability or population densities are drivers of such interannual behavioral changes. Although there are examples of size-dependent changes in interspecific crab behavior (Wasson and Lyon 2005) size in green crabs per se does not explain the interannual difference in aggression levels on the US Atlantic Coast because green crabs from 2006 and 2007 were not significantly smaller or larger than green crabs used in the trials in 2008. Carapace color in green crabs is an indicator of status in the molt cycle. Red, green crabs are closer to molting that green, green crabs. Because molt status can influence aggression levels (Kaiser et al. 1990, Reid et al. 1997) I did not use any red crabs or bright orange crabs for the laboratory trials in this study. Additionally, genetic differences could not account for the decreased aggression levels observed in crabs that had been transported to another coast. Instead, the behavioral change could have been induced by stress due to low oxygen levels during transportation, or stress due to water quality differences between the two laboratories on the US Atlantic and Pacific Coasts where the trials were conducted. The variation in aggression found in this study is intriguing and potential mechanisms driving behavioral shifts could be investigated with further experimental studies, varying environmental condition or crab condition, to determine whether behavioral plasticity represents adaptive strategies. It is important to recognize variation in behavior in terms of methodological approaches using this sort of lab assay. I found no support for the idea that the European green crab underwent strong selection for altered behavior in the introduced range. Or, if there was selection, there may not be sufficient genetic variation to produce a measurable response to selection.

The fact that green crabs do not display increased predatory ability or decreased intraspecific aggression levels in the invaded range, compared to the native range is in accordance with results from a biogeographic study of green crab invasion (Chapter 2, this dissertation) which found that the green crab is more abundant in its native range than in USP, and green crab abundance in USA is similar to that of the native range. In conclusion, the green crab has not become a very abundant invader on the US Pacific Coast and there are no consistent patterns in interspecific or intraspecific aggression level to explain why.

Table 1. Timing and location of the intra- and interspecific aggression experiments. The first three columns specify where and when the different trial types were conducted. Trial type denotes whether the trials were inter- or interspecific trials, and the next column lists the number of that trial type, at a given location, in a given year. "Other crab size" denotes whether the trials were a green crab against a small or large native crab and the last column lists the different native species of other crabs used at a given location in a given year. For species abbreviations, see Table 2.



Region	Location of trials	Year	Trial type	Trials N	Interspecific trial, other crab size	Opposing crab species
USP	LML	2006	Intra	11		
USA	WBNERR	2006	Intra	16		
EAC	RMS	2006	Intra	39		
USP	LML	2007	Intra	19		
USA	WHOI	2007	Intra	28		
USA	JEL	2007	Intra	57		
EAC	RMS	2007	Intra	71		
EAC	NIOO-KNAW	2007	Intra	10		
USP	LML	2008	Intra	84		
USA	WHOI	2008	Intra	64		
USP	LML	2006	Inter	31	Small	*HO, HN, PP, PC*
USP	LML	2006	Inter	10	Large	*CA, CP*
USA	WBNERR	2006	Inter	10	Small	*CS, DS, LD, PH*
USA	WBNERR	2006	Inter	13	Large	*CS, LD, OO*
USP	LML	2007	Inter	15	Small	*CA, CP, PP, PC*
USP	LML	2007	Inter	3	Large	*CA, CP*
USA	WHOI	2007	Inter	18	Small	*HO, HS*
USA	WHOI	2007	Inter	7	Large	*CS, Cancer spp, HS*
USA	JEL	2007	Inter	7	Small	*CB, CI*
EAC	NIOO-KNAW	2007	Inter	25	Small	*HP*
EAC	CNRS	2007	Inter	6	Large	*CPA, LP*
USP	LML	2008	Inter	35	Small	*DS, HO, HS*
USA	WHOI	2008	Inter	51	Small	*DS, HO, HS, LE, PH, PC*

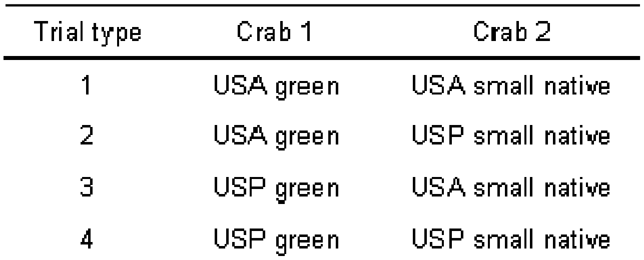
Table 2. Species' abbreviations, scientific names, and region in which they were caught in this study.

Species abbreviation	Species name	Region where species was caught
CA	*Cancer antennarius*	USP
CP	*Cancer productus*	USP
HO	*Hemigrapsus oregonensis*	USP
HN	*Hemigrapsus nudus*	USP
PC	*Pachygrapsus crassipes*	USP
PP	*Pugettia producta*	USP
CS	*Callinectes sapidus*	USA
CI	*Cancer irroratus*	USA
CB	*Cancer borealis*	USA
DS	*Dyspanopeus sayi*	USA
HS	*Hemigrapsus sanguineus*	USA
LD	*Libinia dubia*	USA
LE	*Libinia emerginata*	USA
OO	*Ovalipes ocellatus*	USA
PH	*Panopeus herbstii*	USA
CPA	*Cancer pagarus*	EAC
HP	*Hemigrapsus penicillatus*	EAC
LDP	*Liocarcinus depurator*	EAC

Table 3. Abbreviations and locations of the marine laboratories in Table 1.

Abbreviation	Laboratory/Institution/State or country
CNRS	Station de Biologique de Roscoff, Centre National de la Recherche Scientifique, France
JEL	Jackson Estuarine Laboratory, Univ. of New Hampshire, NH
LML	Long Marine Laboratory, Univ. of Cal. Santa Cruz, CA
NIOO-KNAW	Centre for Estuarine and Marine Ecology, Nederlands Instituut voor Ecologie, Yerseke, The Netherlands
RMS	Rønbjerg Marin Station, Univ. of Aarhus, Denmark
WBNERR	Waquoit Bay National Estuarine Research Reserve, MA
WHOI	Woods Hole Oceanographic Institution, MA

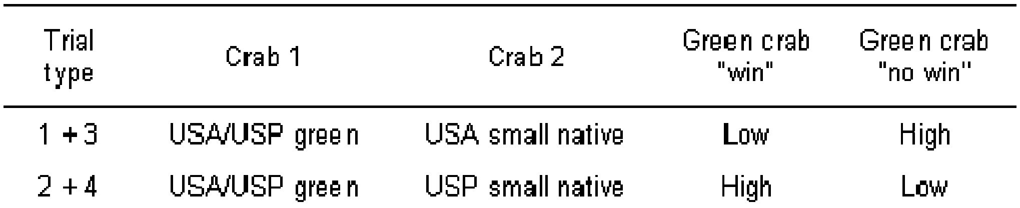
Table 4. The different trial types used to test whether USA small native crabs were green crab resistant or whether USA green crabs were less aggressive than USP green crabs.



Trial type	Crab 1	Crab 2
1	USA green	USA small native
2	USA green	USP small native
3	USP green	USA small native
4	USP green	USP small native

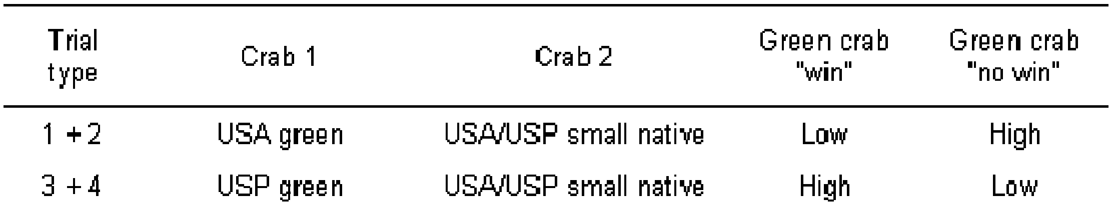
Table 5. A) Trial type combination required to test whether USA small native crabs were more resistant to green crabs than USP small native crabs. The last two columns describe the expected frequency of outcomes of trials if USA small native crabs are more resistant to green crabs than small USP native crabs. B) Trial type combination required to test whether USA green crabs are less interspecifically aggressive than USP green crabs, when encountering a small native crab from either coast. The last two columns describe the expected frequency of outcomes of trials if USA green crabs were less aggressive than USP green crabs.

A



Trial type	Crab 1	Crab 2	Green crab "win"	Green crab "no win"
1 + 3	USA/USP green	USA small native	Low	High
2 + 4	USA/USP green	USP small native	High	Low

B

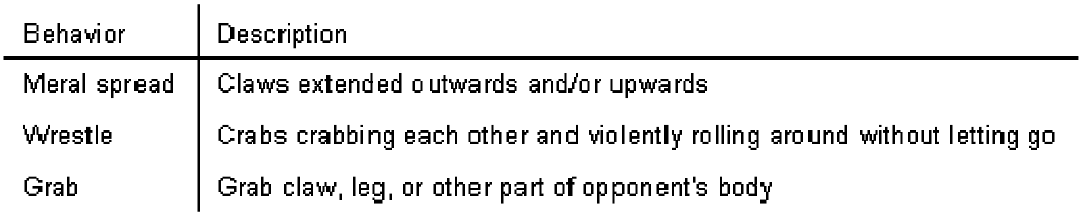


Trial type	Crab 1	Crab 2	Green crab "win"	Green crab "no win"
1 + 2	USA green	USA/USP small native	Low	High
3 + 4	USP green	USA/USP small native	High	Low

Table 6. Experimental design of intraspecific aggression trials designed to test if green crab aggression varied as a function of which region the opponent crab was from. Trial type 1-3 was a reciprocal transplant to test if interregional trials yielded different aggression levels in green crabs, than trials in which the green crab encountered a green crab from its own region. Trial type 4-6 was used to test interregional variation in aggression in trials in which all crabs had been transported.

Trial type	Green crab 1	Green crab 2	Experimental location
1	USA	USA	WHOI and **L**ML
2	USA	USP	WHOI and **L**ML
3	USP	USP	WHOI and **L**ML
4	USA	USA	LML
5	USA	EAC	LML
6	EAC	EAC	LML

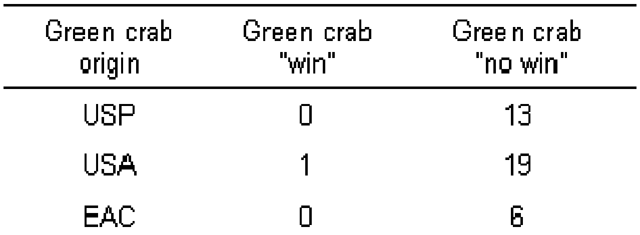
Table 7. Behaviors quantified in the intraspecific aggression trials. Behaviors are adapted from Baird et al. (2006).



Behavior	Description
Meral spread	Claws extended outwards and/or upwards
Wrestle	Crabs crabbing each other and violently rolling around without letting go
Grab	Grab claw, leg, or other part of opponent's body

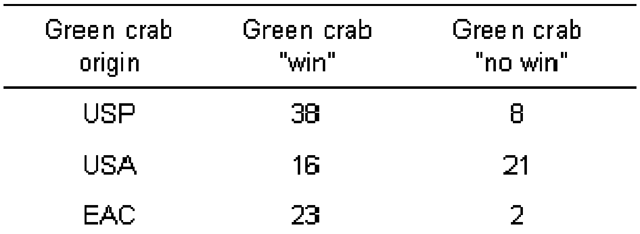
Table 8. Outcome of interspecific trials, green crab vs. small and large native crabs in 2006-2008. A) Frequency of outcomes of trials of green crab vs. large native crabs in 2006-2007. In all trials but one, both crabs were unharmed. B) Frequency of outcomes of trials of green crab vs. small native crab in 2006-2007. Green crabs in USA were the least interspecifically aggressive. C) Frequency of outcomes of trials of green crab vs. small native crab in 2008. Green crabs were approximately equally aggressive in USA and USP.

A



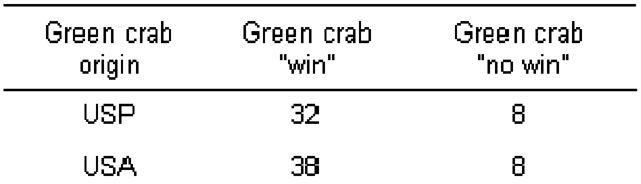
Green crab origin	Green crab "win"	Green crab "no win"
USP	0	13
USA	1	19
EAC	0	6

B



Green crab origin	Green crab "win"	Green crab "no win"
USP	38	8
USA	16	21
EAC	23	2

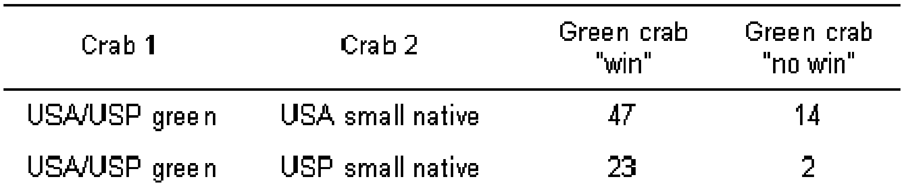
C



Green crab origin	Green crab "win"	Green crab "no win"
USP	32	8
USA	38	8

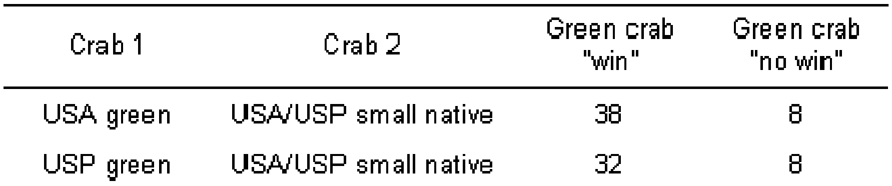
Table 9. A) USA small native crabs were not particularly green crab resistant and B) USA green crabs were not less aggressive than USP green crabs in 2008.

A



Crab **1**	Crab 2	Green crab "win"	Green crab "no win"
USA/USP green	USA small native	47	14
USA/USP green	USP small native	23	2

B



Crab 1	Crab 2	Green crab "win"	Green crab "no win"
USA green	USA/USP small native	38	8
USP green	USA/USP small native	32	8

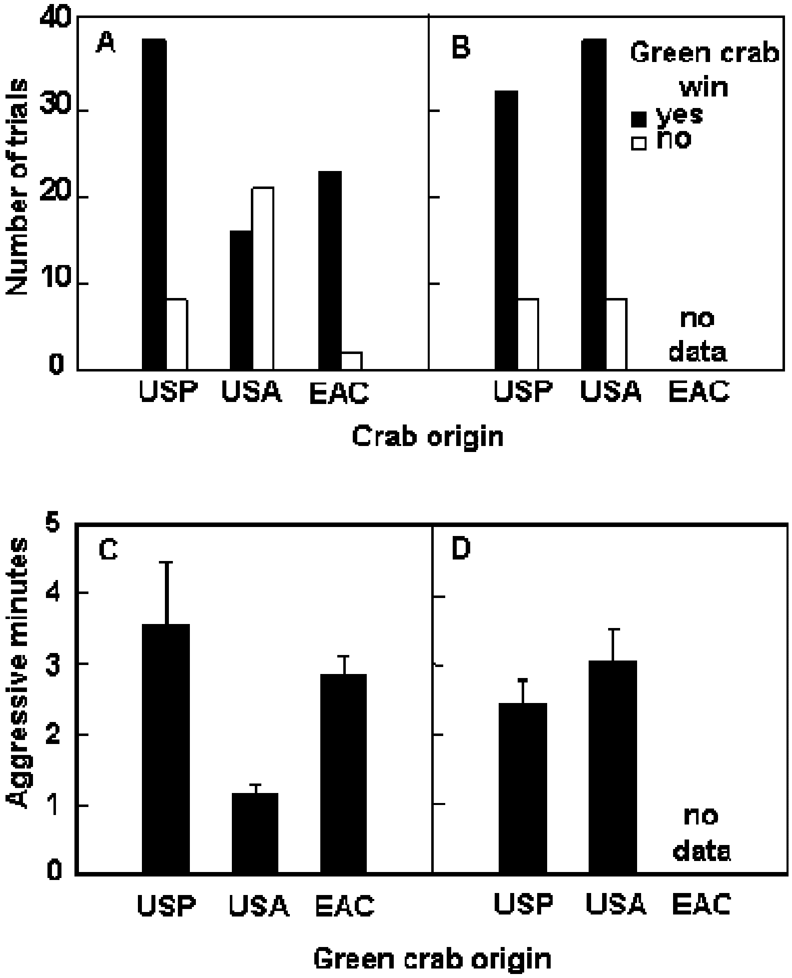


Figure 1. Temporal and spatial variation in interspecific predation and intraspecific aggression in 2006-2008. A) Green crab vs. small native crab in 2006-2007. Green crabs were interspecifically least aggressive in USA. B) Green crab vs. small native crab in 2008. Green crabs were approximately equally aggressive in USP and USA. C) Intraspecific aggression in green crabs encountering a green crab from their own coast in 2006-2007. Green crabs were least aggressive in USA. C) Intraspecific aggression in green crabs encountering a green crab from their own coast in 2008. Green crabs were approximately equally aggressive in USP and USA. There is a positive relationship between inter- and intraspecific aggression levels within a region within a given year. Green crabs that are less interspecifically aggressive (A) are also less intraspecifically aggressive (C).

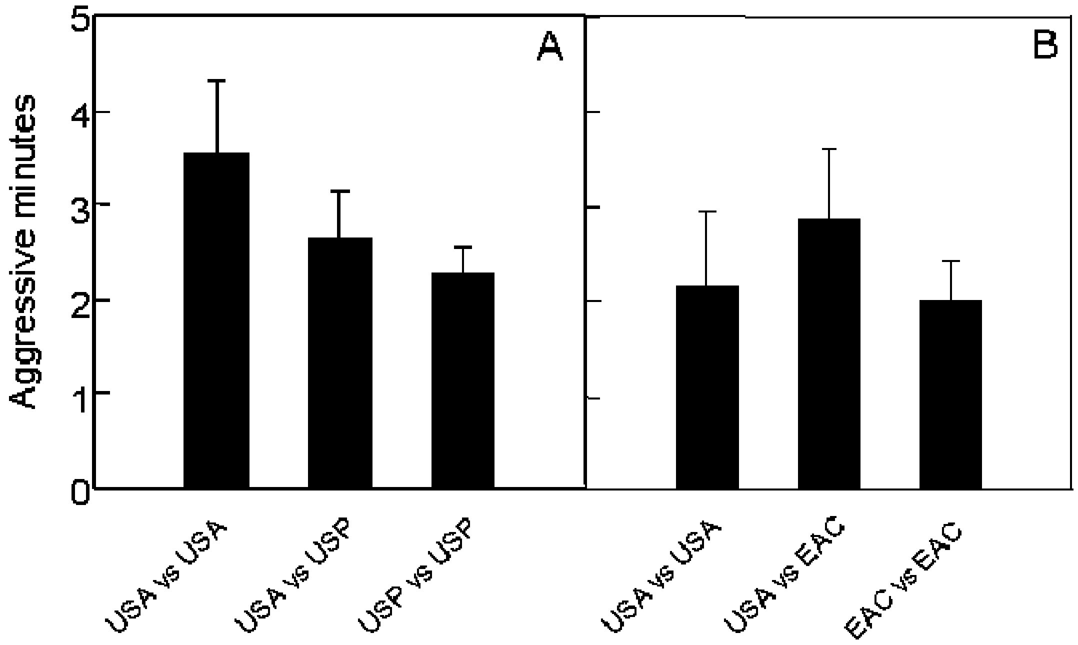


Figure 2. Aggression levels in intraspecific trials in 2008. A) Aggression did not vary whether a green crab encountered a green crab from its own or another coast. B) Aggression levels did not vary whether a green crab from Europe encountered a green crab from its own or any other coast.

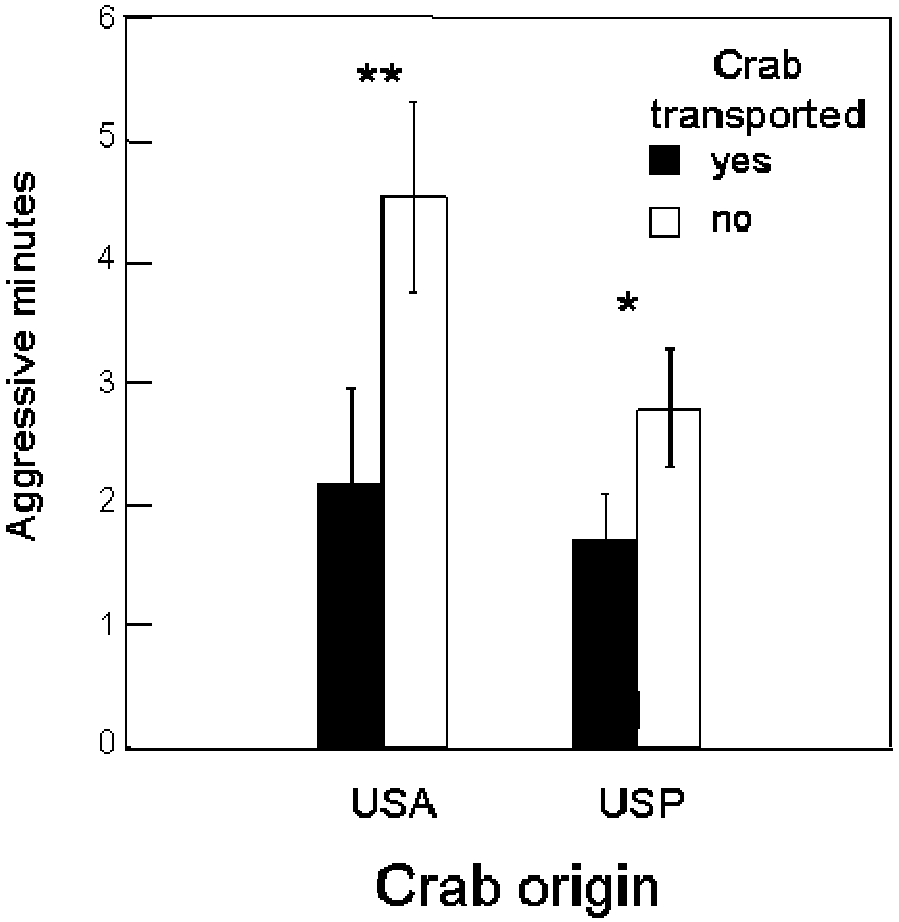


Figure 3. Effect of transportation on green crab intraspecific aggression level in 2008. USA green crabs that had been transported to a different coast were significantly less aggressive in intraspecific trials than green crabs that had not been shipped and USP transported green crabs were marginally significantly less aggressive than non-transported USP green crabs.

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CONCLUSION

This dissertation illustrates two main points. First, long-term monitoring data can be used to evaluate dynamics of a local invasion with respect to temporal and spatial variation and with respect to interactions between native and non-native species. Consequently, it is necessary to carefully consider how to manage for non-native species whose populations are highly variable. It is not uniformly clear when and where potential eradication efforts should be focused, and each invaded area should be evaluated on an individual basis when determining management action. Second, assessment of biogeographic variation in an introduced species may change one's perception of a local invasion. In this study I show how the often untested assumption that invaders are highly successful in the introduced range may not always hold, depending on how invasion success is quantified. However, a non-native species currently found at very low abundance may still be detrimental to, or have a substantially negative effect on a native community. The point is simply that when considering a local invasion from a global perspective, one's evaluation of the severity or trajectory of a local invasion may change. This study provides a valuable framework in which we can study species' invasions, or simply the population characteristics of non-native species at a local level and global level.

Because of support in the plant literature and terrestrial invertebrates for hypotheses such as the enemy release hypothesis, empty niches hypothesis, and decreased aggression levels in the invader, we often automatically assume that introduced species are particularly successful in their introduced ranges. However, studies rarely quantify and compare abundances or niche breadth in the native and introduced ranges to test the assumption that the invader is successful (Hierro et al. 2005). In marine ecosystems, studies of the same species in the native and introduced ranges are particularly rare. When I conducted this study and quantified and compared a marine invertebrate in its native and introduced ranges I found that the assumption of the introduced species being more abundant in the introduced range was not met. However, support for the enemy release hypothesis in the green crab was found by Torchin et al. (2003). Green crabs in the introduced ranges had fewer parasites, and thus attain a larger body size (Grosholz and Ruiz 2003). However, this larger body size did not seem to translate into higher overall abundance. Green crab abundance in the most recently invaded range, the US Pacific Coast, was very low compared to abundance in the native range even if we considered the years on the US Pacific coast where green crab abundance peaked. Instead, I found that generalist predators encountered in the introduced range, such as large rock crabs seem to pose more of a challenge to the success of the European green crab as evidenced by finding higher relative abundance of large crabs on the US Pacific Coast than in the other surveyed regions. A similar pattern was found by deRivera et al. (2005) on the US Atlantic coast where the blue crab *Callinectes sapidus* seems to limit the southern distribution limit of green crab. The long-term monitoring data indicated that recruitment limitation did seem to play a role in low green crab abundance in some years as well. Studies of invasive species' traits have found that lower intraspecific aggression in the invader can contribute to invasion success (Suarez et al. 1999). This yields the prediction of low green crab density and correspondingly lower intraspecific aggression in the introduced range. I did not find support for such predictions in this study. Green crab density was lower on the US Pacific coast; however, I found no consistent evidence for lower intraspecific aggression in this region.

This research highlights a few important points to consider when studying and managing species invasions. First, the challenge of studying this species at the local level is not to accurately predict the outcome of the invasion, but to manage a species in which population dynamics are currently highly variable and most likely will continue to be so in the future. Second, I found that in this marine invader, niche breadth is more limited in the most recently introduced range. On the US Pacific coast, the green crab is limited to estuaries, while on the two Atlantic coast, the green crab is found in open coast habitat as well as in estuaries. Open coast habitat on the US Pacific coast seems to present a novel challenge to the green crab that has yet to be overcome. Perhaps part of this challenge is constituted by the presence of large predatory crab species such as various rock crab species, or the absence of the green crab could be related to high wave action on the open coast (Hampton and Griffiths 2007).

In conclusion, the implications of this study for invasive species management and for general ecology are very different. Current management action for this species is based on the fact that this species has spread to six of the seven continents despite only being native to Europe. Green crab on the US Pacific coast has had documented species level and community level effects on native species despite the abundance of green crab being lower in the introduced than in the native range. From an ecological perspective, the perceived invasion success of the European green crab is in reality highly variable among locations and among years. This illustrates the importance of at least attempting to quantify and compare invasions across regions before determining what factors might limit or facilitate invader success. It seems, at least in a very recently invaded range that there are more novel challenges than opportunities for this species. Even in the range invaded more than two centuries ago, where recruitment limitation is no longer an issue, the invader is not more abundant than in its native range. Hence, for this species it may be the case that there is no place like home.

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