Monitoring and Managing the Spread of Marine Introduced Species:

Development of Approaches and Application to the European Green Crab (*Carcinus maenas*) and the Asian Shore Crab (*Hemigrapsus sanguineus*)

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October 2009

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Doctor of Philosophy in Biology

Table of Contents

List of Tables

List of Figures

Preface

Thesis Format and Style

This thesis is in a manuscript-based format and consists of a set of four papers that make a cohesive whole. In the first two chapters, I increase sampling intensity, refine sampling approaches, and collect data on *C. maenas* and *H. sanguineus* on a regional-scale. In the last two chapters I use the monitoring network and data generated from the first two chapters to document patterns of abundance, distribution, injury, and recruitment of the two invasive species. Then to show how these data are useful not only to managers but also academic studies, I include as appendices a publication in Ecology, which used my 2006 survey data.

Chapter 1: Delaney DG, Sperling CD, Adams C and Leung B (2008) Marine invasive species: validation of citizen science and implications for national monitoring networks. Biological Invasions 10: 117-128.

Chapter 2: Delaney DG and Leung B (In press) An empirical probability model of detecting species at low densities. Ecological Applications.

Chapter 3: Delaney DG, Edwards PK and Leung B (In preparation) Predicting regional spread of invasive species using oceanographic models – validation and identification of gaps.

Chapter 4: Delaney DG, Griffen BD and Leung B (Submitted) Injury as a Moderator of Impacts of Invasive Species.

Appendices A-C: Griffen BD and Delaney DG (2007) Species invasion shifts the importance of predator dependence. Ecology 88: 3012-3021.

Contributions of Co-Authors

Each of the four manuscripts was prepared for publications in peer-reviewed journals focusing on monitoring and/or modeling regional patterns of marine invasive species. To work on a regional-scale, I recruited and trained thousands of people who were participants in the experiments and/or monitored one of my field sites in the large-scale surveys that I coordinated and/or led. Although my work is highly collaborative, I was the primary person who determined the focus of the research, conceived, developed the experimental designs, conducted the experiments, collected the data, analyzed the results, executed the statistical analyses, and created the figures, unless noted below.

Chapter 1: C. Sperling was my field assistant who helped data collection, entry, and offered comments on the manuscript. C. Adams maintained a website for my data on the Massachusetts Institute of Technology Sea Grant's Center for Coastal Resources web page, created the final figures, and offered comments on the manuscript. B. Leung provided comments on the manuscript and the statistical analysis.

Chapter 2: B. Leung played a similar role as in Chapter 1.

Chapter 3: We obtained a model from the Fisheries and Oceans Canada's website and P. Edwards adapted the model and tested if it could predict the drift card and recruitment data that I collected. Both P. Edwards and B. Leung offered comments on the manuscript. P. Edwards produced Figures 3.3, 3.6, and 3.7 and I produced the rest of the figures in this chapter.

Chapter 4: B. Griffen collected field data at one of the 30 field sites and conducted the aggression and feeding experiments. I collected the density and injury data at the other 29 sites. B. Griffen created Figures 4.3 and 4.4 and I produced the rest of the figures in this chapter. Both B. Griffen and B. Leung offered comments on the manuscript and assisted me in executing the statistical analyses.

Original Contributions to Knowledge

Chapter 1

Citizen science (i.e., incorporating volunteers) has been suggested as a solution to monitoring large-scale environmental issues with real-world limitations (e.g., personnel) but validation studies to verify the abilities of citizen scientists are rare, limited in scale and/or poorly designed. Given the lack of validation studies, the data generated by volunteers are rarely published in peer-reviewed journals or considered in management decisions. Some of the cases where the data collected by volunteers have been published in peer-reviewed journals are cited in Chapter 1 and other publications assisted by non-profit organizations such as the Reef Environmental Education Foundation and Reef Check. My study is one of the few peer-reviewed publications that investigated the accuracy of citizen science data (Delaney et al. 2008). Also this study is one of the largest validation studies of citizen science to date, not only validating the abilities of the vast majority of the almost 1,000 participants but also setting quantitative eligibility criteria for volunteers. These criteria will allow accurate monitoring to be conducted in the future and for peer-reviewed publications. The approach developed in this chapter is generalizable to validating the abilities of volunteers in any system or for any species. The survey portion of the study collected data on the densities of native and invasive species in seven northeast states of the USA, which is a scale rarely examined with such sampling intensity. This survey recorded a range expansion of *H. sanguineus*. The most northeastern observation is now a gravid female specimen on Schoodic Peninsula, Maine.

Chapter 2

Quantifying an unbiased estimate of the actual probability of detection is a problem that has challenged ecologists for decades (Geissler and Fuller 1987; MacKenzie 2005; Harvey et al. 2009). While many approaches have been created, my approach is far simpler to execute, requires limited and rudimentary equipment, and is better able to quantify the probability of detection and false negatives. Most researchers and managers assume that the rate of false negatives is negligible for presence-absence survey data even though the probability of not detecting a target if present has been recorded to be as high as 87% (Wintle et al. 2005). In my study, I found the probability of a false negative occurring at a site can be even higher (i.e., 94%). Therefore, researchers examine their data, creating, and analyzing patterns that might be inherently flawed. However, by using my approach to quantify the uncertainty, researchers and managers would be able to incorporate the uncertainty of sampling into models and to quantitatively assess the reliability of the data. For monitoring, the empirical probability model can determine the feasibility of a certain survey or monitoring objective and better interpret the generated data. The manipulative field approach offers managers and researchers a way to refine sampling techniques by comparing alternative techniques in a standardized and quantitative manner. Further, the probabilistic model created from the manipulative field experiments can quantify the amount of personnel needed for large-scale monitoring (e.g., a state, province or country) of invasive species, which allows a quantitative answer to whether monitoring is feasible. Also this field-based approach can quantify an unbiased estimate of the probability of detection or non-detection.

Chapter 3

While ocean currents are critically important for secondary spread of marine invasive species, the ability to use existing oceanographic models to predict larval spread is usually assumed and not validated. This is a challenging problem because physical oceanographic models often do not incorporate biology, and large-scale standardized datasets to validate such models are rare or non-existent. In this study we adapted and improved a physical oceanographic model, incorporated biological behaviors, and then used extensive, large-scale, standardized field data to parameterize and validate the model’s ability to forecast the spread of species.

Density data of adult populations of the two introduced species (Chapters 1 and 2) were collected to estimate sources of larval production. This was coupled with a recruitment study and the first ever drift card study in the Gulf of Maine to allow us to predict spread. It is also one of the few field investigations of recruitment of *H. sanguineus* and again the largest to date. This two-step method of drift card and recruitment studies served to assess the ability of an oceanographic model to accurately forecast the potential spread of intertidal species and to identify research needed to improve these forecasts.

Chapter 4

Predicting the impacts of an invasive species solely by its abundance is common, yet it ignores other potentially important moderating factors. Therefore, to better predict the impact of invasive species we need to examine both abundance and moderating factors. This is the first study to demonstrate how injury may significantly moderate impacts of invasive species. Injury is a novel and understudied predictor of impact. This is one of the few studies to quantify the frequency of injury of invasive species in their non-native ranges. Also it uses manipulative and observational experiments conducted in the field and laboratory to identify a possible causal mechanism and predictors of injury in nature on a regional-scale. It is one of the few studies documenting moderators of invasive species’ impacts. It is only the second study on injury of *H. sanguineus* in its introduced range and it includes over an order of magnitude more data than the only

other study (Davis et al. 2005). This is one of the largest scale studies to date on rates of limb loss of invasive species. This study increases both the magnitude and geographic coverage of crab injury data, allowing the examination of patterns of injury on a regional-scale. In 2006 I collected injury data in a standardized manner at 30 sites along the coast of New England and New York. Also in the more controlled laboratory environment we showed that the amount of time spent in aggression is related to the size of the crabs. Also I examined patterns of injury in nature on a regional-scale and documented that injury is size-dependent and has the potential to reduce economic and ecological impacts of invasive species. Based on the lines of evidence in this study, I proposed a novel mechanism for explaining the relationship of injury and size and argue that injury should be considered in predicting impacts of invasive species.

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Thesis Abstract

Managing introduced species, a current environmental problem, is hindered by real-world limitations of personnel, data, and funding. Monitoring is an important precursor to effective management because detecting an introduced species when its population is localized and at low density (i.e., early detection) maximizes the probability of successful eradication. Often introduced species are only detected years after the initial introduction, when eradication is no longer a viable option. Therefore, in this thesis we developed and analyzed techniques to better monitor and model the spread of the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*). To overcome issues of insufficient amounts of data and personnel, we recruited nearly a thousand volunteers and validated their ability to identify introduced and native species of crabs with high levels of accuracy (Chapter 1). To increase the probability of early detection, we need to not only increase sampling intensity, but also to identify more effective and efficient sampling techniques. Therefore, we developed a quantitative, standardized experimental field approach for comparing the sensitivity of different sampling techniques for detecting organisms at low densities (Chapter 2). Even with an efficient sampling technique and increased resources of a validated volunteer monitoring network, we are still not adequately equipped for early detection monitoring on the large-scale. Since it is infeasible to monitor everywhere a species could be introduced, we should monitor where they are more likely to arrive and manage them where their impact will be greatest. To address this problem we modified an

oceanographic model, incorporated biological behaviors, used extensive field data to parameterize and validate the model’s ability to forecast areas that are most likely to be colonized, so we can optimally allocate our limited resources (Chapter 3). Finally, to determine what areas will be most impacted, we quantified the population densities of these two invasive species and their incidences of injury, which is mainly due to inter- and intraspecific aggression. We propose that injury is an important, but understudied, moderating factor of the impacts of invasive species (Chapter 4). This research increases our ability to monitor and manage the spread of introduced species.

Résumé

La gestion des espèces introduites est un problème environnemental pressant qui est souvent entravé par des limites de personnel, de données et de financement. La surveillance est un prérequis important afin de gérer les espèces introduites de façon efficace puisque la détection hâtive de ces espèces, lorsqu'elles sont peu dispersées et à faible densité, maximise la probabilité de les éradiquer. Il arrive souvent que les espèces introduites soient détectées plusieurs années après leur établissement, lorsqu'il n'est plus possible de les éradiquer. L'un des objectifs de cette thèse est donc de développer et d'évaluer des méthodes servant à détecter et à modéliser la propagation de deux espèces invasives: le crabe vert européen (*Carcinus maenas*) et le crabe asiatique (*Hemigrapsus sanguineus*). Pour surmonter des difficultés courantes liées à un manque de données et de personnel, nous avons recruté mille volontaires et nous avons validé leur aptitude à identifier de façon précise des espèces de crabes natives et introduites (Chapitre 1). Afin d'augmenter la probabilité de détection hâtive, il n'est pas seulement nécessaire d'augmenter la fréquence d'échantillonnage, mais aussi de déterminer quelles sont les techniques d'échantillonnage les plus efficaces. Par conséquent, nous avons développé une méthode expérimentale quantitative et standardisée servant à comparer la sensibilité de différentes techniques d'échantillonnage pour détecter des organismes présents en faible densité sur le terrain (Chapitre 2). Même avec des techniques d'échantillonnage efficaces et un système de surveillance reposant sur des volontaires formés à l'avance, il est très difficile de surveiller des aires à très grande échelle et de permettre la détection hâtive. Étant

donné ces difficultés, il est nécessaire de surveiller les endroits les plus susceptibles d'être envahis et les plus vulnérables aux impacts des espèces invasives. Afin de tenter de résoudre ce problème, nous avons modifié un modèle océanographique en y incorporant des comportements biologiques et en utilisant de nombreuses données de terrain afin de prédire quels seront endroits seront les plus vulnérables d'être envahis et de pouvoir y allouer les ressources disponibles. Finalement, pour déterminer quels endroits seront les plus affectés, nous avons quantifié la densité des populations de *C. maenas* et de *H. sanguineus* et la fréquence de leurs blessures dues à des agressions inter- et intraspécifiques. Nous suggérons que le taux de blessures est un facteur très important, mais sous étudié, pouvant modérer l'impact des espèces invasives (Chapitre 4). Cette recherche permettra d'améliorer notre habileté à surveiller et à modéliser la propagation des espèces introduites en milieu marin.

Acknowledgements

I want to thank the people who have volunteered time to help my research or support me in any way. In the last five years, thousands and thousands of people have participated in my research. Therefore this is too many to name individually but please know that I am eternally indebted for your contribution. I will first thank my funding sources and then thank my family and colleagues.

I would like to first thank NOAA's National Sea Grant Aquatic Invasive Species Research and Outreach Program Grant (NA05OAR4171088) for financially supporting my research. I was also partially supported by the University of Maine's Addison E. Verrill Award. The last year of my research was funded by the Canadian Aquatic Invasive Species Network (CAISN). Also Dr. Judy Pederson and Massachusetts Institute of Technology Sea Grant's Center for Coastal Resources provided countless materials to train volunteers and a web page to disseminate the results.

Most importantly, I want to thank my family. My mother and father inspired me to study science and have been there to help me achieve my goals and dreams. My mother fostered my interest in the ocean by bringing me to the beaches of Massachusetts where I witnessed a stranding of pilot whales along the coast of Cape Cod, and also driving me to classes to obtain my open water diving certification when I was only 12 years old. My father helped foster and hone my scientific abilities and critical thinking skills through support in science fairs and discussing my work. Also thanks to my brother, Chris, who taught me to follow my own path, choose something that is important to me, and whatever I do, give it my all. I have had so much support

from family and friends and I can never thank you enough. I could not have done this without any of you.

Over the years, my volunteers have not only become my colleagues but my friends and I owe the success of my research to them. My monitoring network was successful due to the interest and generosity of countless people, groups and organizations. The following are examples of the thousands of people that were instrumental to my monitoring network and corresponding validation study due to their logistical support, efforts in monitoring, and/or recruiting others to participate. To Tana Glennon-Annoub and her amazing class of the Harbor School, who were my first participants, you went through the rain to do it and really set the tone for others and the monitoring program as a whole! Thanks to Heather Spence who was always generous with her time to read my manuscripts and offer helpful comments. I also want to thank Kelly Fellner, Carl Johnson, Mary Raczko, Dawn Tesorero, Marc Albert, and Captain David Weinstein of Harbor Connections of Boston Harbor Islands National Park. This group organized 250 students in 2005, then the following year, 900 students and by the summer of 2007 the total number reached was greater than 2,000 elementary and middle school students participating in my field work in the Boston Harbor Islands. The experiments and the amount of supervision that I could offer changed but your amazing dedication and talent as leaders and educators never did. I can not thank you enough for helping my outreach program and more importantly your overall environmental message. On that note, I want to give another special thanks to Barbara Warren.

Other people who played important role in my research and citizen science monitoring network include, but are not limited to following people: Zachary Itzkowitz, who volunteered to join my research team and found the specimen of *H. sanguineus* that documented a range expansion. Also I want to thank: Mimi Fong, Donna Cataldo and her 5th grade class from Josiah Quincy Elementary School, John Clancey and Steve Ayer's class from the John Winthrop Elementary School, Kevin Robin from Odyssey High School, Andy Hayes and Crystal Hill from Mary E. Curley Middle School, Carla Veiga and Bob Ettinger's great classes from William McCormack Middle School, Chris Burdman from Mildred Middle School, and Jennifer Felicetti from Boston Public. The New England Aquarium and their amazing staff: Joel Rubin, Sukey Padawer, Dara Wald, Jon Anderson, Jayshree Oberoi, Maria Elena Derrien, Heather Deschenes, Jo Blasi, Dave Wedge, Matt Tweedie, Julia Hammer, Damon Jones, and Dana Crosby. Also I want to thank Julie P. Ainsworth and Maryellen’s Environmental Club of Mystic Aquarium Institute for Exploration, Ailene Rogers, Jacky Farrell, Stacy L. Myers, Mary Morgan, Amity Bentliff, Libby Koch, David Bender, Melissa Griffiths, Katie Granberg, and the great staff of Cornell Cooperative Extension of Suffolk County, Brian Conroy and Deborah Munson of TERC, National Parks Service, Jim McKenna of Schoodic Education and Research Center, David Manski of Acadia National Park. Linda Schier, Joyce Voorhis and the whole Department of Science at Brockton High School, Rob Gough and his amazing artwork, Dr. George Kraemer, Mary Grady from Rhode Island College, Lisa Cody, Helen Dole, Sara Grady and the North South Estuary Program, Linda Healy and Tim Miller from University’s Darling Marine Center, Sue Richman from South Portland High School, Maine, Dora Borlaz and her great science club, Polly Wilson from Portland High School, Ross Henderson's Science Class of Noble and Greenough of Dedham, MA, Linda Hurt, Barbara Carvalho and her amazing class of second graders from Kingston Elementary School, Sara Sweetman, Phil Capaldi and his great 4th grade class from the Melrose School of Jamestown, RI, and Mora Capaldi for the great hospitality and amazing cooking, Abe and Robert Checkoway, Susan Haverstick and Dan Hinnencamp's Science club from Natick, MA, Rich Squillante and Michelle Woods-Robinson classes of Perry School of South Boston, the New York Biology Teacher Association, Jodie York and her great camp staff of Mystic Aquarium Institute for Exploration, Kathy Fisher and her 7th grade class from Rhode Island, Susan Hayhurst, Robert Rocha, Connie Bebis and her class from the Apponequet High School, Chris Pires and his students from New Bedford Vocational-Technical school, Dr. David Welty and students from Fairhaven High School. Elizabeth Stephenson, Esperanza Stancioff and Tracy Hart of Maine Sea Grant Extension, Dr. David Guay, Anne Henshaw, Rose Teng, Dr. Marney Pratt and everyone who planned and/or took part in Bowdoin’s Coastal Science Institute teacher training course, Renee Foreman, Jeff Wilford of York Middle School in Maine, the whole Zaffin Family, and Sam Wilson. Also I would like to thank Nadia Caines of the Massachusetts Water Resource Authority. Daniel Knapp of World Turtle Productions and Armen Varadian for helping to film and produce an educational video to raise awareness of marine invasive species.

Also my research was made possible by the help of my field assistants: Amber Irwin, Kanako Hasegawa, Corinne Sperling, Sylvie Trottier and the personnel of Salem Sound Coastwatch. I would like to thank my committee members of Drs. Brian Leung, Anthony Ricciardi, and Raja Sengupta for advice and insight. Additionally, I want to thank Drs. Gregor Fussmann, Andy Gonzalez, and the Fly Genome Center for lab and office space during parts of my graduate studies. Finally, I would like to thank my lab mates, Catherine Brisson, Corey Chivers, Paul Edwards, Erin Gertzen, Stefanie Kulhanek, Ayaz Hyder, and Dominique Roche, for watching my presentations, reading my manuscripts, always stimulating conversations, and keeping me smiling through many long days of work. I want to thank Dom for translating my work into French. Also I would like to thank George Costanza for inspiring me to a career in marine biology.

For the drift card study, I want to thank volunteers who deployed drift cards at any time of day and night, even at 1:30 and 2:30 AM on a week night. These dedicated individuals, which include scientists, lobstermen, campground owners, and teachers, are Lucas Chioffi, Joan Delaney, Mike Delaney, Kristen LaChance, Sophia Fotopoulos, Steve Engstrom, Sara P. Grady, Thomas Kelly, Scott Large, Cathy Nowacki, Denny O'Brien, Clayton L. Philbrook, the staff of Searsport Shores Campground, Michele Wensman, and Brian Tarbox. For the recruitment study, the deployment and collection activities were assisted by Cliff Spital, Sara Grady, and Barbara Warren. Amber Irwin and Kanako Hasegawa assisted me in processing the samples.

To those I did not mention but volunteered their time to monitor the intertidal, you are the unsung heroes and the reason why citizen science works and are truly my role models. For this reason, this thesis is dedicated to you.

General Introduction

Bioinvasion is a form of global change that is homogenizing the biota of terrestrial and aquatic environments (Carlton 2001; Rahel 2002; Ricciardi 2007). Marine environments are no exception, as they are heavily invaded, and all the world's oceans have been colonized by introduced species (Cohen and Carlton 1998; Ruiz et al. 2000, Carlton and Cohen 2003, Tavares and De Melo 2004). Despite its importance, marine invasion biology lags behind its counterparts in terrestrial and freshwater ecosystems, and arguably, only started as a formal field of science in the 1970s (Carlton 1979). Progress in this field, as with many disciplines in ecology, has been hindered by real-world limitations, especially insufficient resources (e.g., funding, personnel and equipment to extensively monitor vast areas), which leads to the second problem, sparse data (i.e., data do not exist or contain extensive gaps in its spatial and/or temporal records) (Bax et al. 2001; Leung and Delaney 2006; Lodge et al. 2006). These issues are not ephemeral, and invasion biologists need to address them to achieve a central objective—more effective monitoring and management of invasive species to avoid significant economic, ecological and/or human-health consequences (Parker et al. 1999; Pimentel et al. 2000; Carlton 2001; Pimentel et al. 2005).

My thesis examines questions of how to detect the early stages of an invasion, when the population of an invader is localized, at low density, and eradication is still feasible (Rejmanek and Pitcairn 2002) and make monitoring feasible even given real-world limitations, such as limited resources. To examine these questions, I use two established invaders, which allows for experimentation that is not possible with newly arriving introduced species or invaders that are not currently present (e.g., the brush-clawed crabs, *Hemigrapsus takanoi* and *H. penicillatus* and the Chinese mitten crab, *Eriocheir sinensis*). I develop and analyze techniques for these species that allow us to improve early detection of these species as they spread to new regions or for future introduced species. First, there is the need to overcome issues of sparse data by increasing personnel to more thoroughly monitor large areas. Volunteer-based monitoring is a potential solution to this problem (Bonney 1991; Boudreau and Yan 2004), but needs to be validated before academics and resource managers can utilize citizen science data (Chapter 1). For early detection to be more effective, invasion biologists need to quantify the probability of detection and refine sampling techniques for monitoring organisms at low densities (Chapter 2). Also, to effectively and feasibly monitor large areas, we need to better predict spread, so areas at greatest risk of invasion can be identified, allowing managers to optimally allocate their limited resources for monitoring (Chapter 3) and management efforts (Chapter 4). By identifying where marine invasive species are most likely to colonize and cause the greatest impact, invasion biologists can optimally allocate monitoring and management resources to address a growing environmental problem within real-world limitations.

In Chapter 1 I investigated what controls accuracy of monitoring native and invasive species of crabs and create a regional, standardized database for this information. Comprehensive databases of spatial and temporal information for large geographic ranges of native and invasive species are integral to testing scientific hypotheses and validating predictive spread models (Ricciardi et al. 2000). Currently, most databases are disjunct, disparate, and include distributions that are incomplete and often extremely out-dated. Intense monitoring could aid in building comprehensive and up-to-date databases, but such efforts rarely occur due to insufficient personnel. I believe that volunteer-based monitoring is a potential solution to monitor marine invaders, as it has been used successfully in other systems, and could supplement scarce resources (Bonney 1991; Greenwood 1994, 2003; Bray and Schramm 2001; Boudreau and Yan 2004). However, the accuracy of volunteers needs to be assessed before it can be used in academic research.

Hypotheses:

1. If age, education, size of the group, or size of the crabs helps volunteers collect accurate data on crab species, then these factors will be positively correlated with the accuracy of volunteer-based data on the species of a crab.
2. If age, education, size of the group, or size of the crabs helps volunteers collect accurate data on sex of a crab, then these factors will be positively correlated with the accuracy of volunteer-based data on the sex of a crab.
3. If the sex and species of crabs are easy to correctly identify, then volunteers will be able to collect data with high levels of accuracy.

In Chapter 2, I developed a quantitative, standardized experimental field approach for comparing the sensitivity of different sampling techniques for detecting organisms at low densities to increase the probability of detection. Increasing the probability of detection is critically important for invasion ecology, conservation biology and arguably, all fields of ecology (Nichols et al. 2000; MacKenzie 2005). Scientists have detected more than 500 marine introduced species along the coast of North America (Grosholz 2005), and it has been estimated that thousands of species are transported around the world every day (Carlton 1999; Drake and Lodge 2004). Species often remain undetected or are usually only detected years after the initial introduction (Geller et al. 1997), when the population size is large and eradication is no longer an option (Bax et al. 2001; Rejmanek and Pitcairn 2002). It has been recognized that increased monitoring and refined sampling approaches are beneficial since they increase the probability of early detection (US Congress OTA 1993; Bax et al. 2001; Lodge et al. 2006), which offers the best chance for successful eradication (Rejmanek and Pitcairn 2002). Therefore, I examined the frequency of false-negatives (not detecting something that is actually present) in two different approaches, random quadrat sampling and Total Area Search (i.e., freely searching the entire area), for two targets of different levels of mobility (i.e., sessile and mobile).

Hypotheses:

1. If the Total Area Search is more effective for early detection than random quadrat sampling, then it will detect targets faster and at lower densities.
2. If mobile targets are harder to detect than sessile targets then detecting mobile targets will take longer and reduce the probability of detection.

In Chapter 3 I examined the ability to predict the spread of marine introduced intertidal species. Forecasting spread is a central goal of not only invasion biology but ecology as a whole. In the case of predicting the spread of invasive species, it has both pure and applied implications. Although the best management strategy is preventing primary spread, ultimately some species will become established. Therefore, we must be prepared to predict and manage secondary spread as it determines the scale of an invasion and its impacts (Lodge et al. 1998). Given that most marine bioinvaders are highly fecund and have one or more planktonically dispersed life stages (Cohen and

Carlton 1998; Ruiz et al. 2000), ocean currents are arguably an important vector for secondary spread in marine systems. Oceanographic models coupled with larval ecology of an invader theoretically could predict the spread of the organisms. Unfortunately oceanographic models are usually only qualitatively validated using limited data (e.g., Hannah et al. 2001). Validation using biological datasets is rare but important as secondary spread in marine systems has been understudied to determine the extent of invasions. Depending on the duration of larvae, they can be transported hundreds of kilometers so this is a vector that needs further study. In this chapter, I examine the importance of physical and biological processes in determining the spread and dispersal potential of a species.

Hypotheses:

1. If ocean currents are important and oceanographic models can predict them, then these models will be able to predict movement of passive particles (drift cards).
2. If ocean currents and larval behaviors are important factors controlling larval spread and oceanographic models coupled with biological processes can predict them, then these models will be able to predict recruitment of *C. maenas* and *H. sanguineus.*

For this thesis I conducted broad-scale surveys of the abundances of these species along the northeast coast of the United States (Chapter 1) and determined the best way to sample, the accuracy of the data, and examined if we have sufficient sampling for early detection (Chapter 2). Then using the regional datasets of density (Chapter 1 and 2) combined with data from a drift card study and a recruitment study, I determined if physical oceanographic models can predict the spread of marine invasive species (Chapter 3). If the model can not predict the spread of invasive species, I determined if it failed due to gaps in our current understanding of the biology of the organisms (e.g., larval behaviors) or physical processes of ocean currents (e.g., advection) that transport the larvae to new locations.

In Chapter 4 I examine patterns of limb loss in invasive species because injury could be an important but understudied predictor of impact. The impact of invasive species is often predicted solely by their abundance (Crivelli 1983; Medd et al. 1985; Bobbink and Willems 1987; Ricciardi et al. 1995; Alvarez and Cushman 2002; Chumchal et al. 2005; Finnoff et al. 2005; Cacho et al. 2007; Whittle et al. 2007), but other factors, such as injury, might also be important as they can moderate the impacts of invasive species. I document the density, size, and injury (i.e., limb loss) of *C. maenas* and *H. sanguineus* at thirty sites from Shinnecock County Park, New York to Lubec, Maine. Using density of these species at 30 sites and records of thousands of crabs' injury status across these sites, I identify predictors of injury. I examine both individual- and site-level factors. On the individual-level, I examine whether there is a difference in incidence of injury between sex and size of individual crabs. On the regional-level, I examine whether the prevalence of injury was positively correlated with latitude, density, average size of conspecifics and heterospecifics. Given that the focal organisms are both aggressive predators that are having large impacts on prey in the invaded region, aggressively interact with each other, understanding regional patterns of limb loss will help understand and identify where impacts will be reduced by injury.

Hypotheses:

1. If aggression increases as the crabs grows larger then the amount of time spent engaging in aggressive behavior will be positively correlated with the size of a crab.
2. If injury increases with the size and density then the incidence of injury will be positively correlated with size and density.
3. If aggression increases with water temperature, injury rates will be negatively correlated with latitude along the coast of New England.
4. If injury reduces foraging efficiency then the number of bivalves consumed by injured crabs (missing a single cheliped) will be less than for crabs with all claws intact.

Study System and Focal Organisms

My research is conducted at multiple spatial scales but primarily focuses on the regional scale, in the intertidal zone of New England and New York. This area is well-studied and heavily invaded (Say 1817; Verrill 1880; Glude 1955; Taylor et al. 1957; Bousfield and Laubitz 1972; Menge 1976; Brenchley and Carlton 1983; Stachowicz et al. 1999; Lohrer and Whitlatch 2002; Carlton and Cohen 2003) and is predicted to face future invasions by other known invasive species (e.g., *E. sinensis*) (Herborg et al. 2007). To be better prepared for future bioinvasions, research needs to move beyond purely observational studies that only document the presence of invaders to research that tests hypotheses with standardized, quantitative data to identify the general predictors of invasion patterns and optimally manage invasive species. This is only possible for species with rich datasets. Therefore, I will focus on *C. maenas* and *H. sanguineus* because they are well-studied invasive species causing economic and ecological damage and have extensive spatial and temporal invasion histories (Crothers 1967, 1968; Zeidler 1978; McDermott 1992, 1998a, 1998b, 1999; Grosholz and Ruiz 1996; Leonard et al. 1999; Lohrer et al. 2000; Behrens Yamada 2001; Lohrer 2001; Lohrer and Whitlatch 2002; Carlton and Cohen 2003).

Carcinus maenas

The European green crab, *C. maenas* is a voracious omnivore that can consume species from at least 104 families, 158 genera including phyla of animals, plants and protists; therefore, food is usually not a limiting agent (Ropes 1968; Cohen and Carlton 1995; Cohen et al. 1995; Grosholz and Ruiz 1996). As a generalist, it can survive in many of the places to which it is transported (Cohen and Carlton 1995). Once established *C. maenas* can negatively affect many species by predation and competition (Ropes 1968; Grosholz and Ruiz 1995; Grosholz and Ruiz 1996; Leonard et al. 1999; Griffen and Byers 2006; Griffen and Delaney 2007; Griffen et al. 2008). The IUCN has listed *C. maenas* as one of the 100 worst invasive species in the world (Lowe et al. 2000). Its native range is the Atlantic coast of Europe and possibly northwestern Africa, it can now be found on parts of all non-polar continents (Carlton and Cohen 2003). It has obtained this global distribution because it can tolerate a wide range of salinities and temperatures (Broekhuysen 1936; Cohen and Carlton 1995; Cohen et al. 1995; Carlton and Cohen 2003).

Hemigrapsus sanguineus

In common with *C. maenas*, *H. sanguineus* is a generalist, an omnivore, and a highly invasive brachyuran crab that has a distribution on multiple continents (Breton et al. 2002; Schubart 2003). Unfortunately, far less is known about *H. sanguineus* than *C. maenas*. Males can reach a maximum carapace width of 5 cm and are larger than the females. *H. sanguineus* is native to the western Pacific from Sakhalin Island, Russia along the coasts of Korea and China down to Hong Kong and Japan (McDermott 1998a; Lohrer et al. 2000; Ledesma and O'Connor 2001). *H. sanguineus* inhabits waters that range from above 30 to below 5^{o}C (Depledge 1984; Takahashi et al. 1985). It has been detected in multiple locations in Europe, including France and the Netherlands (Breton et al. 2002; Schubart 2003), and during 1988 it was first detected on the eastern coast of North America. This first North America detection was in Cape May County, New Jersey by an undergraduate student on a college field trip (Williams and McDermott 1990). Although *H. sanguineus* was detected in 1988 it probably colonized years earlier as it was discovered as an adult and it was transported as larvae in ballast water of foreign cargo vessels (Lohrer 2001). With a high fecundity in the form of multiple broods of more than 40,000 eggs each breeding season (McDermott 1991), *H. sanguineus* has expanded its invasive range along the eastern coast of the United States, and has colonized from Oregon Inlet, North Carolina to Isle au Haut, Maine (McDermott 1998b; Lohrer 2001; P. Thayer, pers. comm.).

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Linking Statement 1

Given the frequency of new introductions and the global-scale of the problem, we lack sufficient funding to employ enough personnel to document and detect what species are already established or newly arriving to an area. The earlier an invasion is detected, when the invader’s population is localized at low density, the higher the probability of successful eradication. Due to minimal monitoring along the coastline, most introduced species are not detected when eradication is still an option, so it is imperative to increase the amount of monitoring to make early detection more common. The most feasible option to ameliorate this problem, given-real world limitations, such as insufficient funding and personnel to monitor vast amounts of area, is having volunteers monitor the areas that scientists can not monitor themselves. Therefore, I conducted a validation study to determine whether volunteers can collect accurate data on the introduced and native species of crabs along the coast of New England, New Jersey, and New York. If volunteers are accurate, personnel for early detection would be vastly increased. Further, if we can identify factors (e.g., age, education, size of the groups monitoring and the crabs they are identifying) that predict the volunteers’ ability to record accurate data, we can set quantitative eligibility criteria to maintain quality assurance to the data they collect. If a citizen science monitoring network can be validated and sustained, we can use their data to monitor the focal organisms on the large-scale to increase our ability to detect invaders as they colonize and spread. In

Chapter 1 I test whether volunteer-based monitoring is accurate and therefore a potential solution to this problem by supplementing scarce resources.

Chapter 1. Marine Invasive Species: Validation of Citizen Science and Implications for National Monitoring Networks

Abstract

Approximately 1,000 volunteers assessed the presence of invasive (*Carcinus maenas* and *Hemigrapsus sanguineus*) and native crabs within the intertidal zone of seven coastal states of the U.S., from New Jersey to Maine. Identification of crab species and determination of the gender of the observed crabs was documented at all 52 sites across a 725-km coastal transect. Using quantitative measures of accuracy of data collected by citizen scientists, a significant predictor of a volunteer's ability was determined and eligibility criteria were set. Students in grade three and seven had the ability to differentiate between species of crabs with over 80% and 95% accuracy, respectively. Determination of gender of the crabs was more challenging and accuracy exceeded 80% for seventh grade students, while 95% accuracy was found for students with at least two years of university education. We used the data collected by citizen scientists to create a large-scale standardized database of the distribution and abundance of the native and invasive crabs. *Hemigrapsus sanguineus* dominated the rocky intertidal zone from Sandy Hook, New Jersey to Boston Harbor, Massachusetts, while *C. maenas* dominated the northern extent of the sampled coastline. A citizen scientist of this monitoring network detected a range expansion of *H. sanguineus*. We

identified obstacles to creating a national monitoring network and proposed recommendations that addressed these issues.

Introduction

More than 500 marine introduced species have been observed along the coast of North America and it is estimated that thousands of species are transported around the world every day (Carlton 1999; Fofonoff et al. 2003). Species often remain undetected or are usually only detected years after the initial colonization (Geller et al. 1997; Lohrer 2001), when the population size is large and eradication is no longer an option (Bax et. al 2001). Invasion ecology began as a true discipline in the later half of the 20th century and is still in its infancy (Elton 1958; Carlton 1979; Ruiz et al. 1997). In particular, marine systems are still greatly understudied, and so far, only a fraction of the invaders and their impacts have been recorded (Ruiz et al. 1997). Increased monitoring is beneficial since it increases the chance for early detection and thus offers the best chance for eradication (Myers et al. 2000; Bax et. al 2001; Lodge et al. 2006).

Comprehensive databases of spatial and temporal information for large geographic ranges of native and invasive species are integral to rapid assessments, testing scientific hypotheses, and validating predictive models (Ricciardi et al. 2000). Currently most databases are disjunct, disparate, incomplete, and often out-dated. Unfortunately, intense monitoring, as would be necessary to build comprehensive and up-to-date databases, rarely occurs due to resource limitations, such as the availability of funding and personnel. Volunteer-based monitoring is a potential solution to this problem and could supplement scarce resources (Fore et al. 2001; Lodge et al. 2006). For example, a statewide citizen science ornithological study provided more than 200,000 hours of data collection that is valued at over a million dollars, even based on minimum wage (Bonney 1991). It has been shown that citizen science initiatives have not only contributed to reductions in costs associated with research endeavors, but have also been quite useful in previous environmental assessments (Greenwood 1994, 2003).

Citizen science has begun to contribute to the wealth of information about population structures, distributions, behaviors and to assist with the conservation of various organisms. Terrestrial and aquatic resource managers have taken advantage of volunteer networks for ornithology studies, reef ecology, stream and water quality monitoring (Darwall and Dulvy 1996; Ohrel et al. 2000; Bray and Schramm 2001; Fore et al. 2001). While many programs have already incorporated volunteers in environmental monitoring in Europe, fewer groups in North America have realized the value, both economic and educational, of citizen science (Greenwood 1994). The best North American example is the National Audubon Society’s Christmas Bird Counts, which have been generating data for over 100 years about the distribution, range expansions, and other patterns of North American birds (National Audubon Society 2006). These initiatives are valuable both for the scientists, who gain increased personnel to collect more samples, and for the public, who benefit from hands-on learning experiences (Bonney and Dhondt 1997; Fore et al. 2001). With the aid of local volunteers, the program has been able to demonstrate the feasibility of citizen science initiatives and applicability within large-scale bio-monitoring programs (National Audubon Society 2006).

The scientific community, however, seems reluctant to accept citizen science due to a current lack of certified audits to assess the validity of using such data in academic research and resource management decisions. Quality assurance and validation of these initiatives, through compliance to rigorous scientific methodology, is necessary for the scientific community to accept and utilize the data collected by citizen scientists (Boudreau and Yan 2004). Acceptance by the scientific community would also allow additional personnel to participate in bio-monitoring, and thereby increase our biological understanding of these species by creating large standardized spatial and temporal datasets (National Audubon Society 2006). Given the scarcity of knowledge related to marine introduced species (Ruiz et al. 1997) and the novelty of marine-focused volunteer bio-monitoring projects, this study was designed to validate the feasibility and accuracy of a large-scale marine invasive species monitoring network, named “Citizen Science Initiative: Marine Invasive Species Monitoring Organization” (CSI: MISMO 2007).

This study sought to assess the abilities of citizen scientists to compile data about the status and composition of the coastal biota. If, as hypothesized, it was determined that citizen science was a reliable method of conducting research, volunteers could aid in amassing knowledge about both native and invasive intertidal crabs, including the Asian shore crab (*Hemigrapsus sanguineus*) and the European green crab (*Carcinus maenas*). Certain variables were predicted to affect the accuracy of data collected by these volunteers, including the volunteers’ age, education, group size, and size of the crab. We hypothesized that an accurate monitoring network is feasible with the assistance of citizen scientists, if eligibility criteria were determined and enforced. Data confidently generated by such efforts could then contribute to a large-scale, standardized database that would fill gaps in our current monitoring and increase knowledge of marine systems. The abundance and demographics of intertidal crab species could then be mapped to provide baseline data on the distribution of the current biota. The monitoring network could also provide early detection of other invasive crabs, such as the Chinese mitten crab (*Eriocheir sinensis*) and the brush-clawed crab (*Hemigrapsus penicillatus*), both potential invaders to the coast of New England and other locations around the globe.

Study Organisms

As widely distributed organisms, *Carcinus maenas* and *Hemigrapsus sanguineus* were logical choices for this new type of study and validation towards yielding the data needed for the progress of marine invasion ecology. These invasive crabs have many dispersal mechanisms, but the primary vector for these and other marine invaders from their native to invasive range has been via ship's ballast (Cohen et al. 1995). *Carcinus maenas* has invaded the coasts of North America, South Africa, Australia, South America and other places outside of its native range of the Atlantic coast of Europe and possibly northwest Africa (Carlton and Cohen 2003; Hidalgo et al. 2005). *Carcinus maenas* was presumably brought to the Atlantic coast of North America, in 1817, with solid ballast (Carlton and Cohen 2003). By 1989, it started colonizing the Pacific coast of North America starting in San Francisco Bay (Cohen et al. 1995). It was transported accidentally from the east coast by activities associated with the live food and bait trade (Cohen et al. 1995; Carlton and Cohen 2003). Establishment and persistence in these various environments is likely facilitated by its omnivorous feeding strategy and its ability to tolerate a wide range of temperatures and salinities (Crothers 1967; Ropes 1968; Cohen et al. 1995). A single brood of *C. maenas* can contain at least 185,000 eggs (Crothers 1967). High fecundity and the characteristics of a generalist allow *C. maenas* to inhabit a diverse range of marine ecosystems (Carlton and Cohen 2003) and therefore, reduce beta-diversity.

Similarly, *H. sanguineus* is a generalist, an omnivore, and a highly invasive brachyuran crab (Lohrer 2001). *H. sanguineus* is native to the western Pacific (Ledesma and O'Connor 2001) but has colonized multiple locations in Europe (Breton et al. 2002; Schubart 2003) and during 1988 it was first detected on the eastern coast of North America, in New Jersey (Williams and McDermott 1990). Traffic of foreign cargo vessels was presumably the vector that brought the Asian shore crab to North America (Lohrer 2001). In its native range, *H. sanguineus* inhabits waters that range from above 30 to below 5^{o}C (Depledge 1984; Takahashi et al. 1985). With a high fecundity in the form of multiple broods of more than 50,000 eggs each breeding season, *H. sanguineus* has expanded its invasive range along the eastern coast of the United States, and has colonized from Oregon Inlet, North Carolina to Isle au Haut, Maine (McDermott 1998; Lohrer 2001; P. Thayer pers. comm.).

Methodology

Systematic surveys, using randomly placed quadrats, were conducted from May through August, 2005, with approximately 1,000 volunteers across 52 sites (Fig. 1.1) from Sandy Hook, New Jersey (40°27.103N, 074°00.135W), to Machias, Maine (44°42.451N, 067°18.823W). Intertidal habitats suitable for the invasive crab species *H. sanguineus* and *C. maenas* were selected, and our sampling site was defined as a 30 by 30 meter area using two tape measures. The tape measures were run parallel (X) and perpendicular (Y) to the coastline, to allow X-Y coordinates to be identified. The top left corner of each one square meter quadrat was placed at the intersection of two randomly selected X-Y coordinates. Crabs were collected and removed from each quadrat, taking care to systematically examine under macrophytes and rocks. On site, volunteers were instructed to record the species, gender, and carapace width for each crab. Carapace width was measured between the antero-lateral teeth furthest away from the eye-stalks (Crothers 1968). Citizen scientists placed the crabs into buckets corresponding to the different species and gender combinations (e.g., male *C. maenas*, female *H. sanguineus*) for validation. All rocks were returned to their initial state to minimize any disturbance. This process was repeated for as many quadrats as was feasible during low tide.

The volunteers varied in age and education level, which allowed identification of volunteer eligibility criteria. The education level ranged from pre-kindergarten to Ph.D., and age ranged from 3 to 78 years old. The participants at each site were divided into subgroups (1 to 10 people). In total, 190 groups participated in the experiment. Before the sampling started, the research team introduced the volunteers to the methodology in an hour-long training session. Participants were given magnifying glasses, buckets, rulers, as well as Massachusetts Institute of Technology Sea Grant’s “Hitchhikers Guide to Exotic Species” and field guides, which served as teaching tools to increase the accuracy of citizen scientists monitoring at each site. After each sampling session, all of the crabs collected by volunteers were checked and re-counted by the research team to verify the degree of accuracy with which the citizen scientists had recorded the data.

Statistical Approaches and Issues

To develop eligibility criteria, we identified independent variables (age, education, and group size of participants, as well as the size of the crab) to examine their effect on the ability of volunteers to accurately determine crab species and gender. As expected, age and education were highly collinear (r = 0.813). Therefore, only education was included in the analysis because it was assumed to be a more accurate predictor of citizen scientists’ abilities. Further, of the 190 groups in the monitoring network, 135 of them had measured the carapace width for every crab that they had collected, and thus, these were the only groups included in the validation analysis. The volunteer groups were used as independent sampling units (N = 135), since our purpose was to validate the accuracy of volunteers.

The experimental design has an issue of repeated measures, because each group collected multiple crabs and had unequal sample sizes. Thus, a randomization program selected an individual crab collected from each group at random, such that each group provided a single data point. Each multiple logistic regression served to test the relationships between the predictor variables (volunteer group size, education and crab size) and a binary dependent variable (correct identification of crab species or gender). The program randomized the predictor variables with respect to the dependent variables, and a multiple logistic regression on this randomized set created the null comparison point (Manly 1997). The program repeated this process 10,000 times, each time selecting, with replacement, a crab from each group. This allowed statistics to be calculated using all crabs in the dataset, thereby providing a better idea of the generality of the results and avoiding inflated Type I errors associated with non-independence from multiple measurements per group. For independent variables that were significant, the eligibility criteria to provide high levels of accuracy (80% and 95%) were determined using back-transformation from the averaged logistic model results.

Results

Validation of Citizen Scientists

Education was a highly significant predictor of the volunteers' ability to correctly identify both the species and gender of a crab (Table 1.1). Based on the data, it was concluded that third-grade students were, on average, at least 80% accurate when discerning the differences between the native and invasive crab species, while seventh-grade students were over 95% accurate. Determination of crab gender was more challenging requiring at least a seventh grade education to obtain 80% accuracy.

Volunteers required two years of university education to exceed 95% accuracy. The analysis did not find that volunteer group size and crab size were significant predictors of a citizen scientist’s ability to identify the gender or species of a crab correctly (Table 1.1).

Abundance, Diversity and Distribution

Once the statistical analysis provided eligibility criteria for participants of CSI: MISMO volunteers, the further analysis on crab distributions presented here used only the data of the citizen scientists who satisfied the requirements that exceeded 95% accuracy. These results depict the distributions and relative densities of *C. maenas* and *H. sanguineus* in their invasive range in the seven sampled northeast coastal states (Fig. 1.2 and Table 1.2). Latitudinal correlation analysis showed a pattern of H. *sanguineus* abundance that was inversely proportional with a correlation coefficient of -0.583. The Asian crab dominated the rocky coasts from Sandy Hook, New Jersey (Site 1) to Quincy, Massachusetts (Site 21). At all sites north of Boston Harbor (Sites ≥ 25), C. *maenas* populations were larger than those of H. *sanguineus*. Several sites in the central locations, particularly New Bedford, Massachusetts (Site 11), East Providence, Rhode Island (Site 17) and Saco, Maine (Site 30), were relatively diverse with regard to native species (Fig. 1.2).

Finally, the volunteer network recorded a range expansion of H. *sanguineus*. The most northeastern observation is now a gravid female specimen, measuring 22.11 mm, on Schoodic Peninsula (Site 43), which is the northeast limit of Acadia National Park in

Maine. This range expansion, discovered on July 21, 2005 by a citizen scientist of CSI: MISMO, is approximately 60-kilometers northeast of previous records of *H. sanguineus* on Moores Harbor, Isle au Haut, Maine (Fig. 1.3).

Discussion

Eligibility and Implications for a National Monitoring Network

Based on this study, we have established a large-scale, standardized database and eligibility criteria for citizen scientists monitoring marine introduced species. Now we will outline the issues that may arise in the future for monitoring to be successful and for extending to other marine introduced species. The utilization of citizen scientists could face issues concerning the endurance of citizen scientists' patience. For example, in this pilot study, some volunteers failed to complete the size measurements of all their crabs because they found it to be too difficult or tedious. However, all groups did record the species and gender of the crabs, which is extremely useful information for early detection and helps to fill in the gaps in current monitoring by professionals (Fore et al. 2001). Early detection has been recognized by invasion biologists and the US Government to increase the probability of successful eradication (US Congress OTA 1993; Myers et al. 2000; Lodge et al. 2006).

For better management of introduced species, not only is there a need for more data but it is crucial to have the data readily available to managers. One solution is the use of global technologies such as the worldwide web and geographical information systems as a means for data entry and sharing. A dynamic database linked with online mapping technology (e.g., Google Earth) would make an ideal medium for the first completely graphical global database of the native and introduced ranges of species. To make such a database comprehensive, it would need to incorporate data from already established databases such as the Global Invasive Species Database (GISD 2007), Marine Invader Tracking Information System (MITIS 2007), National Institute of Invasive Species Science database (NIISS 2007), and the USGS Nonindigenous Aquatic Species information resource (USGS NAS 2007). Another approach, as used by the NISbase, is to link decentralized databases through a single-user interface (Ricciardi et al. 2000; NISbase 2007). This option also has great potential but requires a level of standardization by the creators of the individual databases that has been quite elusive. Thankfully, this appears to be slowly changing. No matter what medium, a comprehensive, up-to-date internet-based database will be vital because it will enable global accessibility to standardized data that facilitates rapid response, increasing our probability of successful eradication. It will provide information to all the stakeholders such as researchers, resource managers, policy makers, educators and the public.

Another challenge will be the sustainability of the monitoring network itself given issues of limited funding and the challenge of large-scale coordination and training. CSI: MISMO and the National Park Service produced a video to train citizen scientists and raise awareness of people all along the coasts of North America, while keeping the investment of time and money for traveling and training expenses at a minimum. Sustainability is possible with the right tools, and high quality data can be maintained by enforcing the eligibility criteria determined in this study. For example, education was a significant predictor variable but the size of the crab was not a significant dependent variable for the abilities of citizen scientists to identify the species or gender of a crab correctly. There are a few possible hypotheses to explain this surprising result. One explanation is that citizen scientists did not collect the smaller size classes of crabs and therefore, did not extensively encounter the threshold size of crabs at which citizen scientists could not discern the gender or species. Another possible factor is that citizen scientists used magnifying glasses to identify smaller crabs, and therefore, size was not an important factor.

Although there are issues with using citizen scientists, given proper training, they can collect data with high accuracy (Darwall and Dulvy 1996; Fore et al. 2001; Boudreau and Yan 2004). Citizen scientists are a valuable source of information for early detection (Lodge et al. 2006). In fact, the first Asian shore crab in North America was discovered by a college student (Williams and McDermott 1990). Unfortunately, discoveries by citizen scientists are not usually published or disseminated to resource managers and scientists, with the possible exception of ornithological studies (Lodge et al. 2006; National Audubon Society 2006). The presence of *H. sanguineus* in Massachusetts first came to the general attention of invasion ecologists and New England marine biologists in 1993 because of the specimens collected by the students of the Children's School of Science (J.T. Carlton pers. comm.). In South Portland, a 9-year old child discovered the first site colonized by H. *sanguineus* in the state of Maine (J. Sandler pers. comm.). This study sets a baseline for eligibility of citizen scientists and lays the groundwork to extend and validate monitoring for other marine introduced species. Given the low eligibility needed to identify crab species and gender correctly, it is quite feasible that citizen scientists can accurately monitor less conspicuous introduced organisms.

It would be unrealistic, however, to believe that validation of citizen scientists' abilities to collect data is the only element necessary for the establishment of a national monitoring network. Creating a large-scale network is a multi-year, tiered process, requiring a great deal of investment to enable it to flourish, expand, and remain sustainable. Necessary investments include time, dedication, and financial backing. Since data quality is an important issue, state-level supervision could play an important role. We propose the ideal groups for this would be programs funded by National Oceanic and Atmospheric Administration (NOAA), such as the National Sea Grant College Program, a university-based research program located in 30 states. NOAA already funds LiMPETS (Long-term Monitoring Program and Experiential Training for Students), which uses students and other volunteer groups to monitor various marine habitats of five west coast national marine sanctuaries (Pearse et al. 2001; Osborn et al. 2005). NOAA has already set the framework for a national program monitoring introduced aquatic plants (Crawford et al. 2001). Comprehensive national monitoring of aquatic systems for all introduced organisms would be the logical expansion of this work and NOAA is best prepared for this monumental challenge. Collaboration between NOAA and other established groups, such as the National Park Service, NGOs (e.g., Salem Sound Coastwatch) and extension programs (e.g., Cornell Extension Program of Suffolk County), would be beneficial and these partnerships would serve to promote the use of local experts in confirming the data for their area, to create the first national marine monitoring network (M. Raczko, C. Smith, and B. Warren pers. comm.).

The creation and proliferation of “bio-blitzes”, with volunteers gathering samples to be identified by scientists, could be an ideal avenue for sustained citizen science monitoring. These are heavily used by the National Park Service and many other conservation groups. The Boston Harbor Islands National Park has already organized such “bio-blitzes” that brought together personnel from the Harvard Museum of Comparative Zoology and CSI: MISMO in which professionals were coupled with volunteers to monitor native and invasive invertebrates of various Boston Harbor islands. Other events organized by the National Park Service conduct a survey of Coleoptera, Formicidae, and Lepidoptera diversity in Acadia National Park and complete inventories such as the ‘All Taxa Biodiversity Inventory’ in places such as the Great Smoky Mountains National Park (D. Manski pers. comm.). These all serve to demonstrate that interest in public monitoring events facilitates the interaction of professional scientists and resource managers with citizen scientists who share mutual goals (Fore et al. 2001). Due to the large work force needed to monitor these huge areas, citizen science is a vital component for the success of properly monitoring the spread of invasive species.

This study sought to demonstrate that a large group of people working together could collect enough scientifically valid data for use in detecting the spread of recently introduced non-native species. Increased monitoring is beneficial since it increases the chance for early detection that offers the best chance for eradication, which is the most cost-effective management option (US Congress OTA 1993; Bax et al. 2001). Increased knowledge about baseline biota could not only enable the prediction of future marine invaders but also allow more informed policy decisions for the prevention of future bioinvasions and the management of introduced species (Leung et al. 2005). It is no revelation that collecting this data is an overwhelming feat to achieve and requires large numbers of individuals. Citizen scientists are a key solution to limited funding and personnel needed to carry out such research. Given proper training, citizen scientists are able to monitor their coastlines for these species, and help scientists by providing additional data on the distribution of marine introduced species, especially in areas scientists cannot monitor themselves. Such efforts would improve the efficiency of detecting new introduced species and serve to compile baseline information about the changing biota of the intertidal zone.

Distribution of Invasive Crabs

Abiotic factors can explain many of the observed large-scale patterns of crab distribution and abundance. *Hemigrapsus sanguineus* is significantly less abundant as latitude increased. This is probably due to many factors but latitude could act as a rough proxy for one of the most important factors, water temperature, which decreases from New Jersey to Maine. Lohrer et al. (2000) revealed that habitat complexity is another important predictor of abundance, with more complex sites offering more shelter and supporting higher densities of crabs. For example, high densities of H. *sanguineus* were found within the abundant cobble of Centerport (Site 3 and 4), but low abundance was found in the muddy areas of East Providence (Site 17) and Taunton Bay (Site 50), and in the varied but largely sandy substrate of Roque Bluffs, Maine (Site 51).

Biotic factors, in addition to abiotic factors, appear to influence the patterns of distributions and abundances of these crabs. Initially, researchers believed that *H. sanguineus* was exploiting a niche previously unoccupied by other brachyurans, but it was later found that this invasive crab interacts with and can out-compete and exclude *C. maenas* (Lohrer and Whitlatch 2002). The overlap of these two species is not clearly defined, but it appears that *H. sanguineus* is far more aggressive than any other crab and can exclude all other species from the rocky intertidal zone as seen in the southern sites. In northern New England, *C. maenas* still dominated the intertidal zone (Fig. 1.2).

Logistical issues and environmental heterogeneity can also influence the observed crab abundances. The crab abundances found in this study were almost certainly underestimates due to logistics involved in sampling the rocky intertidal zone and monitoring a mobile organism. Many sites (e.g., Sites 1, 2, 11, and 37) were comprised of large, immovable rocks with only small crevices, and sampling was difficult at times. Given the mobile and evasive nature of the crabs, even in more accessible locations, it was arduous to capture all crabs in any given quadrat and the densities recorded are probably lower than the actual densities. In addition, sampling large 30 by 30 meter sections will encompass optimal, suboptimal and possibly uninhabitable locations, reducing the overall average abundance. Other factors that could influence the data are tidal height, wave exposure, and seasonality but these were minimized by consistently sampling at dead low tide and randomly moving to different geographic areas of the transect throughout the four months of the spring and summer (May to August), instead of sampling from north to south.

Sampling intensity and behavior of the organism could have been important factors in explaining the observed pattern of crab distribution. It is imperative to note that even during this study, some of the sampled sites in northern Maine may have been invaded by *H. sanguineus* unbeknownst to the research team and volunteers who monitored the coasts, because the introduced crab was at very low densities and therefore might have gone undetected. Another challenge to consider is that *H. sanguineus* can migrate to the subtidal zone during the winter months to avoid challenges of the colder temperatures (Ledesma and O'Connor 2001). This organism could possibly be utilizing this behavior year-round in northern Maine. This adaptation could initiate unknown interactions, as well as decrease the probability of detection. There is a 60-kilometer range expansion between the newly detected northernmost limit of H. *sanguineus* at Schoodic Peninsula, and the previous northern record at Moores Harbor, Isle au Haut, Maine (Fig. 1.3). The monitoring network did not detect H. *sanguineus* at any of the five sites between these two locations or at the four additional sites further northeast. Thus, further analysis should experiment with different sampling techniques and variations in sampling intensity to determine how to optimally allocate effort and determine the probability a species is present, if not detected (i.e., false-negatives).

These aforementioned issues raise the question of whether Schoodic Peninsula will be the final extent of H. *sanguineus*' migration north. The Asian shore crab found at Schoodic Point was a gravid female, demonstrating that even at this northern extent of the invasive range, *H. sanguineus* is reproducing. The unresolved matter is whether the population is sustainable. The colder water temperatures of Maine increase the obligate minimum time that larvae of *H. sanguineus* spend as plankton and therefore the crab may not be able to recruit due to increased advection and a mean southwestward flow (Byers and Pringle 2006). The ultimate explanations for the patterns of distribution and abundance could be due to abiotic tolerances, advection, competition, propagule pressure, or a time lag in the expansion of the H. *sanguineus* in the northeastern region. It is more likely the synergy of a few of these factors. Arguably, large systematic databases generated by citizen scientists will be vital for testing which factors and interactions are important. The final extent of its range can only be determined by joint models that incorporate invasibility, propagule pressure and climate change models. These complex models will need large-scale standardized datasets, such as the one created by citizen scientists in this study, to validate these models.

Acknowledgements

This research was funded by NOAA's National Sea Grant Aquatic Invasive Species Research and Outreach Program (NA05OAR4171088). We also want to thank Acadia Institute of Oceanography, J. Ainsworth, Bowdoin College, Cornell Cooperative Extension Program of Suffolk County, R. Crossman, Darling Marine Center, M. Delaney, E. Ely, J. Farrell, K. Fellner, R. Foreman, E. Gertzen, Island Alliance, Z. Itzkowitz, S. Myers, National Park Service, New England Aquarium, J. Pederson, M. Raczko, A. Rogers, H. Spence, Capt. D. Weinstein, and especially all the volunteers.

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Tables

Table 1.1 The p-values from the multiple logistic regression to determine the significance of the predictor variables, education, group size, and size of crab, on the two dependent variables the volunteers' ability to correctly identify the species and gender of a given crab.

	Education	Group Size	Crab Size
Identification of Sex	0.007	0.355	0.153
Identification of Species	0.004	0.375	0.413

Table 1.2 For each site, a number from 1 to 52 is assigned according to its location from South to North ("Code") , the latitude ("LAT"), longitude ("LONG") , and the density of crabs, including the total density of all crabs ("Crabs"), the individual densities of the invasive *Hemigrapsus sanguineus* ("Asian"), *Carcinus maenas* ("Green") and the pooled density of all native species ("Native"), are given. The densities are given as crabs/m^2.

Code	LAT	LONG	Crabs (Crabs/m^2)	Asian (Crabs/m^2)	Green (Crabs/m^2)	Native (Crabs/m^2)
1	40°27.103N	074°00.135W	2.19	2.19	0	0
2	40°33.683N	073°52.951W	2.11	2.11	0	0
3	40°54.384N	073°22.673W	24.6	24.6	0	0
4	40°54.401N	073°22.051W	43.83	43.83	0	0
5	41°06.664N	073°19.739W	20	20	0	0
6	41°14.971N	072°32.556W	28.25	28.25	0	0
7	41°19.646N	071°54.311W	18.5	18.25	0.25	0
8	41°29.347N	071°23.012W	1.97	1.26	0.71	0
9	41°29.485N	071°25.270W	2.63	2.06	0.13	0.44
10	41°36.178N	070°51.799W	7.38	5.69	0.92	0.77
11	41°36.369N	070°54.211W	1.4	0.28	0.4	0.72
12	41°36.550N	070°54.265W	18.24	17.91	0	0.33
13	41°36.567N	070°54.285W	2.76	2.32	0.2	0.24
14	41°37.985N	070°54.150W	23.46	23.46	0	0
15	41°46.278N	070°31.068W	9.38	9.38	0	0
16	41°46.406N	070°29.973W	31.7	31.65	0.05	0
17	41°48.059N	071°22.636W	1.36	0.57	0.22	0.57
18	41°59.214N	070°41.947W	5.16	3.83	1.25	0.08
19	42°05.501N	070°38.546W	4.5	4.08	0.17	0.25
20	42°09.434N	070°42.262W	3.1	1.3	0.7	1.1
21	42°18.226N	071°00.838W	3.67	1.89	1.78	0
22	42°19.830N	070°55.820W	1.75	1.1	0.65	0
23	42°19.865N	071°01.775W	5.58	3.5	2.04	0.04
24	42°21.311N	070°58.111W	3.65	3.26	0.39	0
25	42°34.572N	070°44.227W	3.86	2.8	0.33	0.73
26	43°02.506N	070°42.890W	3.7	0.09	3.06	0.55
27	43°04.866N	070°42.526W	8.93	2.86	5.93	0.14
28	43°12.268N	070°35.413W	2.21	0.13	2.08	0
29	43°20.651N	070°29.686W	1.82	0.19	1.46	0.17
30	43°26.811N	070°20.167W	4.38	0	2.63	1.75
31	43°33.934N	070°11.942W	7.33	0.14	7.05	0.14
32	43°38.281N	070°13.313W	1.6	0	1.37	0.23
33	43°38.876N	070°13.545W	2	0.06	1.94	0
34	43°43.064N	070°00.173W	5.93	0	5.93	0
35	43°47.027N	069°43.283W	1.58	0	1.53	0.05
36	43°48.511N	070°04.291W	2.85	0	2.85	0
37	43°50.189N	069°30.447W	1.23	0	0.88	0.35
38	43°55.553N	069°15.507W	3.23	0	3.17	0.06

39	43°56.081N	069°34.759W	2.6	0	2.6	0
40	44°05.401N	069°02.805W	1.57	0	1.41	0.16
41	44°17.087N	068°24.529W	3.63	0	3.63	0
42	44°17.711N	068°14.598W	1.55	0	1.33	0.22
43	44°20.281N	068°03.200W	2.42	0	2.42	0
44	44°22.897N	068°49.168W	2.12	0	2.06	0.06
45	44°23.726N	068°13.219W	1.1	0	0.9	0.2
46	44°23.963N	068°12.587W	2.41	0	2.41	0
47	44°27.426N	067°52.833W	1.83	0	1.83	0
48	44°28.267N	068°52.458W	2.35	0	2.35	0
49	44°32.075N	067°35.585W	1.17	0	1.17	0
50	44°33.506N	068°16.446W	0.04	0	0.04	0
51	44°36.619N	067°28.976W	0.4	0	0.4	0
52	44°42.451N	067°18.823W	1.11	0	1.11	0

Figures

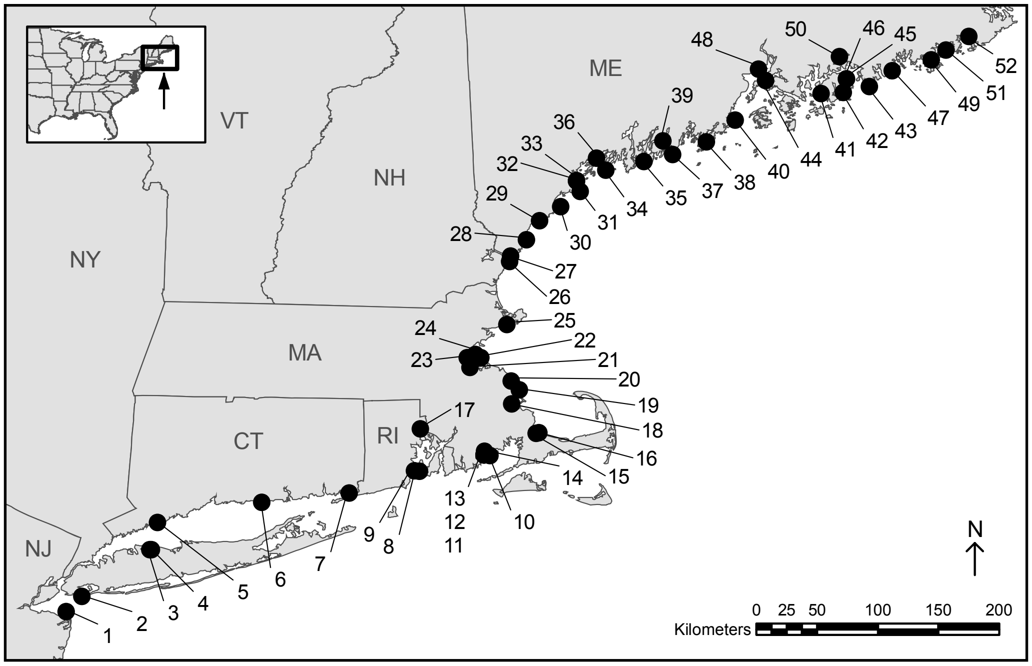

Figure 1.1 The 52 sites that were monitored along the 7 coastal states of United States of America, New Jersey to Maine. The numbers correspond to the “Code” in Table 1.2.

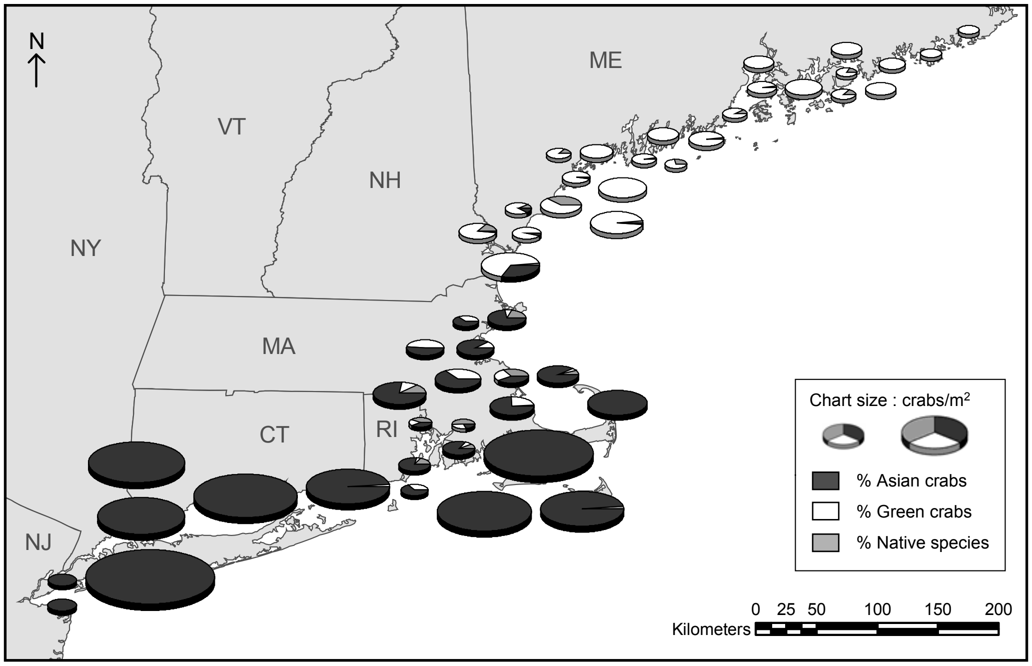

Figure 1.2 The size of the pie chart for each site is scaled to represent relative abundance of crabs at that site. Divisions in the pie charts indicated abundance of each species, *H. sanguineus*, *C. maenas*, and pooled native species.

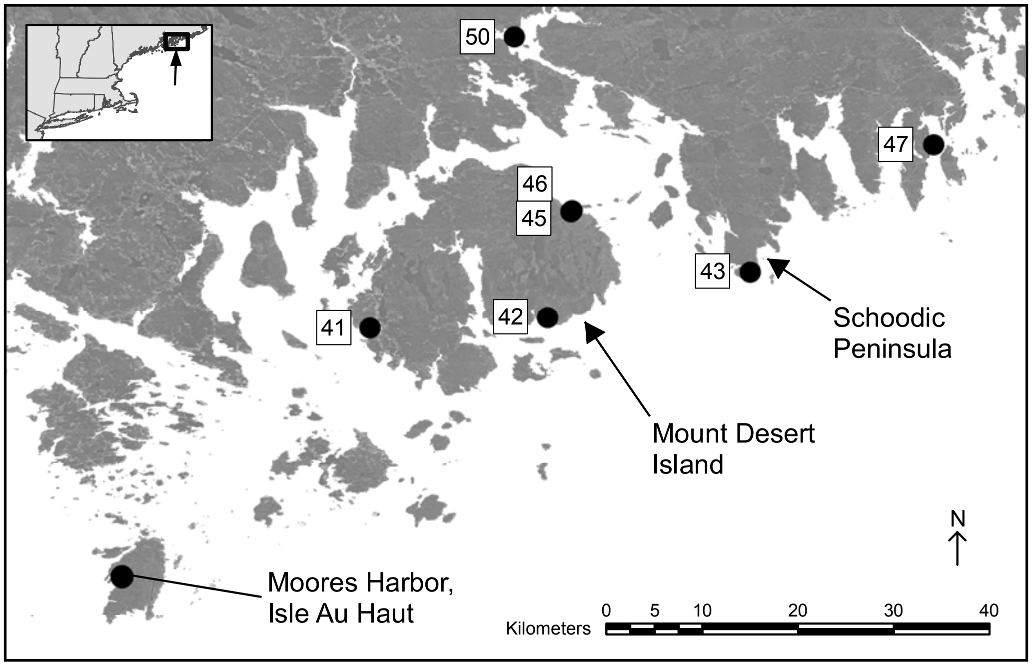

Figure 1.3 An aerial photograph of Maine from Moores Harbor, Isle au Haut to Narraguagus Bay. The circles that are numbered are sites that have been monitored in this study. While Moores Harbor was the previous known northernmost extent of *H. sanguineus*, current findings suggest that it is now found as far northeast as Schoodic Peninsula, Maine.

Linking Statement 2

In Chapter 1 I validated that the majority of volunteers I recruited can monitor native and invasive crabs with high levels of accuracy. From 2005 to the present I coordinated and maintained this citizen science monitoring network to survey the coast of New England and New York. The goal of this network was to detect newly arriving invasive species when their populations are localized and low in density, since this is when eradication may be possible. The creation of the citizen science network has greatly increased the amount of personnel monitoring for marine invasive species. Yet, the next logical and important question is whether the increased sampling intensity achieved by including volunteers is sufficient for effective early detection on various scales (e.g., a site, province, state, or country) with high probability of detection (POD) and how much personnel is needed for a certain monitoring objective. The answers to these questions depend on the sampling technique being used and the objective that is trying to be achieved (e.g., early detection). Therefore to make sampling less intensive, we need to devise a refined sampling technique to use personnel most effectively for early detection. In this chapter, I develop an approach to evaluate sampling techniques and determine whether a given objective is feasible.

Chapter 2. An Empirical Probability Model of Detecting Species at Low Densities

Abstract

False negatives, not detecting things that are actually present, are an important but understudied problem. False negatives are the result of our inability to perfectly detect species, especially those at low density such as endangered species or newly arriving introduced species. They reduce our ability to interpret presence-absence survey data and make sound management decisions (e.g., rapid response). To reduce the probability of false negatives we need to compare the efficacy and sensitivity of different sampling approaches and quantify an unbiased estimate of the probability of detection. We conducted field experiments in the intertidal zone of New England and New York to test the sensitivity of two sampling approaches (quadrat versus Total Area Search, TAS), given different target characteristics (mobile versus sessile). Using logistic regression we built detection curves for each sampling approach that related the sampling intensity and the density of targets to the probability of detection. The TAS approach reduced the probability of false negatives and detected targets faster than the quadrat approach. Mobility of targets increased the time to detection but did not affect detection success. Finally, we interpreted two years of presence-absence data on the distribution of the Asian shore crab (*Hemigrapsus sanguineus*) in New England and New York, using our probability model for false negatives. The type of experimental

approach in this paper can help reduce false negatives and increase our ability to detect species at low densities by refining sampling approaches, which can guide conservation strategies and management decisions in various areas of ecology such as conservation biology and invasion ecology.

Introduction

Bioinvasion is a form of global change that is homogenizing the biota of terrestrial and aquatic environments (Ricciardi 2007). Marine environments are no exception, as they are heavily invaded and colonization by new introduced species continues (Grosholz 2002, Grosholz 2005). Despite its importance and recent progress, marine invasion biology still lags behind its counterparts in terrestrial and freshwater ecosystems, and arguably, only started as a formal field of science in the 1970s (Carlton 1979, Ruiz et al. 1997, Grosholz 2002). Progress in this field, especially in our ability to manage marine introduced species, has been hindered by real-world limitations such as insufficient resources (e.g., funding, personnel, and equipment to extensively monitor vast areas), limited data, and an inability to perfectly detect organisms (Bax et al. 2001, Lodge et al. 2006). These problems are not ephemeral, so invasion biologists need to address them to achieve a central objective—more effective monitoring and management of invasive species to avoid significant economic, ecological, and/or human-health consequences (Carlton 2001).

Monitoring is an important precursor to effective management of invasive species. For instance, detection of bioinvaders at an early stage, when the population is localized and at a low density, will maximize the probability of successful eradication (Rejmanek and Pitcairn 2002). Often introduced species remain undetected or are only detected years after the initial introduction, when the population size is large and its distribution is already widespread (Geller et al. 1997). In the applied field of invasion biology, early detection can be the difference between successful eradication, which means a one time investment of money and personnel, or the costly establishment of an invasive species and the perpetual investments for control efforts. Optimal sampling approaches that minimize the probability of false negatives are vital to maximizing the success of monitoring efforts.

The ability to detect new invaders will be strongly affected by the monitoring approach used and the biological characteristics of the species. For instance, the random quadrat approach is arguably one of the most common sampling approaches (Chiarucci et al. 2003); it can provide data on population structure (Wernberg 2009), abundance (Rueda and Salas 2008), diversity of an ecosystem (Liuzzi and Gappa 2008), and is often used for monitoring and detection (Hewitt and Martin 2001, Robinson et al. 2004, Delaney et al. 2008). While this approach is useful for monitoring newly introduced species, it arguably falls short; it underestimates the presence of organisms at low abundance (Miller and Ambrose 2000). In contrast, it may be far simpler and more effective to perform a Total Area Search (TAS) – a modified time transect search of an entire area - rather than along a single line and not be constrained to searching small restricted areas defined by quadrats. The trade-off is that the TAS approach covers more area while the quadrat approach searches less area but in greater intensity and completeness. Further, there may be an interaction with species characteristics such as mobility. Motile organisms might be more difficult to detect than sessile organisms since they can hide from searchers as they do from predators, and this may differentially affect the efficacy of alternative sampling approaches. Alternatively, mobility might increase the probability of detection by alerting the searchers to the location of the organism. For monitoring to be more effective, we need to assess the probability of false negatives for different approaches and given different species characteristics (e.g., mobility).

Creating and comparing the efficacy of alternative approaches for early detection has been recommended as an urgent area of research (National Management Plan for the Genus *Eriocheir* 2003). However, research on the topic is limited (Hayes et al. 2005 and references therein). Capture-recapture approaches have shown promise to quantify an unbiased estimate of the probability of detection and false negatives (Otis et al. 1978, Pollock et al. 1990, MacKenzie et al. 2005). In this manuscript, we modify capture-recapture theory, integrating it with experimentally manipulated target and searcher densities in natural intertidal areas along the east coast of the USA, to test detection efficacy (i.e., the ability to detect at least one individual of a species in an area, if it exists). Further, we test different sampling approaches (quadrat versus TAS) and different target characteristics (mobile versus sessile). We produce a model to estimate the probability of detecting one individual in an area given different target densities and search effort. Finally, we link these models to two years of survey data.

Study system

The focal organisms for this study, the European green crab, *Carcinus maenas,* and the Asian shore crab, *Hemigrapsus sanguineus*, are both global invaders (Lohrer 2001, Breton et al. 2002, Schubart 2003, Carlton and Cohen 2003). These species are of great interest and importance to resource managers as both species can not only cause ecological damage but also prey upon economically important species such as shellfish and other crabs (Elner 1981, McDonald et al. 2001, Walton et al. 2002, Griffen and Delaney 2007). The areas sampled were sites within the intertidal zone of New England, New Jersey, and New York, which have already been invaded by *C. maenas* for almost two hundred years and have been colonized by *H. sanguineus* in the last twenty-five years (Williams and McDermott 1990, Carlton and Cohen 2003, Kraemer et al. 2007). Furthermore, this region is at risk for invasions by other decapod species such as the Chinese mitten crab, *Eriocheir sinensis* (Herborg et al. 2007), which has colonized the central section of the east coast of the USA and has been detected as far north as New York can cause ecological and economical impacts (NY DEC 2009). For these reasons, the IUCN has listed *E. sinensis* as one of the 100 worst invasive species (Lowe et al. 2000).

Methods

Manipulative field experiment

In the summer of 2006 we conducted field experiments to determine the relationship between detection of at least one individual and the following factors: sampling intensity (i.e., number of searchers or time searching), target density, sampling technique (quadrat and Total Area Search, TAS), and target mobility. The study was conducted across 40 sites from Rye, New York to Seal Harbor, Maine. Each site had from 1 to 49 people searching four 200 m^2 sections of the rocky intertidal zone, resulting in a sampling intensity ranging from 0.005 to 0.245 searchers/m^2. Therefore in total 160 areas were searched for the experiment. Each search group used both the TAS and quadrat sampling for 10 minutes per 200 m^2 area. Participants randomly placed 1 m^2 quadrats and sampled as many as were possible during the time period. At each site, the order that study areas were searched was randomized. We explicitly controlled for target density, by randomly placing different numbers of banded *H. sanguineus* and *C. maenas* crabs or oval marbles, to obtain a range of densities from 0.005 to 0.14 targets/m^2 (1 to 28 targets). At each site one density level was used at all four 200 m^2 areas. Banding of crabs allowed us to distinguish targets from other crabs in the area, thereby controlling density. The crabs were banded with a single 6.35 to 25.4 mm metal ring on one of their chelipeds (i.e., claws), rather than on their walking legs, so as not to reduce their mobility. To minimize edge effects (crabs moving out of the search area), we created a buffer region around the study area in which we distributed the banded crabs at the intended density but over a larger total area (900 m^2). To simulate sessile targets, we used flat oval marbles as a proxy, given the lack of sessile crabs. If the random coordinates where the marbles were to be allocated to locations where rocks occurred, the marbles were placed under that rock. These marbles, ranging from 12.7 to 25.4 mm, were in the middle of the size range for *H. sanguineus* and *C. maenas* as the average size (i.e., carapace width) for the 11,244 specimens of *H. sanguineus* and *C. maenas* collected during the 2006 survey was 19.7 mm (sd = 12.1 mm). The marbles were randomly allocated to a 400 m^2 section of the rocky intertidal zone at each site, which encompassed the two 200 m^2 study areas so there was a study area to be searched by each of the two approaches, separately.

Statistical Analysis

We tested whether sampling approach (quadrat versus TAS) and mobility (crabs versus marbles) affected detection by examining detection success (yes/no) as well as time to first detection (seconds) on a per site basis. We used 2x2 contingency tables with two-tailed chi-square tests with Yates' correction for continuity to determine whether mobility of target was a significant predictor of detection success (i.e., detectability) for either sampling approach, and to test whether there was a difference between the detection efficacy of the two sampling approaches. We used a block design ANOVA for time to first detection, with site as a blocking variable and two fixed effect within-block factors (mobility of target and the type of sampling approach). At one randomly selected site, Lovells Island, Boston, MA, we recorded the sizes of all crabs collected by each sampling approach. Neither distribution was normally distributed (Kolmogorov-Smirnov test, $P < 0.010$), so the non-parametric Mann-Whitney test was used to determine if the TAS sampling approach collected individuals that were significantly different in size.

Detection model

We used multiple logistic regression to test for a relationship between probability of detection of at least one individual in an area (POD), measured as the binary yes/no at each site, versus sampling intensity and density of targets:

$$POD = \frac{e^{(a+bT+cS)}}{1+e^{(a+bT+cS)}} \tag{2.1}$$

where *T* is the density of targets, *S* is the density of searchers, and *a*, *b*, and *c* are the regression coefficients. The compliment of POD is the probability of a false negative. From the regression model we can calculate the sampling intensity needed to detect a certain target density with a given POD. To quantify the density of searchers and targets, we need to know the amount of area of intertidal zone for the region of interest (e.g., state, country). Unfortunately, the area or width of the intertidal zone is not always known but the length of shoreline is known (Millhouser et al. 1998). From this, and by assuming that the average width of the intertidal zone is 30 m, we estimated the area of the intertidal zone for a region from its shoreline length (length of the shoreline multiplied by 30 m). This is an underestimate of the intertidal zone area, as it can almost reach a width of 1 km in certain areas of the Bay of Fundy. In 2005, all 52 sites within 7 states (New Jersey to Maine) surveyed had an intertidal width greater than 30 m at low tide. Therefore this is a conservative estimate of the sampling intensity needed for monitoring.

Presence–absence surveys for Hemigrapsus sanguineus

To apply our detection model to a current environmental problem, we conducted systematic surveys using the TAS approach and randomly placed quadrats from May through August, in 2005 and 2006. In 2005, 52 sites were sampled from Sandy Hook, New Jersey, to Machias, Maine. A sampling site was defined as a 30 by 30 meter section of rocky intertidal zone, which were suitable habitat for the introduced crab species *H. sanguineus* (Delaney et al. 2008). The sampling intensity varied from site to site, ranging from 1 to 69 people (0.001 to 0.077 searchers/m^2). In 2006, 30 sites were sampled from Rye, New York to Lubec, Maine with constant sampling intensity across the sites with 16 randomly placed 1 m^2 quadrats and 12 people each searching 10 minutes within an area of 200 m^2 (0.06 searchers/m^2), which was 10 vertical meters by 20 horizontal meters (Griffen and Delaney 2007).

Results

Comparing sampling approaches and quantifying false negatives

Mobility of the target did not affect the detection success of the quadrat (χ^2 = 0.564, df = 1, P = 0.452) or TAS approach (χ^2 = 0.779, df = 1, P = 0.377). Therefore, detection success data for sessile and mobile targets were aggregated for each sampling approach. However, mobility of the target did increase the time to first detection ($F_{1,117}$ = 4.89, P = 0.029). Sampling strategy was highly significant for both the continuous ($F_{1,117}$ = 108.41, P < 0.001) and binary (χ^2 = 46.692, df = 1, P < 0.0001) response variables in the corresponding statistical tests. TAS was a significantly better approach for detecting targets at lower densities of targets and searchers (Fig. 2.1). The searchers using the TAS approach detected the first target more quickly than with the random quadrat approach (Fig. 2.2). The TAS approach is more effective at detecting a species at lower target density but is biased towards collecting larger individuals on average than the quadrat approach (Mann-Whitney test, $P < 0.001$). Twenty-nine percent of the crabs collected by the random quadrat approach were smaller than 1 cm, compared to only 10% of the crabs in this size class for the TAS approach. The large size class of >3 cm comprised 1.1% of the crabs collected by the quadrat approach but comprised 7.7% of crabs collected by the TAS approach.

In a multiple logistic regression, the density of targets and sampling intensity were significant for both the quadrat and TAS approach (Table 2.1). For the TAS approach, the highest density of targets that was not detected was 0.07 targets/m^2, at a sampling intensity of 0.005 searchers/m^2 (i.e., a single searcher) and was half of the highest target density that the quadrat approach missed, 0.14 targets/m^2 (Fig. 2.1).

Detection Model

The multiple logistic regressions generated the needed coefficients (Table 2.1) to parameterize the statistical model based on equation 2.1. The model coefficients were used to calculate contour plots of the probability of detection as a function of the density of searchers and targets (Fig. 2.3). This model applies when the sampling intensity and density of the targets are both greater than zero. Using an estimated intertidal width of

30 m, the model was used to calculate the amount of time needed to monitor the coast of a certain area, such as a site, an entire state or a country. To realize a 95% POD of at least one invader present in a 200 m^2 section of intertidal zone, would require a total of 2.2 hours of TAS sampling, but for the quadrat sampling approach 9.5 hours of total searching would be required. To monitor New Hampshire, the state with the smallest coastline in our study area (211 km), would require a minimum of approximately 301,000 hours of quadrat sampling to have a 95% POD of an invader at a low density of 0.005 crabs/m^2. The TAS approach would require 68,300 hours of sampling along the coast of New Hampshire. On a national-scale, to have this level of effectiveness, using the quadrat approach, would require at least 203,000,000 hours of sampling and with the TAS approach would require 46,200,000 hours of sampling. Other states in the study area were somewhere in this range for sampling intensity needed (Fig. 2.4). Given these conditions, the TAS approach requires less than a fourth of the sampling intensity than random quadrat approach to achieve the same level of effectiveness, however, both require an exorbitant amount of effort.

Presence – absence surveys for Hemigrapsus sanguineus

In 2005, 1 to 69 people conducted the random quadrat sampling technique and the TAS approach, so the POD varied from site to site due to different sampling intensities. If one crab was present at a site, a single person carrying out a search would have a POD of 1.2% and 13.5% for the quadrat and TAS approach, respectively. For 69 people searching a site with the same target density, the POD would be 7.4%

and 97.4% for the quadrat and TAS approaches, respectively. Both the TAS and quadrat surveys conducted in 2005 showed a discontinuous distribution of *H. sanguineus* (Fig. 2.5A, B). The 2006 quadrat survey (Fig. 2.5C) found a discontinuous distribution, while the 2006 TAS survey (Fig. 2.5D) documented a continuous distribution. In the 2006 quadrat survey, given a constant sampling intensity across sites, there was a 6.0% POD where the TAS approach had a 93.1% POD.

Discussion

Detection

Detection is a critical component of management strategies, maximizing the ability to respond rapidly and most effectively to novel invaders (Lodge et al. 2006). Further, it is highly relevant for interpretation of survey results, which often rely on presence-absence data (e.g., National Parks Service's All Taxa Biodiversity Inventory). Presence-absence data are becoming more popular given new statistical approaches to use the data and as it is readily available, cheaper, and easier to obtain on the large-scale (Pereira and Itami 1991, Hanski 1994, MacKenzie et al. 2002, MacKenzie et al. 2003, Tyre et al. 2003, Wintle et al. 2005). Although widely acknowledged, it is difficult to quantify the uncertainty in detection by a sampling approach. Therefore, many researchers and managers assume the rate of false negatives is negligible for presence-absence survey data even though such errors have been recorded to be as high as 87% (Wintle et al. 2005). In this study, we found the probability of a false negative in survey data can even be higher (94% for quadrat sampling). Therefore, researchers examine their data, creating, and analyzing patterns that might be inherently flawed. However, if identifying and quantifying uncertainty were possible, researchers and managers would be able to incorporate it into models or at least quantitatively assess the reliability of data. For monitoring, consideration of false negatives can determine the feasibility of a certain survey or monitoring objective.

Quantifying the probability of detection

Given the importance of quantifying false negatives, researchers have developed different methodologies to assess and ameliorate these issues (MacKenzie et al. 2005 and references therein). Our experimental approach yields an unbiased estimate of the probability of detection, since we know that one or more targets are present at each site, so every non-detection is a false negative and is quantified. This type of experimental approach can quantify the actual probability of detection and false negatives and can help better understand and interpret presence–absence survey data and design better monitoring programs.

The probability of detection is strongly affected by the density of searchers and targets but many other factors could also negatively or positively affect the probability of detection. These factors include but are not limited to the size, behaviors, and color of the organism and external factors (e.g., habitat, weather). What factors increase or decrease the probability of detection could have management implications. For example, the probability of detection may be lower for small and young individuals.

Nevertheless, if we can detect the invader before sexual maturity, theoretically eradication may still be possible (Edwards and Leung, *in press*).

The methods and experiment developed in this paper would allow researchers to determine if these and other factors for species detection are important and quantify an unbiased estimate of the probability of detection, which would allow for better management of a species. Particularly, the approaches presented in this manuscript are most applicable for sessile (e.g., algae, barnacles, bryozoans, hydroids, tunicates, etc.) and slow moving organisms (e.g., clams, chitons, other species of crabs, limpets, nudibranchs, sea urchins, sea stars, snails etc.), which will remain in the study area, permitting estimation of their densities. Such slow moving or sessile organisms are common invasive species and are highly abundant in the intertidal zone. Therefore, this experimental approach will be relevant for a large subset of invasive species.

A case study: Monitoring invasive species in Salem Sound

Refining sampling approaches can increase the abilities of monitoring groups to detect newly arriving invasive species. Salem Sound is a large, well studied embayment north of Boston, Massachusetts with an intertidal zone area of approximately 4.8 million m^2 (1186.58 acres) (Chase et al. 2002). To date, the intertidal zone of Salem Sound has been documented to contain at least 12 introduced species, including *C. maenas* and *H. sanguineus*. This area is at risk for future invasions by other decapod crustaceans such as *E. sinensis* and the brush-clawed shore crab *Hemigrapsus takanoi*, and it is currently monitored by a non-governmental organization (NGO) called Salem Sound Coastwatch.

This organization, like most NGOs is small, having only one to three paid staff at any time, so they train volunteers to monitor the coastline for introduced species in Salem Sound. In 2005 and 2006, Salem Sound Coastwatch trained 30 volunteers to monitor Salem Sound (B. Warren, *personal communication*). The methodology was used to conduct monthly monitoring in the summer using randomly placed quadrats in the high and the low intertidal zone to detect introduced species that were present in Salem Sound.

Using the model developed in this paper, we can quantify the probability of detecting an invader at any density, given their sampling intensity, for the area of intertidal zone of Salem Sound using their current sampling approach and compare it to their effectiveness of using the TAS approach. We estimate that with a sampling intensity of 30 people each searching 10 minutes, there is a 1.4% or 14.7% probability of detecting an introduced species at a density of 0.005 crabs/m^2 in the intertidal zone of Salem Sound using the random quadrat sampling or TAS approach, respectively. The TAS approach is an order of magnitude more effective in its ability to detect species at low densities than the quadrat approach. Unfortunately, even with the better sampling approach early detection is still a low probability, labor-intensive task. To have a 95% probability of detecting an invader in Salem Sound at a density of 0.005 crabs/m^2 would require 26 or 115 full-time personnel (i.e., 2,000 hours/person) monitoring with the TAS and quadrat approach, respectively. In 2007 the personnel and volunteers of Salem Sound Coastwatch switched from mainly using the random quadrat sampling approach, which they had used for the previous three years, to primarily using the TAS approach based on our recommendation (B. Warren, *personal communication*).

Comparing alternative sampling approaches

We recommend quantitative experiments to determine the abilities and limitations of a sampling approach as every sampling technique has different strengths and weaknesses. We offer a search theory approach that will help scientists and practitioners quantitatively compare alternative sampling approaches in a standardized manner. Although random quadrat sampling is the most common way to sample an area (Chiarucci et al. 2003) because it can enumerate estimates of population structure (Wernberg 2009) and abundance (Rueda and Salas 2008), it is not effective at detecting organisms at low densities (Figs. 2.1 and 2.2). The TAS approach is more effective at detecting organisms low in abundance; the trade-off is that TAS is biased toward finding larger individuals. Also the TAS approach is currently not able to quantify the density of a species but this may be possible and should be an area for future research. However, the TAS approach is a more powerful and simpler technique than random quadrat sampling. It is more easily performed by volunteers, which increases sampling intensity, as seen in Salem Sound. This type of program should be done in other regions as the entire east coast of North America is at risk for the establishment of *E. sinensis* (Herborg et al. 2007). We have demonstrated that these sampling approaches have significantly different abilities to detect the focal organisms and this can have important ramifications. For this reason, we need to better understand what the best sampling approach is for a given objective. The type of experimental approach in this study can be used to compare other sampling techniques (e.g., trapping). For early detection to be possible, we need new sampling approaches and experiments to evaluate their efficacy and sensitivity for monitoring various species at low densities.

Avoidance

The probability of detecting a species at low densities, which has been shown to increase the probability of successful eradication, could be species-specific (Hayes et al. 2005). The optimal sampling approach may be determined by the biological characteristics of the focal species, such as mobility. Certain sampling approaches, such as quadrat or transect sampling, take initial setup before sampling occurs that could allow motile organisms to move out of the sampling area and therefore not be detected (Hayes et al. 2005). This has been called avoidance and could be an important factor affecting the detection of motile organisms (Bohnsack 1979). We found that motile organisms took longer to detect than our proxy for sessile organisms, which is evidence of the existence of avoidance, but did not significantly affect detection success. We hypothesize that this is the case for the focal species of this study because when startled they usually hide under the closest rock. In other environments or for other species the disturbance of placing a quadrat or laying out a transect could result in the organisms leaving the search area and increase the importance of avoidance in the form of reduced detection success (Hayes et al. 2005). Therefore, avoidance should be studied further with different species as it may hinder our ability to rapidly and effectively detect species at low densities, which is critical for successful control and eradication programs.

To date there have only been a handful of successful eradications of marine introduced species and early detection was key (Bax et al. 2001, Kuris 2003). Our review of the relevant peer-reviewed literature found that all the marine introduced species that have been successfully eradicated are organisms with completely sessile adult life stages. The only possible exception is the eradication of a tube-dwelling sabellid polychaete *Terebrasabella heterouncinata* from Cayucos, California by removing adult snails, which act as host species for the invader (Culver and Kuris 2000, Kuris 2003). An example of a sessile adult organism being successfully eradicated is the black-striped mussel *Mytilopsis sallei* (Kuris 2003). It was detected in Darwin, Australia possibly within the first 6 months after it was introduced (Bax 1999, Kuris 2003) and nine days after it was detected a rapid response plan was agreed upon and initiated, which resulted in successfully eradicating *M. sallei* (Bax et al. 2002). Understanding how biological characteristics affect detectability will help select a sampling approach for detecting a target species or at least identify what species might be easier to detect and eradicate and guide funding and policy decisions.

Detectability in presence – absence surveys

Non-detection does not necessarily mean non-occurrence of a species. The 2006 quadrat survey displays a discontinuous distribution of *H. sanguineus*, since the organism was not detected at one site within its known distribution. The probability that our 2006 quadrat survey missed detecting *H. sanguineus*, if present, at this site could be as high as 94%. Therefore, there is a high probability of a false negative being recorded at this site. This is confirmed by the fact that the TAS approach detected *H. sanguineus* at this site on the same day that it was not detected by the quadrat approach (Fig. 2.5C, D). The 2006 TAS survey dataset (Fig. 2.5D) depicts a continuous distribution of *H. sanguineus* with a boundary of its distribution in Maine, but how confident are we in this conclusion? This question is similar to observing an apparent gap in the surveyed distribution of a species. The probability of the conclusion being correct (PCC) decreases with the probability of not detecting (POND) a species and increases with the number of repeated surveys (N) in a gap or boundary region with no detections:

$$\mathrm{PCC} = 1 - \mathrm{POND}^{N} \qquad (2.2)$$

In this case we surveyed 10 sites in northern Maine and did not detect the presence of *H. sanguineus* at any of these sites. The POND for a single invader if present was 6.9%. Therefore the probability of this actually being a boundary is >> 99.9%. This is supported by the fact that to date *H. sanguineus* has not been detected along the coast of Canada.

Solution to a personnel problem

Limited sampling intensity can lead to false negatives and survey data with misleading depictions of species distributions (e.g., Fig. 2.5C). Accurately recording this type of data and for early detection of newly arriving invasive species requires high levels of sampling intensity. To illustrate this point, we have considered the minimal amount of personnel or time that would be needed to monitor the coastline in its entirety with equal level of sampling intensity (Fig. 2.4). Even with TAS, the more efficient sampling approach, 23,100 people working full-time would be needed to monitor the coast of the USA. This is too labor-intensive to be feasible and more effective and practical strategies must be found.

To overcome this challenge we recommend a multipronged approach of prevention, increased funding for monitoring, creating a predictive spread model to prioritize areas to monitor, and incorporating trained volunteers in monitoring. Prevention can be more cost-effective than managing the impacts of an invader (Leung et al. 2002, Bax et al. 2003). Unfortunately, no matter how effective prevention programs are, they will never be 100% effective and species will still be colonizing, so we must continue to monitor, especially in certain areas of the coast that are more likely to be colonized (e.g., seaports, most suitable habitats of the invader) (Lodge et al. 2006). Advances in theoretic understanding are occurring in invasion biology, that predict habitat suitability and dispersal patterns for a species (e.g., Leung and Mandrak 2007). These advances allow us to identify areas at highest risk and would provide a way to ameliorate the personnel limitations for large-scale monitoring. The most cost-effective option is incorporating citizen scientists (i.e., trained volunteers) in monitoring. Scientists can easily recruit volunteers in large numbers and with the aid of a field guides volunteers can identify native and invasive species of crabs with high levels of accuracy (Delaney et al. 2008). Citizen scientists can increase the sampling intensity in areas that are currently being monitored and monitor areas that are not currently being monitored. Also the TAS approach, which is more effective for detecting species at low densities, is simpler and easier for volunteers to execute. Even with the most effective approach and incorporating volunteers in monitoring, we may not have sufficient personnel to monitor the entire coast with the level of intensity that is needed for early detection. We probably still need to further reduce the amount of labor by continued experimentation on other sampling approaches (e.g., trapping) to optimally monitor.

This problem of limited resources and vast amounts of area to monitor is a common and challenging problem for practitioners and ecologists but the solution may come from a different field that has had to deal with a similar problem: optimal allocation of search effort (Koopman 1953, Stone 1989). During World War II, search theory was developed by Bernard Koopman and the Anti-Submarine Warfare Operations Research Group of the US Navy to optimally detect German submarines in the Atlantic Ocean with limited resources (Koopman 1946, Koopman 1980). The goal was to determine the best way to detect enemy submarines and to maximize the chance of success by using different search patterns, while minimizing the amount of equipment and personnel needed. Later, search theory helped the US Coast Guard guide search and rescue missions doubling or tripling successful rescues (Cooper et al. 2003). Although this area of research has been mainly used by the military, recently it has been suggested to have useful applications in the field of ecology (Cacho et al. 2007) but has not yet been used in ecological surveys in marine systems. We propose that search theory could inform ecologists and resource managers how to optimally allocate limited resources, such as personnel, and determine what is the best approach for a certain survey or monitoring objective.

In summary, since labor is limited, our ability for early detection is greatly hampered and this leads to many false negatives in large-scale presence-absence survey data. Predictive spread models would identify areas of high risk for colonization, so if we can not monitor everywhere, given the same sampling intensity, we maximize our chance for detection by searching high risk areas. We recommend involving citizen scientists and conducting quantitative search theory experiments to determine optimal sampling techniques and areas to search. Our experimental approach used in this study allows quantitative comparison of sensitivity and efficacy of different approaches and quantifies the probability of detection. We created a model that dynamically calculates sampling intensity needed depending on different levels of effectiveness and spatial scales (a site, region, state, or country). The problems, as well as the approaches, are generalizable. By quantifying the limitations of sampling approaches and data, researchers and managers can better understand patterns in presence-absence survey data, which allows for better research, management, and policy decisions.

Acknowledgements

This research was funded by NOAA’s National Sea Grant Aquatic Invasive Species Research and Outreach Program (NA05OAR4171088). Field work was assisted by C. Sperling and S. Trottier. We thank M.F. Delaney, H.R. Spence, and two anonymous reviewers for offering comments that greatly improved the manuscript.

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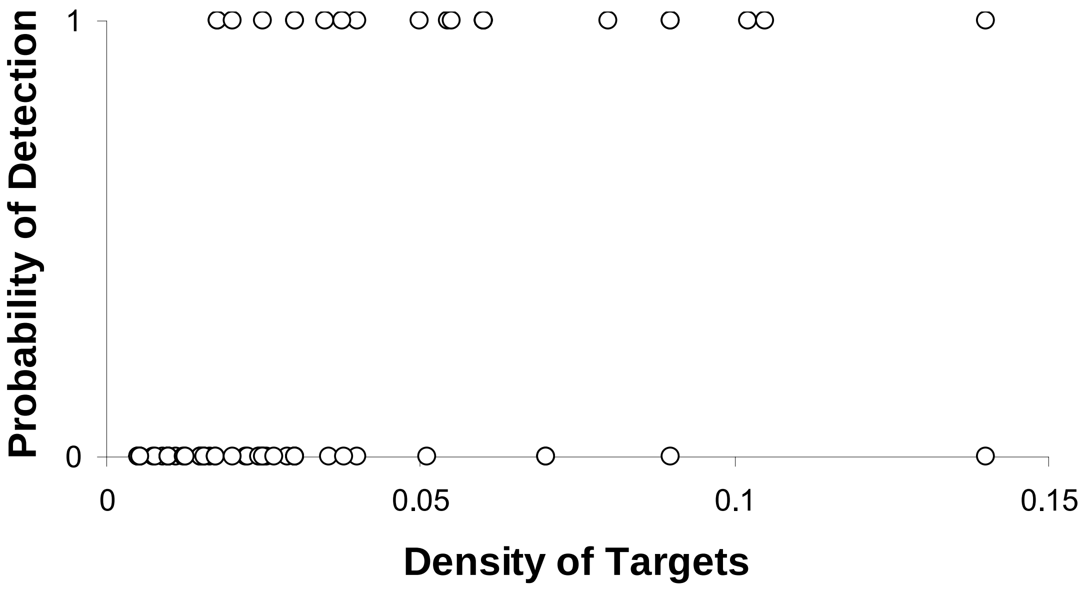
Tables

Table 2.1 The multiple logistic regression coefficients (“Coef.”) used in equation 2.1 are displayed with standard error (“SE”), Z-score (“Z”) and P value (“P”) for the two sampling approaches.

Sampling Approach	Parameter	Symbol	Coef.	SE	Z	P
Total Area Search	Constant	*a*	-1.988	0.791	-2.51	0.012
	Target Density	*b*	45.340	23.032	1.97	0.049
	Sampling Intensity	*c*	72.723	20.989	3.46	0.001
Quadrat Search	Constant	*a*	-4.512	0.948	-4.76	<0.001
	Target Density	*b*	48.380	12.214	3.96	<0.001
	Sampling Intensity	*c*	25.297	8.178	3.090	0.002

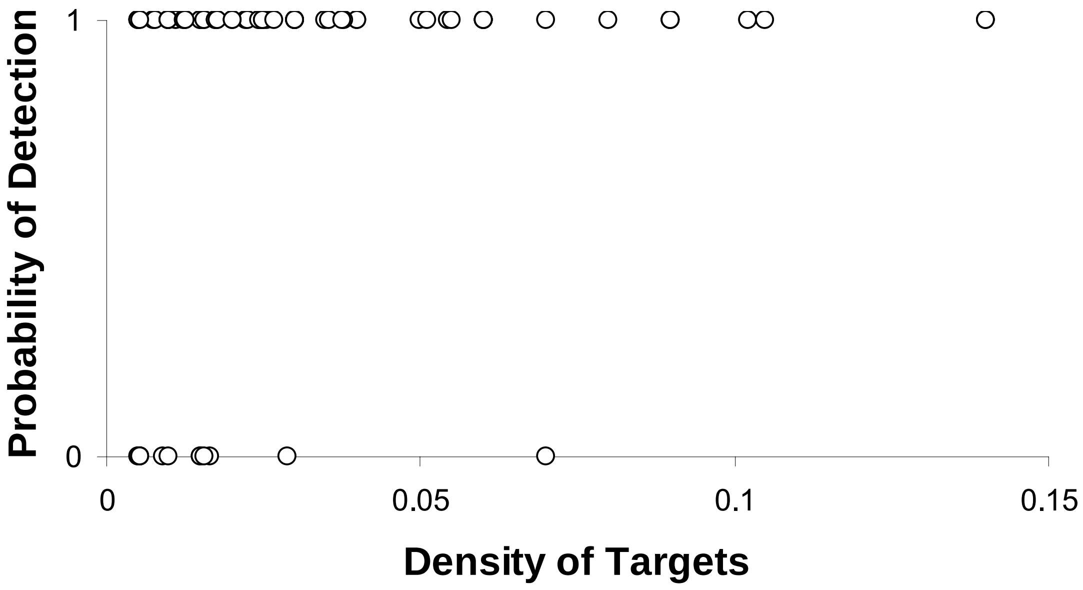
Figures

A



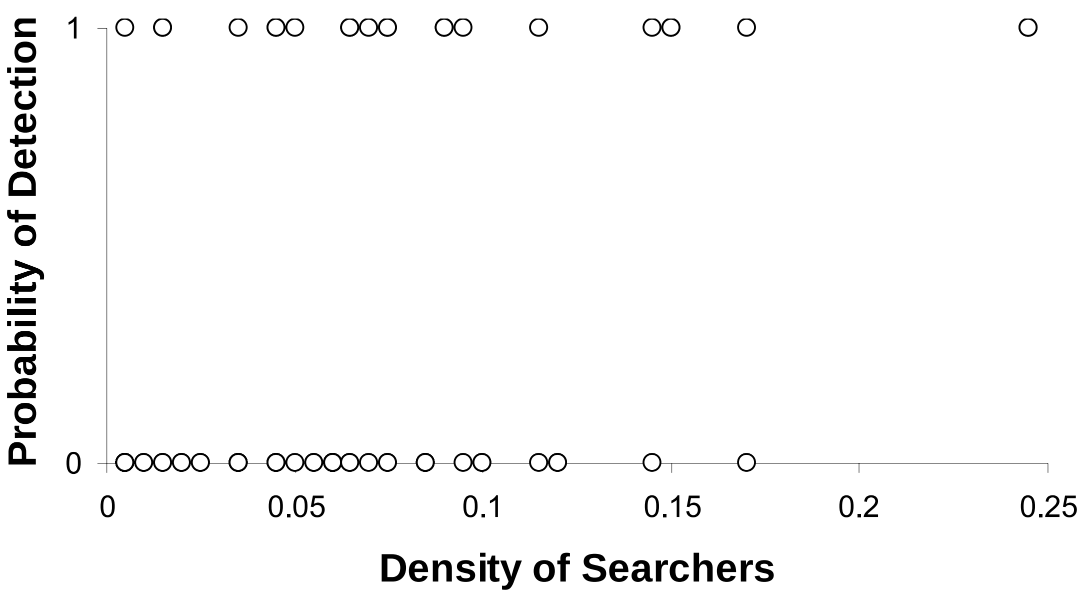
Probability of Detection
1
0
0
0.05
0.1
0.15
Density of Targets

B



Probability of Detection
1
0
0
0.05
0.1
0.15
Density of Targets

C


Probability of Detection
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0
0
0.05
0.1
0.15
0.2
0.25
Density of Searchers

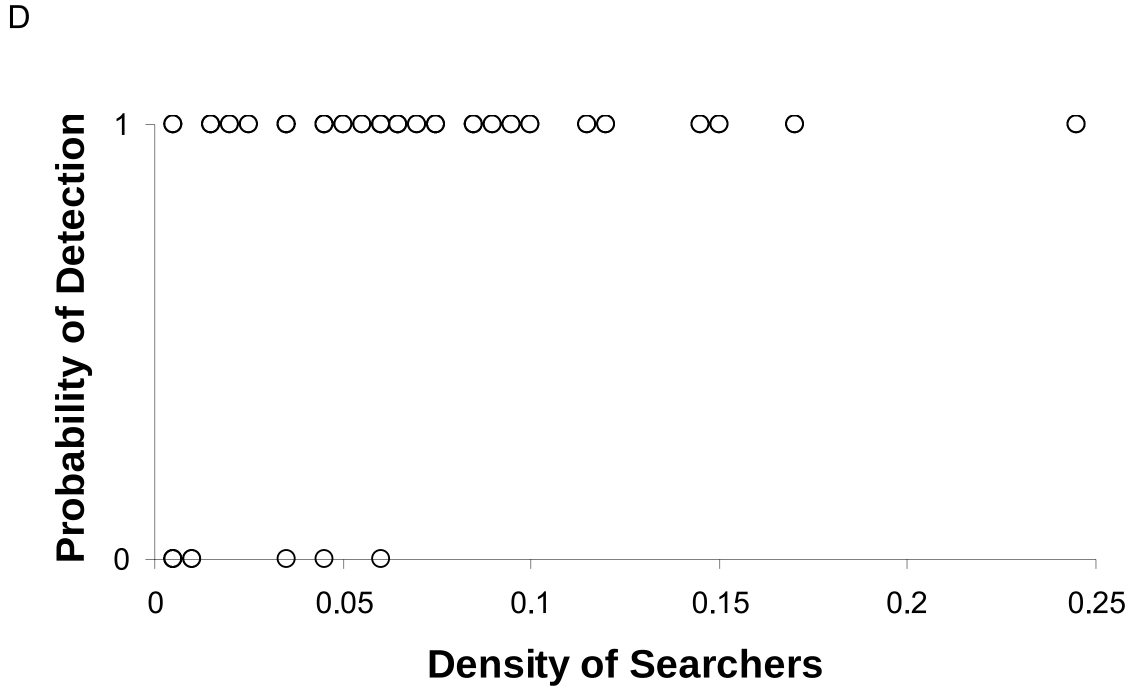
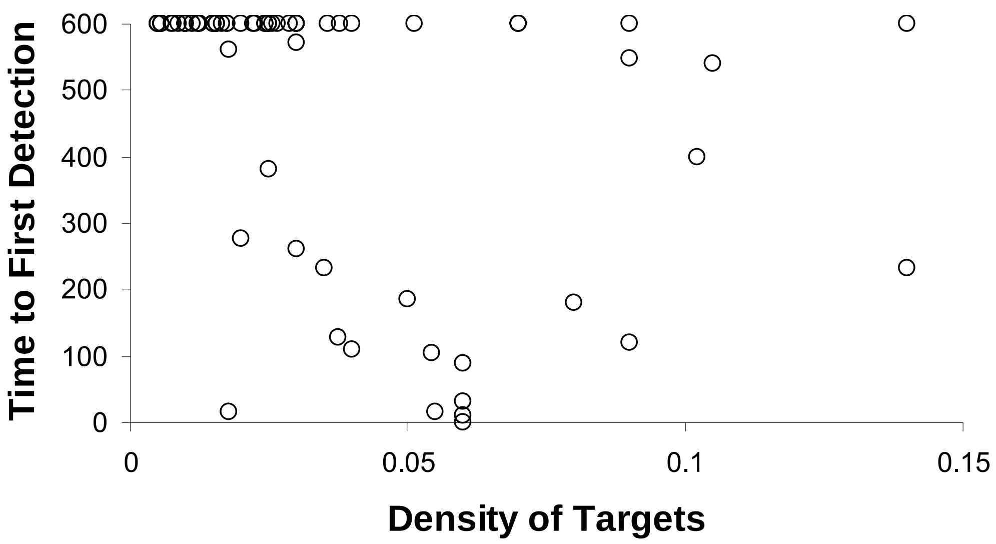
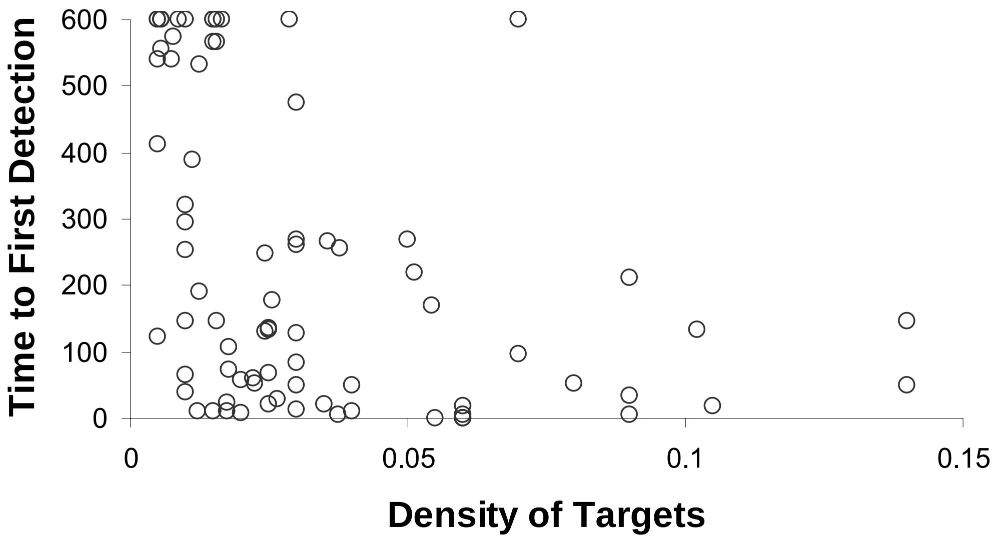


Figure 2.1 Probability of detection data (1 = detected, 0 = not detected) versus density of targets (targets/m^2) for A) Random quadrat sampling and B) TAS sampling. Probability of detection data versus density of searchers (searchers/m^2) for C) Random quadrat sampling and D) TAS sampling. Since there was at least 1 target at each sampling area, all zeroes represent false negatives.

A


Time to First Detection
600
500
400
300
200
100
0
0
0.05
0.1
0.15
Density of Targets

B


Time to First Detection
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400
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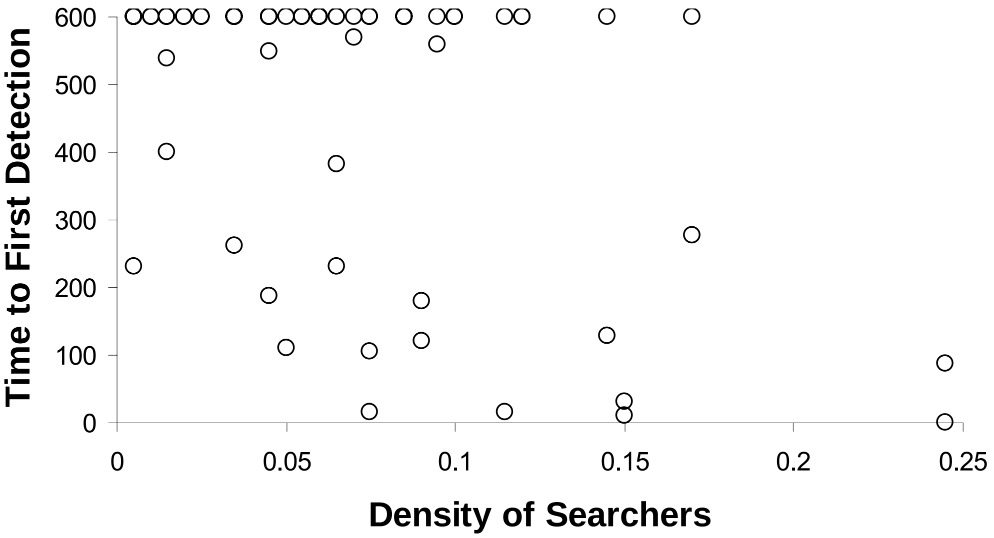
200
100
0
0
0.05
0.1
0.15
Density of Targets

C



D

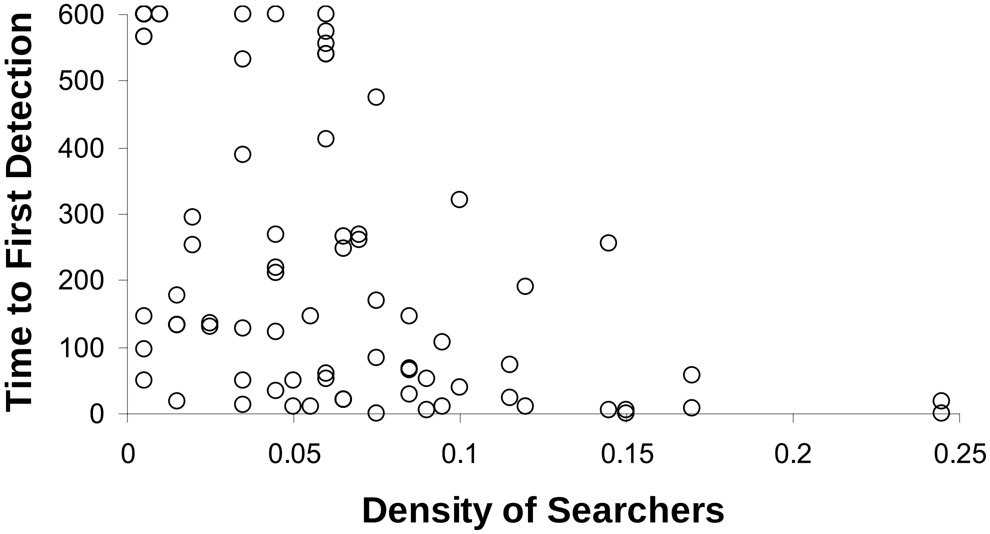


Figure 2.2 Time to first detection (seconds) versus density of targets (targets/m^2) for A) Random quadrat sampling and B) TAS sampling. Time to first detection versus density of searchers (searchers/m^2) for C) Random quadrat sampling and D) TAS sampling. The maximum search time is 10 minutes, so data points at 600 seconds are false negatives.

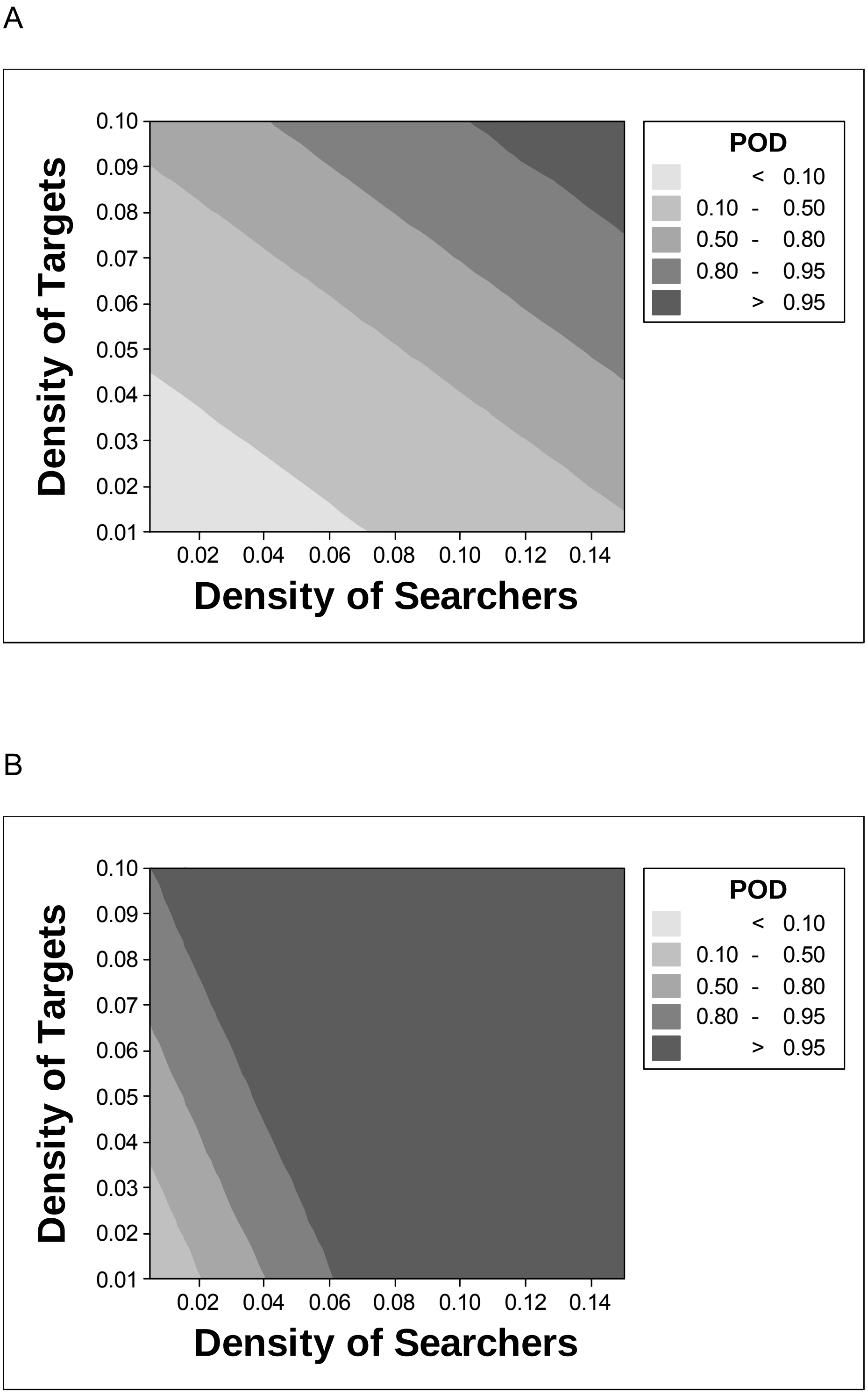


Figure 2.3 Contour plots of predicted probability of detection (POD) versus density of searchers (searchers/m^2) and density of targets (targets/m^2) for the random quadrat (A) and the TAS approach (B).

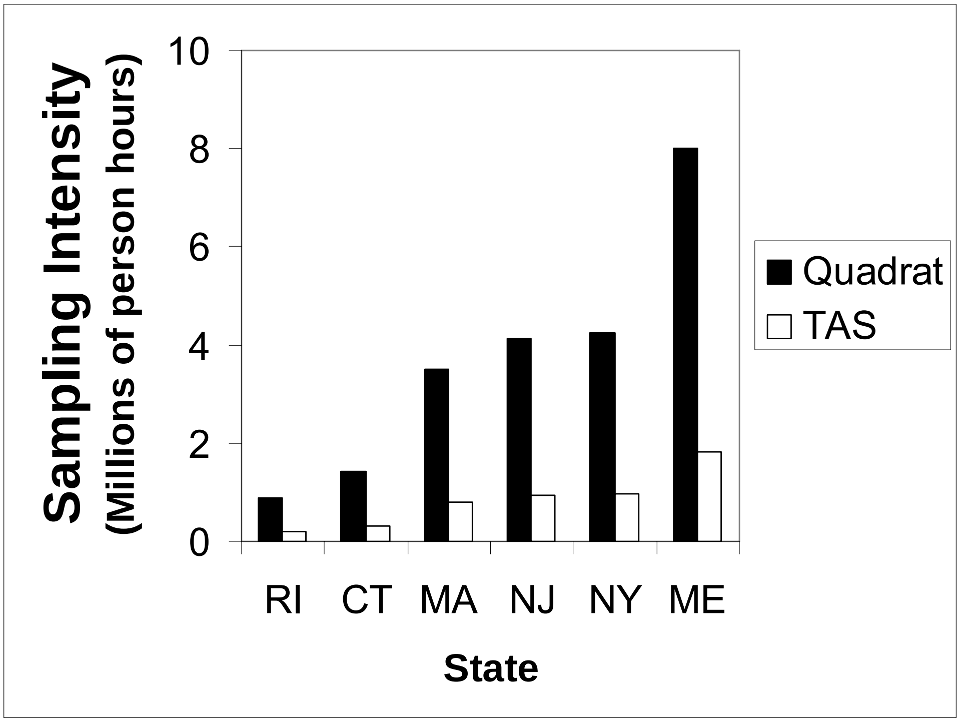
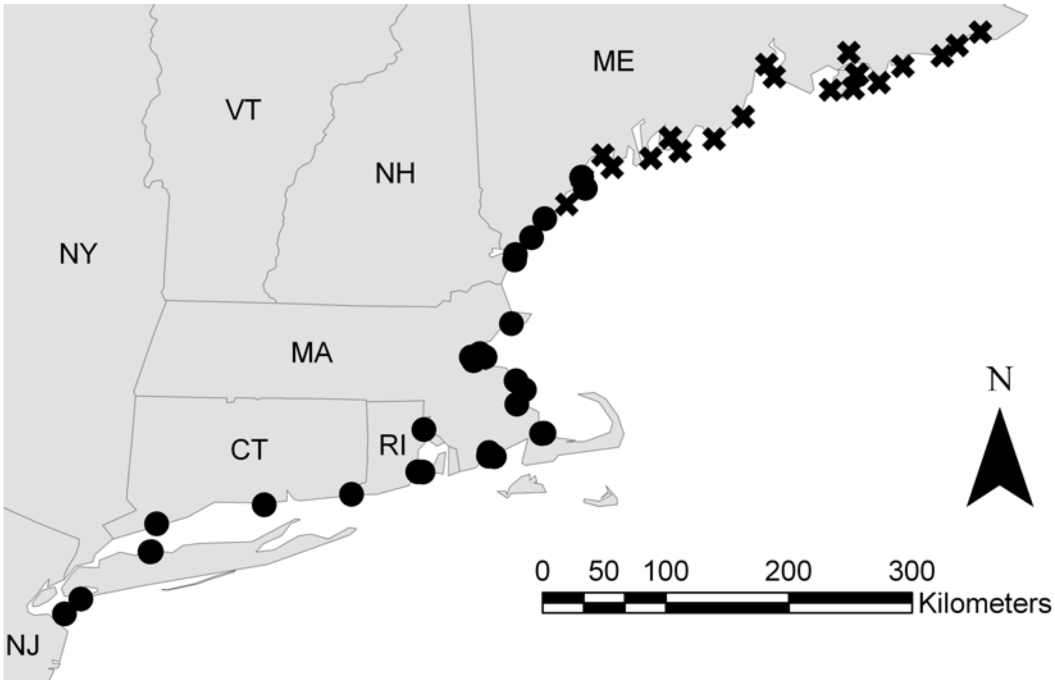


Figure 2.4 Estimated minimum number of hours needed to detect an invader at a density of 0.005 crabs/m^2 with a 95% probability of detection for the TAS approach (whites bars) and the random quadrat approach (black bars) for the coasts of Connecticut (CT), Maine (ME), Massachusetts (MA), New Jersey (NJ), New York (NY), and Rhode Island (RI).

A


ME
VT
NH
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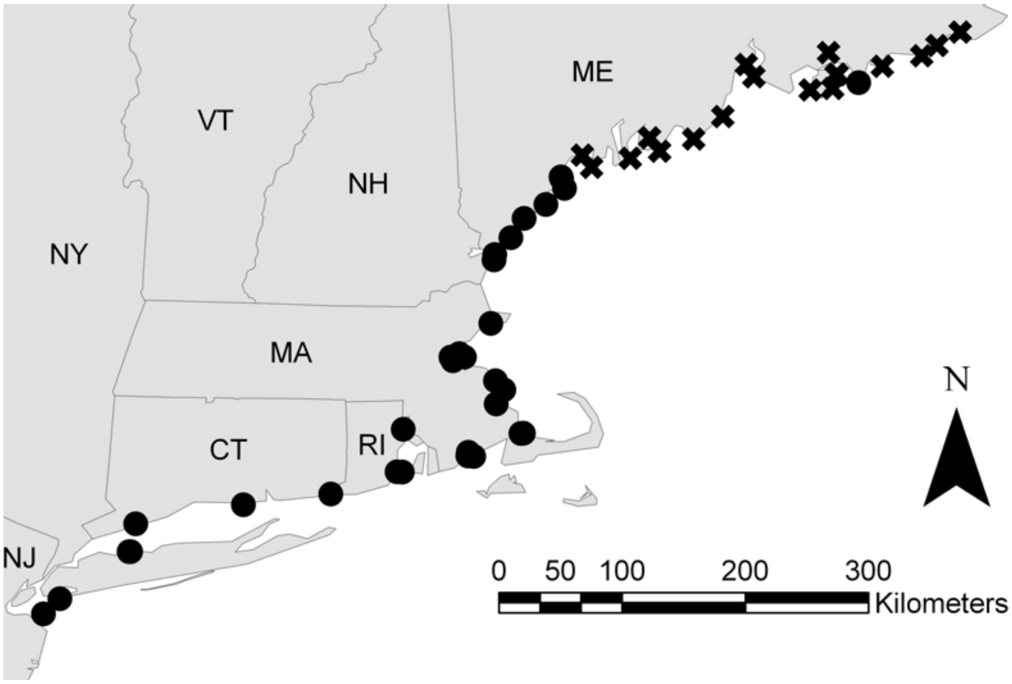
MA
CT
RI
NJ
N
0
50
100
200
300
Kilometers

B


ME
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NH
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MA
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N
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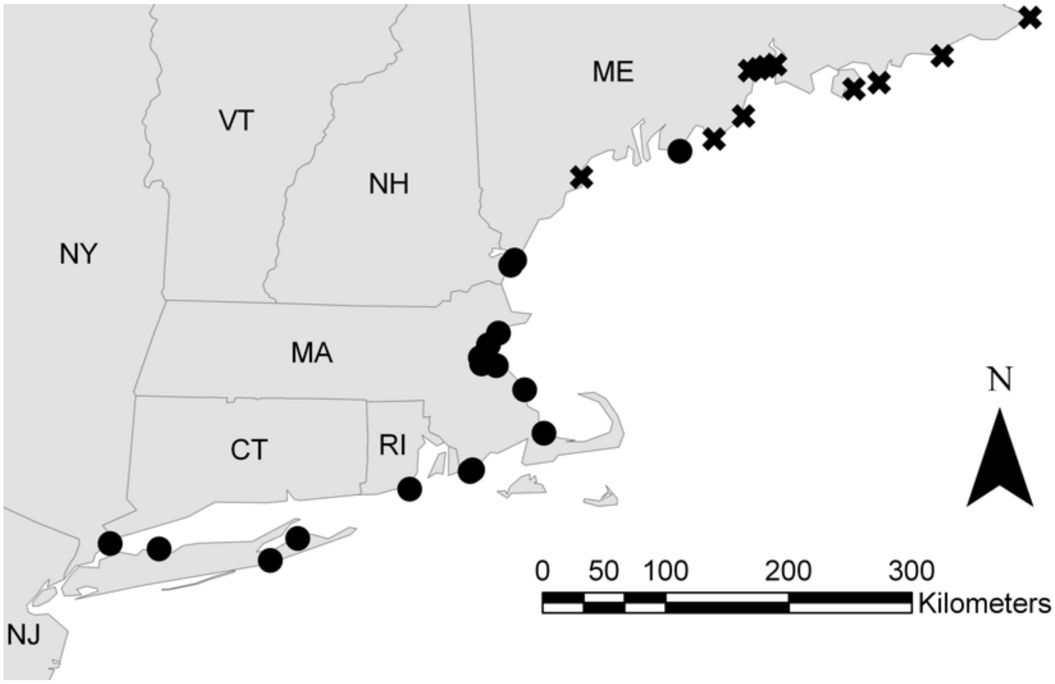
200
300
Kilometers

C



D

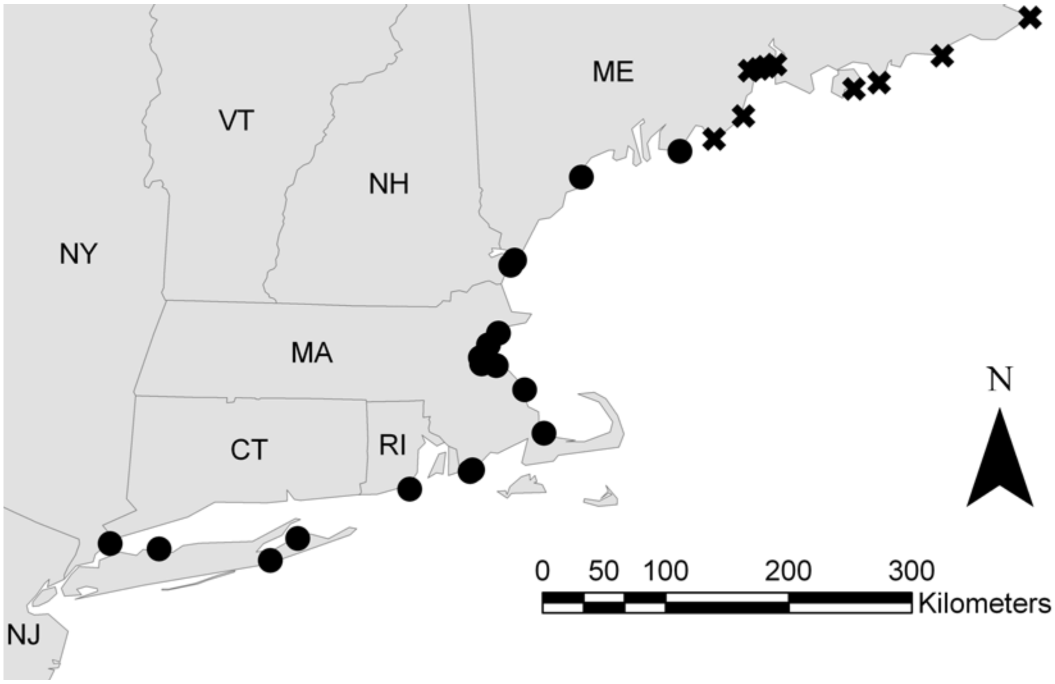


Figure 2.5 The 2005 survey (A and B) consisted of 52 sites from Sandy Hook, New Jersey (NJ) to Machias, Maine (ME). The sampling intensity varied across sites. A) Random quadrat sampling, B) TAS sampling. The 2006 survey (C and D) was conducted with even sampling intensity at 30 sites from Rye, New York (NY) to Lubec, Maine. C) Random quadrat sampling, D) TAS sampling. The circles denote locations that *Hemigrapsus sanguineus* was detected and an “X” denotes a site that was sampled but *H. sanguineus* was not detected.

Linking Statement 3

Although the citizen scientist monitoring network increased our sampling intensity (Chapter 1) and the efficiency of the Total Area Search technique decreased the sampling intensity needed (Chapter 2), given real-world limitations, there is still insufficient resources for early detection monitoring of invasive species on the large-scale (Chapter 2). Therefore we need to know where introduced species are likely to be transported so we can allocate our limited resources to those areas. Most marine organisms, whether native or introduced, have planktonically dispersed life stages that allow them to be transported to a range of locations. If oceanographic models can predict what areas are most likely to be colonized, we can optimally allocate limited resources for monitoring (e.g., funding, personnel) to those areas at high risk for secondary spread, increasing the probability of early detection and successful eradication. Therefore early detection can be effective, even with real-word limitations since we would not have to monitor the entire coastline with equal sampling intensity. To do this I use the density data collected in Chapters 1 and 2 combined with data from a drift card study and a recruitment study, which were also assisted by volunteers, to create a large-scale standardized dataset to examine if an oceanographic model can predict the spread of intertidal invasive species.

Chapter 3. Predicting Regional Spread of Invasive Species Using Oceanographic Models – Validation and Identification of Gaps

Abstract

Predicting spread is a central goal of ecology that has intrigued and challenged biologists for decades. Given the growing problem of invasive species, predicting spread now has both important pure and applied applications. The coast of New England, USA is currently invaded by the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*), which are still spreading throughout the Northwest Atlantic. We conducted two empirical studies, a recruitment study and a drift card study, to explicitly evaluate the ability of oceanographic models to predict patterns of spread. The drift card recovery data were used to establish the validity of a physical oceanographic model, excluding biological processes. The model was then expanded by incorporating biological processes to capture pertinent aspects of larval behavior (diel vertical migration, ontogenetic migration) that could cause the larvae to disperse differently from passive particles. To model the spread of invasive species, we devised a way to estimate propagule pressure from data we obtained by monitoring the adult densities of the two established species for two successive years at sites from New York to Maine. The joint biological-physical model could not predict the spread of *C. maenas* and *H. sanguineus*. Given the model's ability to predict drift cards, its inability to correctly predict the spread of intertidal invasive species could be due to incompletely incorporating larval behavior into the model. Therefore while marine

debris, oil spills, and other passively transported items could be predicted, further modeling and larval ecology research is needed before the spread of intertidal organisms can be reliably predicted by oceanographic models.

Introduction

Invasive species are a current and growing environmental problem that is a form of global change (Ricciardi 2007). Thousands of introduced species are being transported around the world every day (Carlton 1999). When an invasive species becomes established, it can reach high densities and cause secondary spread by producing propagules that are transported to new locations by physical and biological processes. Researchers and managers need to detect and manage secondary spread as it determines the extent and impact of biological invasions (Lodge et al. 1998).

Forecasting spread has been studied for decades due to the important pure and applied ramifications (Fisher 1937; Skellam 1951; Shigesada and Kawasaki 1997; Yoshimura et al. 1999; Leung and Mandrak 2007). The ability to accurately forecast spread of invasive species has been limited, particularly in marine systems (Grosholz 1996). While increased computational capacity and research have greatly increased the capability of physical and biological models, rich, large-scale datasets to parameterize and validate these models for application to invasion biology are scarce.

Data quantifying propagule pressure in open systems and over large-scales are needed to predict spread, but such datasets are rare or non-existent. Lacking more direct information, using proxies of propagule pressure may be the only way to proceed on the large-scale. The density of intertidal adult populations, which should be directly related to the amount of offspring produced, could be used as a surrogate of propagule pressure. Therefore, we extensively surveyed the spatial distribution and density of adult crab populations along the coast from New Jersey to Maine. From the data we can model the amount of propagules entering the 3-dimensional system driven by complex ocean currents. Oceanographic models should be important for forecasting spread. However, this is currently an open question because existing models are often built to predict large-scale general particle movements far from shore (Werner et al. 1993, Hannah et al. 2000, 2001). For intertidal species, other factors are relevant, including nearshore dynamics, diffusion, and biological processes. Given that the direction and strength of currents vary both in the horizontal and vertical, any behaviors that change the organism's position in the water column may affect their resultant transport. Therefore, we need to incorporate larval behaviors into oceanographic models to predict the spread of larvae.

The majority of larval ecology research has focused on diel vertical migration (DVM) and ontogenetic migration (i.e., the vertical migration pattern of the larvae as it develops), both of which are common behaviors for invertebrate larvae. Larvae of *C. maenas* and *H. sanguineus* both undergo DVM and ontogenetic migration (Zeng and Naylor 1996; Park et al. 2004; Queiroga and Blanton 2004), which may need to be modeled to properly predict their spread. In ontogenetic migration, as larvae mature they usually inhabit deeper sections of the water column and increase the amplitude of their DVM (Queiroga and Blanton 2004).

Beyond data used to incorporate biological (e.g., DVM) and physical processes (e.g., diffusion), further regional and standardized datasets are needed to quantitatively validate the predictive ability of the models. Such data are quite expensive and labor-intensive to collect and even more scarce than the models themselves. Most models make no attempt to validate their abilities to predict the recruitment of species along the intertidal zone for various reasons. For example, nearshore currents are not usually incorporated or fully considered in large-scale models (Werner et al. 1993; Hannah et al. 2001), so physical models might not be able to predict the spread of intertidal invasive species.

In this study, we examine the ability of existing oceanographic models to predict spread, comparing output of the model to observed patterns of drift cards and larval settlement in the Gulf of Maine. If the model is unable to capture the physical processes or has inadequate spatial or temporal resolution, we should find poor concordance with both drift card and larval settlement patterns. If the model adequately describes physical processes but not biological ones, then we predict that the model should fit the drift card patterns but not the larval settlement patterns. Finally, if the existing model simulates the most important processes driving biological spread, then we hypothesize that we should find concordance with not only the drift cards but also the larval settlement patterns.

Secondarily, we extended the model and incorporated aspects of larval behavior and additional physical processes (diffusion) into an oceanographic model. If stochastic diffusion and larval behaviors are important, we hypothesized that their inclusion in the oceanographic model would improve concordance between model predictions and the observed larval settlement densities.

Study Organisms

In this study, we focus on the European green crab (*Carcinus maenas*) and Asian shore crab (*Hemigrapsus sanguineus*) as they are both global invasive species that can cause ecological and economic impacts in their non-native distributions (Grosholz and Ruiz 1995; Grosholz and Ruiz 1996; Walton et al. 2002; Brousseau and Baglivo 2005; Griffen and Delaney 2007; Kraemer et al. 2007; Griffen and Byers 2009), in which they are still spreading (Klassen and Locke 2007; Behrens Yamada and Gillespie 2008; Delaney et al. 2008). *C. maenas* can be found on all non-polar continents (Carlton and Cohen 2003). It obtained this global distribution because it is an omnivore, so food is probably not a limiting agent (Ropes 1968; Grosholz and Ruiz 1996) and can be transported by multiple vectors (Carlton and Cohen 2003 and references therein). As an adult and to a certain extent as a larva, the species can tolerate a wide range of salinities and temperatures (Broekhuysen 1936; Eriksson and Edlund 1977; Dawirs 1985; Dawirs and Dietrich 1986; Anger et al. 1998). The timing and duration of the breeding season of *C. maenas* varies by geographic region (Behrens Yamada 2001), but we commonly observed ovigerous females along the coast of New England from May to August. *C. maenas* are highly fecund (Broekhuysen 1936; Crothers 1967). The free swimming, planktonically dispersed larvae are transported by surface currents as they undergo four zoeal stages before metamorphosing into megalopae that become benthic adults (Crothers 1967; Behrens Yamada 2001). While the amount of time spent as plankton is temperature-dependent, at 18^{o}C, each of the four zoeal stages lasts for approximately 4 to 6 days before a 13 day long megalopa stage (Dawirs 1985). *C. maenas* undergoes vertical migration as a zoea and megalopa (Zeng and Naylor 1996; Queiroga et al. 1997; Behrens Yamada 2001).

The ecology and larval behaviors of *H. sanguineus* are similar to *C. maenas*. Both the adults and larvae of *H. sanguineus* are tolerant to a wide range of temperatures and salinities (Epifanio et al. 1998; McDermott 1998). The breeding season along the east coast of North America is late April through September (McDermott 1998). *H. sanguineus* can produce multiple broods in a single breeding season and is highly fecund (McDermott 1991,1998). Also similar to *C. maenas* and most other marine larvae, the rate of development and duration of the planktonic zoeal stages is temperature-dependent and has been shown to vary from 16 to 55 days before metamorphosing into a megalopa (Epifanio et al. 1998). *H. sanguineus* has an additional fifth zoeal stage before becoming a megalopa (Epifanio et al. 1998). Yet the general timing and length of its breeding season for the population found along the east coast of North America is similar to *C. maenas* (McDermott 1998).

Methods

Drift card study

During June to September 2007 we conducted a drift card study with multiple deployments of drift cards released from the intertidal zone throughout the breeding season from 11 locations from Oak Bluffs, Massachusetts (41.433N, -70.556W) to

Schoodic Peninsula, Maine (44.336N, -68.056W) (Fig. 3.1). The locations provided coverage across the coast, but the specific locations were subject to the availability of groups to deploy the cards. Each of the 83 deployments comprised 30 cards labeled with a unique identification number that allowed us to know the location, time, and date of its release. Contact information was printed with non-lead-based paint, on the biodegradable cards, so people that detected the cards could report the locations and dates that the drift cards were found. Cards were released throughout the breeding season at various tidal conditions at each of the sites.

Recruitment study

We conducted a recruitment study during the summer of 2007, at 20 sites from New Bedford, Massachusetts (41.595N, -70.911W) to Machias, Maine (44.628N, -67.385W) (Fig. 3.2). At each site, we deployed 5 collectors in the intertidal zone approximately 0.5 m below the mean lower low water line. A collector is a 20 cm x 20 cm piece of green indoor/outdoor plastic carpeting that was approximately 2 to 3 cm thick. The carpeting is widely available and imitates macroalgae and acts as a standardized settlement collector for larvae of decapod species and is easily processed in the laboratory (Amaral and Paula 2007). We used white cable ties to attach the piece of carpeting to a 20.32 cm × 40.64 cm × 5.08 cm red brick, which acted as an anchor. The collectors were deployed in an interspersed order across the study range to avoid confounding latitudinal changes with seasonal changes. After approximately a month, we retrieved the collectors in the same random order in which they were deployed. The deployment and recovery of all the collectors was executed in a week. The retrieved settlement collectors were removed from the water, the carpeting was detached from the brick, placed into labeled Ziploc bags, and transported to a laboratory for processing. The samples were soaked and rinsed with freshwater, which was then filtered to free the larvae from the carpeting (van Montfrans et al. 1990). Then the material was put into a Petri dish for examination under a dissecting microscope to identify the larvae of all decapod species. The specimens were classified into two groups, non-native and native species. Non-native species were identified to the species level using descriptions and figures in the literature (Muraoka 1971; Hebling 1982; Williams 1984; Hwang et al. 1993; Behrens Yamada 2001; Johnson and Allen 2005; Kornienko et al. 2008; Lee and Ko 2008). This process was repeated for a second set of 5 collectors deployed at 18 of the 20 original study sites from mid-July to mid-August. The collectors were processed using the same methodology as described above.

Oceanographic model

We used a 3-D vector field of currents through time generated by a hydrodynamic model developed by Hannah et al. (2001). The domain of the model is from the outer tip of Cape Cod, Massachusetts to the southern tip of Nova Scotia, Canada. This model uses circulation derived from the tides, the seasonal mean circulation, wind-driven circulation, and a surface-wind drift as a vector field for offline particle tracking (Hannah et al. 2000, 2001). The existing advection model was modified to incorporate stochasticity by including a parameterized spread term that incorporates diffusion and other factors (e.g., eddies, nearshore dynamics) not explained in the original model. Often diffusion is used as a surrogate for the combined effect of these processes. We incorporated stochastic spread into the model using Eqn. 3.1 and validated the fit and predictive power provided using the observed recovery locations of drift cards:

$$\rho = \alpha e^{-\alpha d} \tag{3.1}$$

where ρ is the probability of a given spread distance, d, and α is a diffusion coefficient that controls the magnitude of spread. This spread routine was executed at each time step of the model run (i.e., 15 minutes). The α parameter was fit to the observed drift card data using a simple one-dimensional fitting algorithm that minimized the Minimum Energy Test score between the predicted (modeled) and observed (drift card recoveries) datasets (Baringhaus and Franz 2004; Aslan and Zech 2008).

Before larval behavior was added, the stochastic model was validated using experimental drift card data to examine whether it could predict the spread of passive particles. Only 6 of the 11 drift card deployment sites were located within the domain of the model, so we used three of these sites (Deer Island, MA; Monhegan Island, ME; and Searsport, ME) to fit the diffusion coefficient (Eqn. 3.1). Then the stochastic oceanographic model used the fit parameter to predict recovery locations of drift cards deployed from the other 3 sites (Marshfield, MA; Matinicus Island, ME; and Schoodic Peninsula, ME).

We compared the model fit to the observed recovery locations of cards released from the three validation sites to determine the accuracy of the model. Since a binning technique was not obvious for these spatial sets, the scoring was done on different scales by bounding the domain of analysis at each site to the minimum and maximum coastal extent of recovery points for the site and dividing that distance into 3 to 99 bins, and calculating the rank Spearman correlation coefficient for each bin size (Costanza 1989). The model predictions were evaluated against complete spatial randomness (CSR) - a classical null model for spatial analysis (Gillis et al. 2006). CSR was formulated such that each bin had an equal probability of receiving a point. We plotted the cumulative distribution of the observed drift cards and predicted locations along the coast compared to CSR.

We then applied the model using recruitment data, to see if we could predict biological spread. We included parameters for the average depth and amplitude of DVM for young (i.e., first 10 days), intermediate (i.e., from 10 to 20 day period), and old larvae (i.e., last 10 days), which were quantified by taking minimum and maximum values for brachyuran species as quantified in Queiroga and Blanton (2004) (Table 3.1). The simulations were run for 30 days from mid-June to mid-July – corresponding to the period of time the settlement collectors were left out. Then the model was run for the mid-July to mid-August period during which the second set of collectors were deployed. For both *C. maenas* and *H. sanguineus* the propagule pressure from a site was estimated from the abundance of crabs in regional surveys of the coastline from New Jersey to northern Maine conducted in 2005 and 2006 (Chapters 1 and 2). For sites we monitored both in 2005 and 2006, we averaged the densities for both years. Using our adult density data, we estimated the density along the entire coast using a linear interpolation of our data. We used 52 discrete points evenly spaced along the coast, simulating propagules release based on the interpolated adult densities. We assumed no density dependence, so the number of propagules released from a site would scale linearly with the number of adults at the site. Due to computational limitations, the number of propagules was scaled:

$$f(\rho_i) = \frac{1000\rho_i}{\rho_{\max}} \tag{3.2}$$

$$n_i = \begin{cases} \lfloor f(\rho_i) \rfloor & ; f(\rho_i) > 1 \vee f(\rho_i) = 0 \\ 1 & ; 0 \leq f(\rho_i) \leq 1 \end{cases} \tag{3.3}$$

where ρ_i is the density of adults at site *i*, ρ_{max} is the maximum density of adults across all sites, $\lfloor x \rfloor$ is the floor function which rounds the value of *x* to the lowest integer that is less than or equal to *x*, and n_i is the number of propagules deployed from site *i*. That number of propagules was released at the start of the simulation then every 7 days during model runs. The predicted recruitment data were compared to the actual recruitment data. Only the 18 northern recruitment study sites were within the domain of the model in the June/July dataset, so only these sites were used for parameterization. For comparison, the coast was divided into 18 bins between the midpoints of the 18 sites where the collectors were deployed. This segmented the coast *a priori* based on the data (Fig. 3.3). The number of propagules predicted to arrive at the 18 sites was counted and divided by the coast length for that section. For the July/August data, only 16 of the sites where collectors were deployed were within the model, so the methodology was executed in an identical manner but with only 16 bins. Then, we examined if the observed recruitment was positively correlated with the predicted recruitment. Each species was analyzed in a separate regression. Also, the analysis was conducted on each temporal dataset separately.

Results

Drift card study

Of the 2,490 cards deployed, 1,005 (40.36%) were recovered and reported. The majority of the cards were found along the coast of Massachusetts, New Hampshire, and Maine (Fig. 3.4). The majority of drift cards were recovered in close proximity to the deployment site with a tendency to be recovered south of the deployment site (Figs. 3.1 and 3.4). There was some long-distance dispersal – some cards reached locations far north of where they were deployed and some reached the Canadian coast of New Brunswick and Nova Scotia (Fig. 3.4). One card was recovered in Norway and another along the coast of England.

Recruitment study

After approximately a month, over 90% of the settlement collectors were recovered from the June/July (97/100) and July/August (82/90) deployments. Over 80% the sites were colonized by invasive decapods in both datasets (Tables 3.2 and 3.3). Sites that were not colonized in June/July were also not colonized later in the breeding season (Tables 3.2 and 3.3). The recruitment of both species generally declined with increasing latitude but to different extents. *C. maenas* recruited from the most southern to the second to the most northern site; while the recruitment of *H. sanguineus* was limited to southern sites (Fig. 3.5). The most northern site where *H. sanguineus* was detected was Kittery, Maine in the June/July data (Table 3.2) and South Portland, Maine in the July/August dataset (Table 3.3). Therefore *H. sanguineus* was not detected in 9 and 8 of the most northern study sites in the June/July and July/August datasets, respectively. The most northern site, Machias, ME, was not colonized by either native or introduced decapod species. Recruitment of invasive species was higher in the June/July (4.2 recruits/collector) than July/August period (1.1 recruits/collector). The overall level of observed recruitment was inversely related to latitude in both June/July and July/August datasets (Fig. 3.5).

Oceanographic model

For drift cards, the stochastic oceanographic spread model consistently produced better fits to the observed data than CSR at all three sites (Fig. 3.6). Depending on the scale, the r ranged from 0.35 to 0.82 for Marshfield, MA, 0.38 to 1.00 for Matinicus Island, ME, and 0.11 to 0.87 for Schoodic Peninsula, ME (Fig. 3.7). The model was not able to consistently predict the spread of *C. maenas* and *H. sanguineus*. We found that for the recruitment data of collectors retrieved in mid-July (Table 3.2), on which the model's diffusion parameter (Table 3.1) was fitted, the model prediction was significant for *H. sanguineus* (r = 0.544, P = 0.020) but was not significant for *C. maenas* (r = 0.254, P = 0.309). For validation, the model parameters generated from the June/July data (Table 3.2) were used to predict the July/August recruitment data (Table 3.3). This resulted in an r of 0.389 (P = 0.136, Fig. 3.8A) and -0.227 (P = 0.398, Fig. 3.8B) for *H. sanguineus* and *C. maenas*, respectively.

Discussion

In this study our coupled biological-physical oceanographic model could predict the spread of drift cards but could not correctly predict the spread of the larvae of two invasive species. These results could be due to physical or biological shortcomings of the models or artifacts in the data. Most of our understanding of maturation and larval behaviors has been obtained by laboratory studies that may not accurately represent natural behavior (Byers and Pringle 2006). Other biological processes could include post-settlement processes that have been shown to be quite important in understanding observed patterns of recruitment (Eggleston and Armstrong 1995; Scheibling and Robinson 2008) and may have started to occur on the collectors during the month they were deployed. These processes include competition, predation and even cannibalism (Lohrer and Whitlatch 2002). Cannibalism occurs for both species, but is far more prevalent for *C. maenas* than *H. sanguineus* (Griffen and Byers 2009) and has been shown to regulate populations (Moksnes 2004). This could explain the lower than predicted larval density of *C. maenas* in northern locations, which have higher adult densities, compared to southern sites, which have low adult densities and the highest levels of observed recruitment.

For both species we found their recruitment was inversely related to latitude. This could be due to declining water temperature with latitude that is known to increase the duration of time that the organism spends as planktonic larvae (Dawirs 1985). The fact that our recruitment study was conducted in the first half of the recruitment season could explain this pattern of greater observed recruitment at southern than northern sites, which have colder water temperatures and this leads to a prolonged duration of larvae in the water column and a later peak time of settlement (Berrill 1982; Behrens Yamada 2001).

While the aforementioned biological explanations may account for the model's inconsistent predictions of recruitment data, the reason could be fully or at least partially physical in nature. The model does not incorporate nearshore dynamics, which may be vital for predicting the spread of intertidal species, whether introduced or native. While the original model successfully predicted the recruitment of species such as cod and haddock that have larval behaviors (Werner et al. 1993), these simulations were run in essentially the center of the model's domain. No previous attempt to validate this model has been conducted for predicting the recruitment of species along the intertidal zone on the edge of the model's domain. Boundary conditions in the model, such as nearshore currents are not usually incorporated or fully considered in large-scale models such as the one we used (Hannah et al. 2001).

Since we were not able to consistently predict recruitment data we need to examine if this was due to shortcoming in incorporating physical forcings into the model (e.g., ignoring nearshore currents). To do this we conducted a drift card study to determine if the model could predict the physical transport of passive particles. We found that the model could predict drift card data suggesting that the physics used in the model and its lack of explicit nearshore dynamics was adequate for predicting the spread of passive particles deployed from the intertidal zone.

In this paper we adapted a deterministic physical oceanographic model to include stochastic spread and biological behaviors (DVM, ontogenetic migration) of the organisms to predict the spread of intertidal and invasive species. Validated and accurate predictive models would provide both applied and pure applications. On the theoretical side, it can help us better understand connectivity of metapopulations (Jones et al. 2009; Rasmussen et al. In Press), dispersal potential of a species (Gaines and Bertness 1992; Harwell and Orth 2002), and regional recruitment patterns (Connolly et al. 2001). On the applied side, it will quantify and predict the spread rates of marine invasive species, harmful algae blooms (Wong and Lee 2007; Dyble et al. 2008), and determine the number and spatial arrangement of marine protected areas to optimize connectivity and biodiversity (Palumbi 2003; Robinson et al. 2005).

Most marine introduced species are highly fecund and have one or more planktonically dispersed life stages (Ruiz et al. 1997; Ruiz et al. 2000). While ocean currents are arguably the most important vector for secondary spread in marine systems, there are other vectors that could also facilitate spread (e.g., ballast water). Determining whether marine introduced species have spread by larval drift or multiple independent introductions (i.e., propagules transported from the native or a different non-native distribution) is a challenge. The actual vector for the spread of *H. sanguineus* up the coast of New England remains unclear. *H. sanguineus* recruits were only found as far north as southern Maine, which is almost 200 km south of where a range expansion of this species was previously detected (Delaney et al. 2008). This isolated, northern population could have been founded by larval drift from southern populations, as was the case for the spread of *C. maenas* along the west coast of North America (Behrens Yamada 2001) or it could be due to a second and independent human-mediated introduction. Larval drift is less likely to explain this northern Maine range expansion of *H. sanguineus* since the prevailing currents of the Northwest Atlantic (e.g., Labrador current, Maine coastal current) are from north to south. Yet this range expansion was detected two years before our 2007 recruitment study. Inter-annual variability could be important (Grosholz 1996) and recruitment studies like this one need to be conducted for multiple years to quantify inter-annual variability of recruitment before we can confidently exclude larval drift as the vector for the northern population. Further, spread is stochastic and long distance dispersal events, although rare, may be quite important in explaining and predicting range expansions of introduced species.

Alternatively, the range expansion of *H. sanguineus* may be due to multiple, independent introductions rather than larval drift. Roman and Palumbi (2004) showed with genetic evidence that the distribution of *C. maenas* in the Northwest Atlantic was the result of multiple introductions. Therefore, we recommend that further genetic studies should be conducted as they could provide critical insight into what vector(s) cause a range expansion. This question is of great relevance since New England is just north of New Jersey and New York, which is being invaded by *E. sinensis* (NY DEC 2009) and could be transported by larval drift, ballast water, or other vectors. Below Cape Cod, MA, the prevailing currents are from south to north, driven by the Gulf Stream. These northward currents could potentially bring propagules of *E. sinensis* to the coast of New England via larval drift. To determine this, further modeling will need to be conducted.

Accurate and predictive coupled physical-biological models are important for managing both introduced and native species and their populations. For native species, this type of model can possibly forecast annual recruitment of economically important species, such as crabs, lobsters, mollusks, and fish, and also to help set quotas to make a fishery sustainable (Jamieson 1993; Pauly et al. 2002). While the model could provide many benefits, we were interested in the spread of intertidal decapods and validating it on a large-scale standardized dataset. When successful, this theoretical predictive model could make monitoring feasible within real-world limitations by identifying where to optimally allocate our limited sampling intensity. Yet before these models can be used for these purposes, they need to be tested rather than assumed to be predictive.

As adapted by us, the model should be able to predict areas likely to be affected by marine debris (Barnes 2002), oil spills (Crawford et al. 1996), and the spread of non-native plants by the passive transport of their seeds (Ayres et al. 2004). Drifting plant material, which can transport a rich community of species by rafting (Highsmith 1985), can also be predicted by the current model. Further, drift card and recruitment studies offer useful data to test the abilities of regional oceanographic models so they can be refined and improved until they can predict the actual spread of larvae from non-native animals in addition to rafting species, oil, and marine debris that is harming our coastal environment.

In summary, we conducted two studies collecting different types of data on the large-scale patterns of spread that allowed us to validate a model, determine gaps in its ability, and identify the direction for future research for predicting the spread of species. We found that we could predict the spread of passive drift cards but we could not predict the recruitment of active larvae. Therefore, the physical models were able to predict passively transported particles but until larval ecology is better understood and quantified, especially under natural settings, we currently can not predict the spread the intertidal invasive species.

Acknowledgements

This research was funded by NOAA's National Sea Grant Aquatic Invasive Species Research and Outreach Program (NA05OAR4171088). D. Delaney was partially supported by an Addison E. Verrill Fellowship from the University of Maine. The deployment of drift cards and settlement collectors was assisted by C. Spital and B. Warren of Salem Sound Coastwatch and more than a dozen volunteers including S. Large. A. Irwin and K. Hasegawa assisted with processing the samples. We thank M.F. Delaney and H.R. Spence for offering comments on the manuscript. Also we would like to thank Jason Chaffey of Bedford Institute of Oceanography for providing extended vector data and source code.

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Tables

Table 3.1 The parameters for both *C. maenas* and *H. sanguineus*. Diffusion ("DIFF") was fitted using the mid-June to mid-July data. The amplitude ("AMP1") and mean depth ("ZBAR1") of young larvae, the amplitude ("AMP2") and mean depth ("ZBAR2") of more developed larvae, the amplitude ("AMP3") and mean depth ("ZBAR3") of the most developed larvae were quantified using the minimum and maximum values for brachyuran crabs in Queiroga and Blanton (2004).

DIFF of *C. maenas*	DIFF of *H. sanguineus*	AMP1 (m)	ZBAR1 (m)	AMP2 (m)	ZBAR2 (m)	AMP3 (m)	ZBAR3 (m)
0.0074	0.1641	17.5	17.5	25.0	25.0	50.0	50.0

Table 3.2 Average number of *Carcinus maenas* and *Hemigrapsus sanguineus* recruits per collector deployed at 20 sites from mid-June to mid-July, 2007.

Latitude	Longitude	# of *C. maenas*	# of *H. sanguineus*	# of collectors recovered
41.595	-70.911	1.8	0.8	5
41.715	-70.637	9.8	3.4	5
41.927	-70.543	2.0	0.8	4
42.119	-70.672	1.8	5.0	5
42.355	-70.969	10.8	3.6	5
42.417	-70.907	3.8	0.8	5
42.500	-70.838	2.2	0.0	5
42.524	-70.884	14.2	1.0	5
42.674	-70.665	9.2	2.2	5
43.041	-70.713	0.6	0.0	5
43.081	-70.709	1.2	0.2	5
43.651	-70.227	1.3	0.0	4
43.935	-69.577	0.2	0.0	5
43.960	-69.213	0.4	0.0	5
44.394	-68.084	0.3	0.0	4
44.439	-68.932	4.8	0.0	5
44.481	-68.423	0.0	0.0	5
44.499	-67.854	0.0	0.0	5
44.607	-67.560	0.2	0.0	5
44.628	-67.385	0.0	0.0	5

Table 3.3 Average number of *C. maenas* and *H. sanguineus* recruits per collector deployed at 18 sites from mid-July to mid-August, 2007.

Latitude	Longitude	# of *C. maenas*	# of *H. sanguineus*	# of collectors recovered
41.595	-70.911	0.8	2.8	5
41.715	-70.637	0.4	0.8	5
42.355	-70.969	1.6	0.6	5
42.417	-70.907	0.3	0.5	4
42.500	-70.838	0.8	0.5	4
42.524	-70.884	1.0	0.3	4
42.674	-70.665	3.4	1.2	5
43.041	-70.713	0.6	0.2	5
43.081	-70.709	0.2	0.2	5
43.651	-70.227	0.5	0.3	4
43.935	-69.577	0.5	0.0	4
43.960	-69.213	0.3	0.0	4
44.394	-68.084	0.5	0.0	4
44.439	-68.932	1.4	0.0	5
44.481	-68.423	0.0	0.0	4
44.499	-67.854	0.0	0.0	5
44.607	-67.560	0.2	0.0	5
44.628	-67.385	0.0	0.0	5

Figures

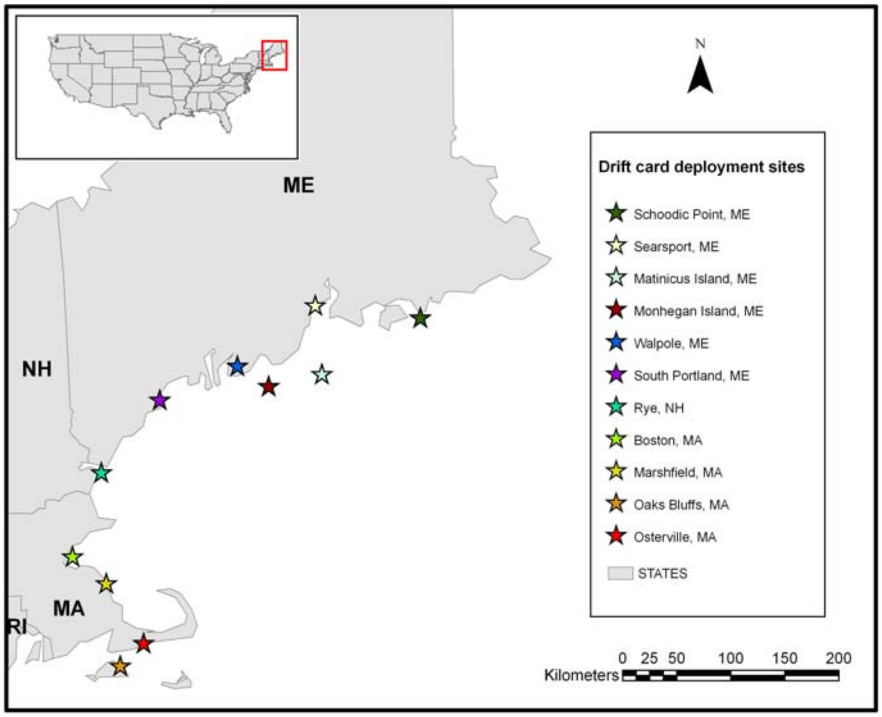


Figure 3.1 The 11 locations, from Oak Bluffs, MA to Schoodic Peninsula, ME, where drift cards were deployed from June to September, 2007.

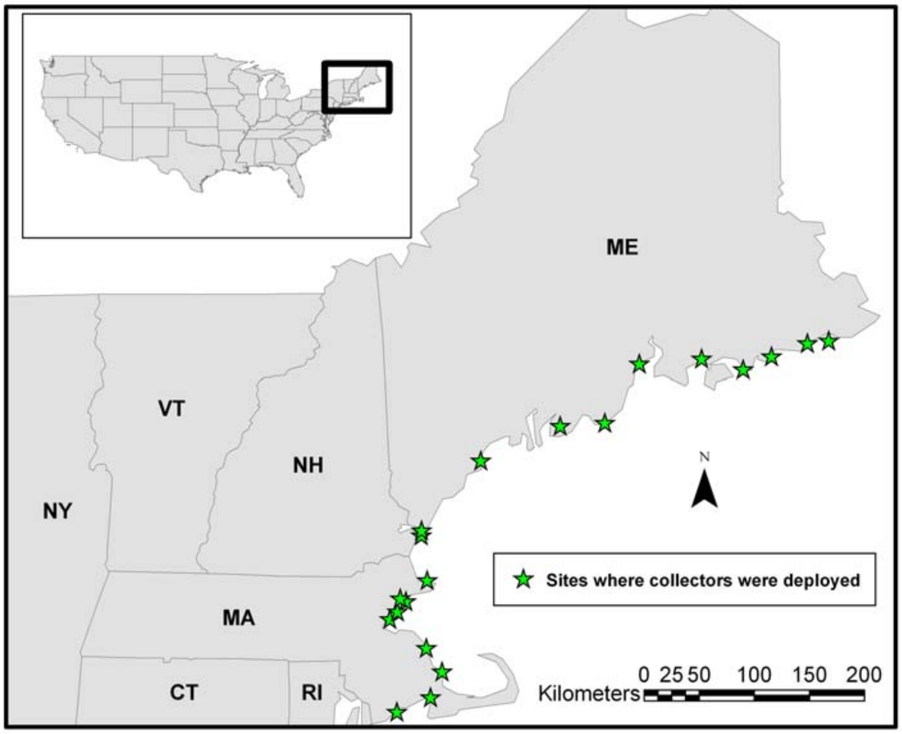


Figure 3.2 The locations from New Bedford Massachusetts (MA) to Machias, Maine (ME) where settlement collectors were deployed from June to August, 2007.

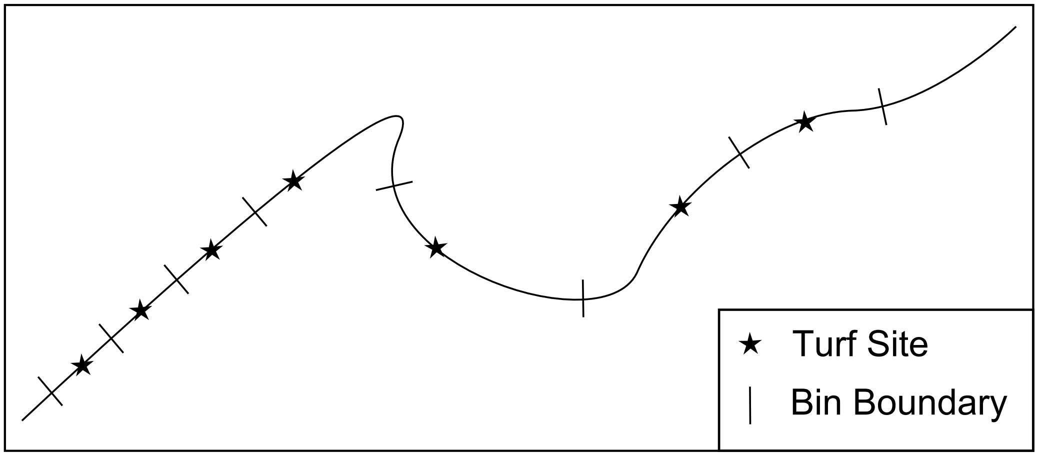


Figure 3.3 A conceptual diagram to explain how the coast was divided for statistical analysis. The coastline is divided into bins (delineated by perpendicular lines) at the midpoint between study sites (as denoted by stars). The first bin boundary (as seen from left to right) is located at a distance before the first study site at a distance equivalent to half the distance from the first study site to the second study site. Similarly the last bin is placed to the right of the last study site at a distance equivalent to half the distance from the last study site to the second to the last study site.

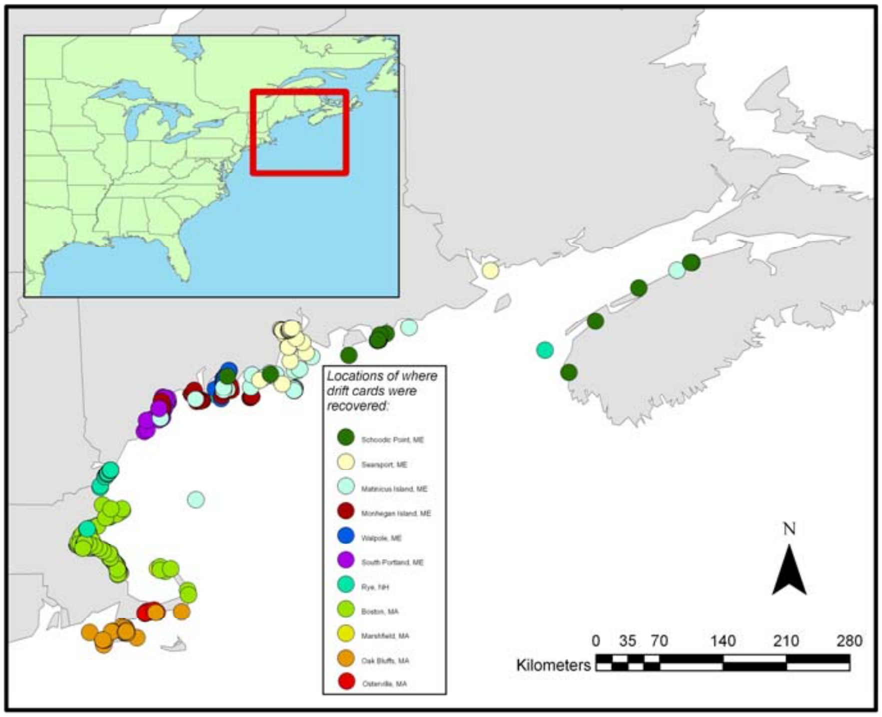
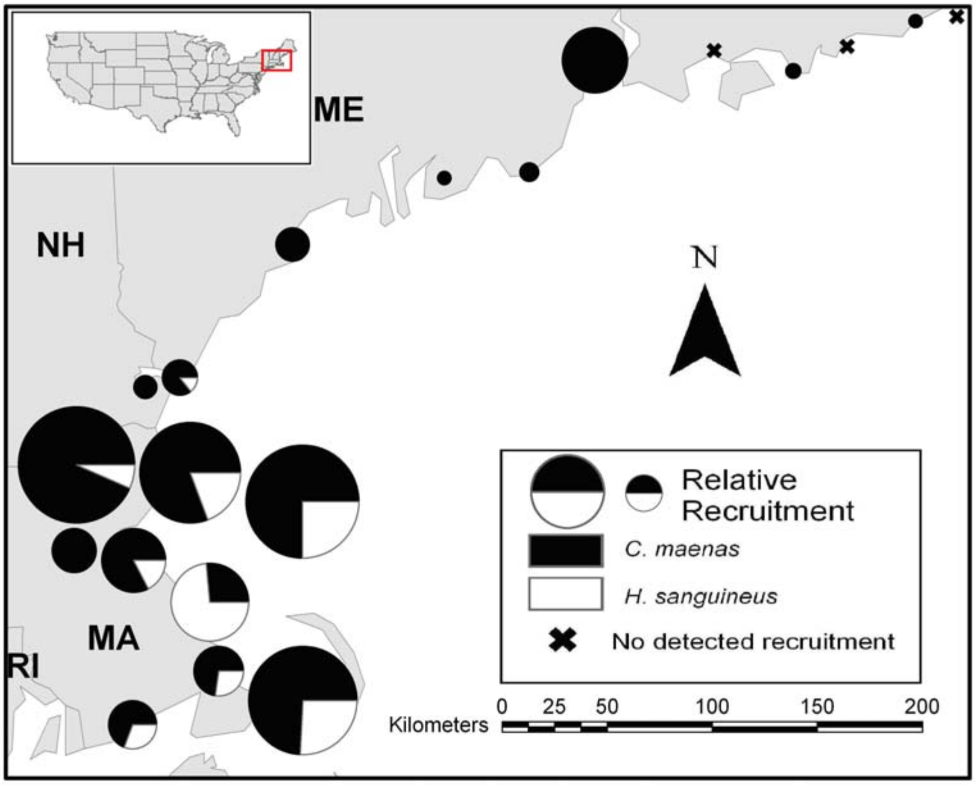


Figure 3.4 The recovery locations of the drift cards, color-coded by the site where they were deployed.

A



ME
NH
MA
RI
N
Relative Recruitment
C. maenas
H. sanguineus
No detected recruitment
Kilometers
0
25
50
100
150
200

B

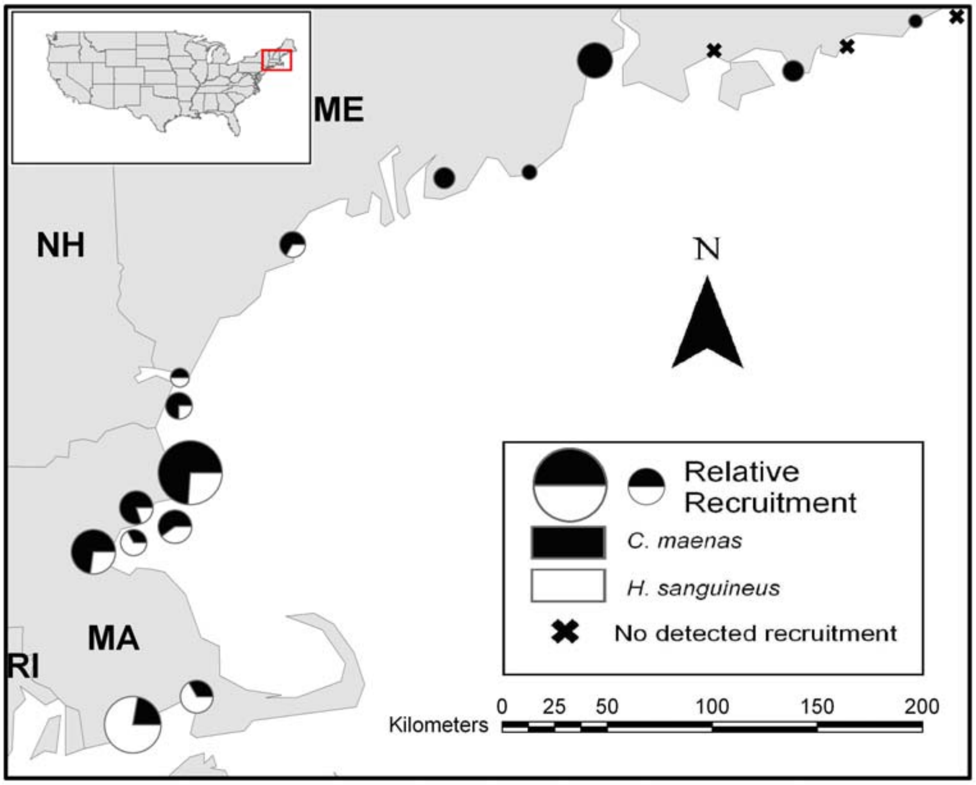
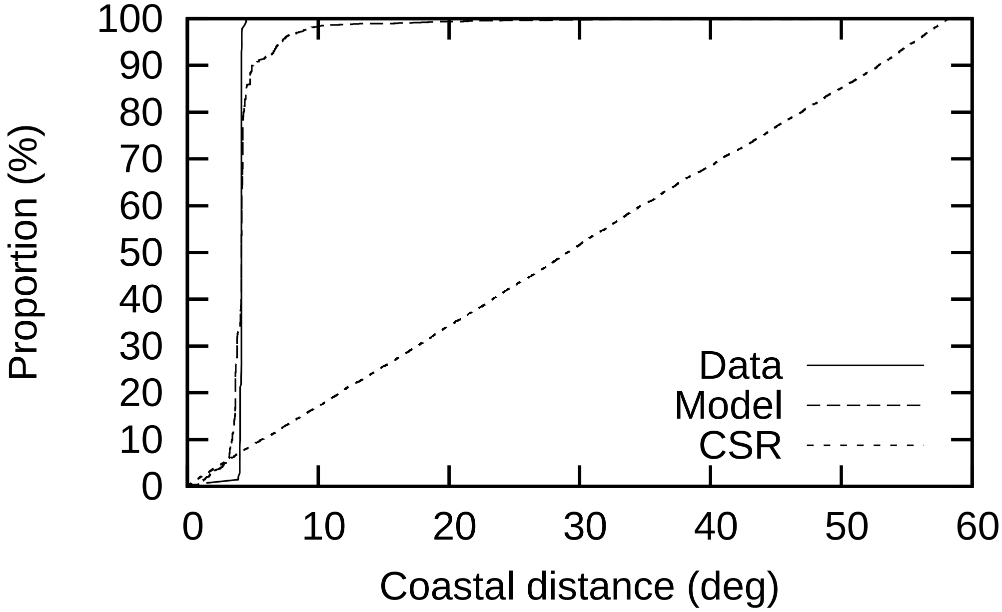
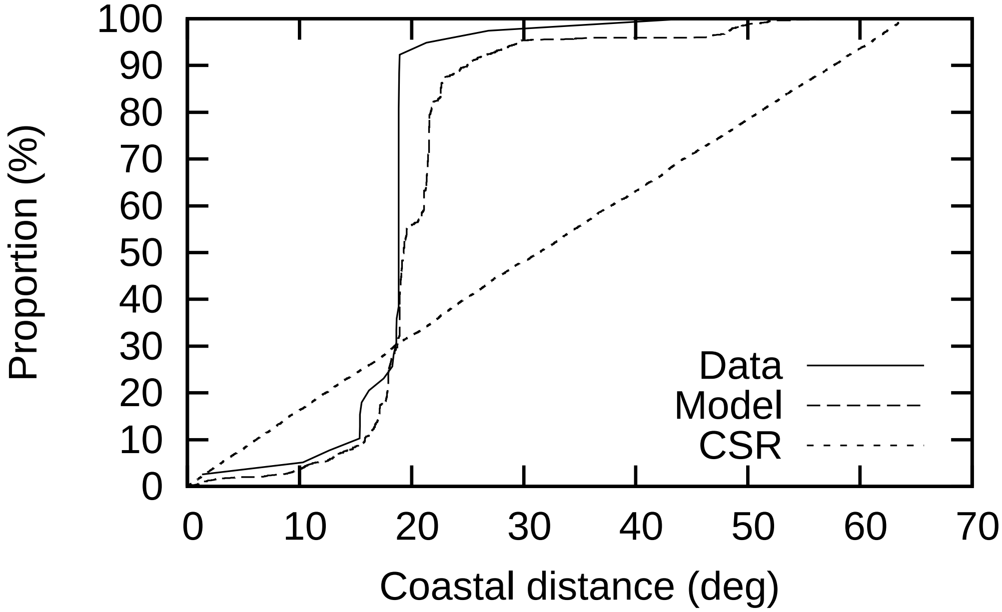


Figure 3.5 The relative recruitment of invasive decapods to 20 sites from New Bedford, MA to Machias, ME. The size of the pie chart is proportional the amount of recruitment by introduced species. The proportion of the larvae of *C. maenas* and *H. sanguineus* is displayed in black and white pie portions, respectively. A: Collectors deployed from mid-June to mid-July during the 2007 breeding season. B: Collectors deployed from mid-July to mid-August during the 2007 breeding season.

A


Proportion (%)
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
Coastal distance (deg)
Data
Model
CSR

B


Proportion (%)
100
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30
40
50
60
70
Coastal distance (deg)
Data
Model
CSR

C

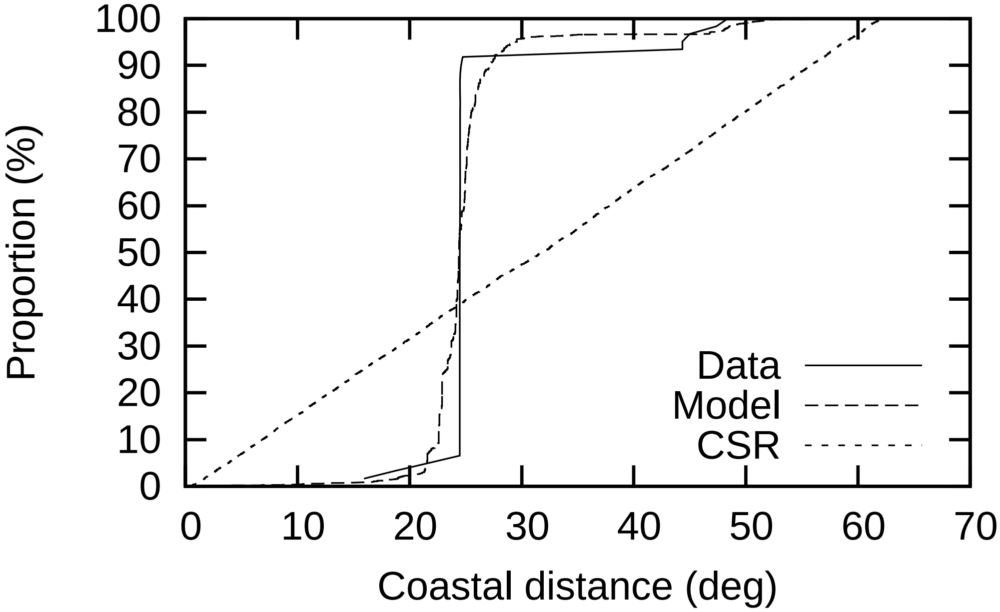

Figure 3.6 The cumulative, proportional distribution of drift cards (“Data”), the predicted recovery locations (“Model”) and the null model (“CSR”) along the coast line at three deployment sites. A: Marshfield, MA. B: Matinicus Island, ME. C: Schoodic Peninsula, ME. A degree of coastal distance is a length of approximately 111 km.

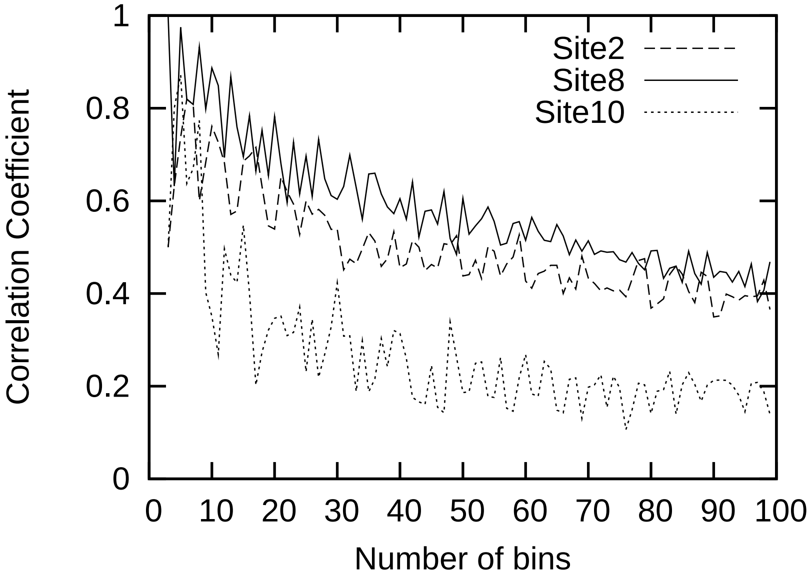

Figure 3.7 The multi-scale rank Spearman correlation coefficient between the observed recovery locations for the drift cards and the locations predicted by the model for the three deployment sites: Site 2 - Marshfield, MA. Site 8 - Matinicus Island, ME. Site 10 - Schoodic Peninsula, ME. Correlations were done with various sizes from 3 to 99 equal size bins.

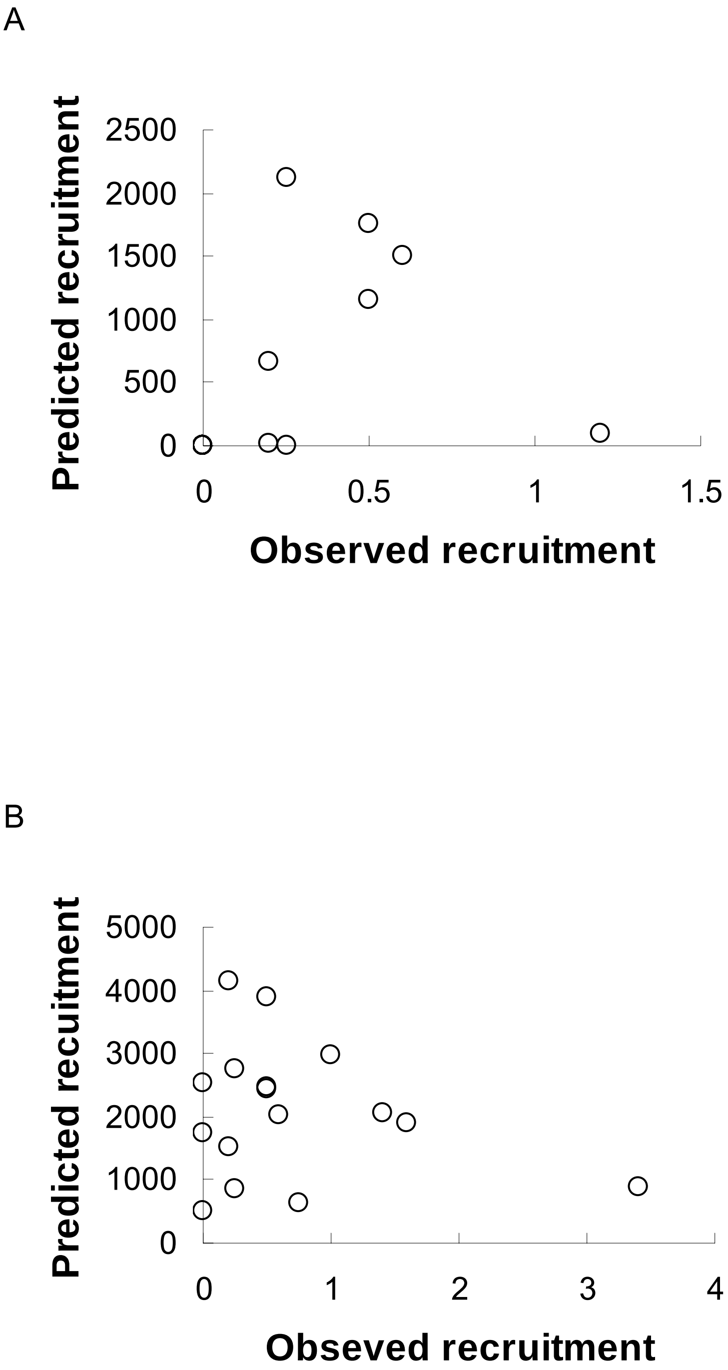

Figure 3.8 The average observed recruitment (recruits/collector) versus predicted recruitment for the July/August data. A: *H. sanguineus*. B: *C. maenas*.

Linking Statement 4

In Chapter 1 we greatly increased sampling intensity for monitoring using citizen science. Monitoring can have many purposes, such as early detection and quantifying various factors such as abundance and distribution of species. In Chapter 2 we quantified the amount of personnel needed for early detection to be effective on the large-scale (e.g., coastline of a state or country). In Chapter 3 we found that an oceanographic model was not able to accurately predict the spread of both species' larvae, so it could not be used to determine where to allocate our limited resources for monitoring. Therefore, invasive species will go undetected, establish, spread, possibly reach high densities and cause impacts. At this point, eradication is no longer possible but managing the invader and mitigating its ecological and economic impacts can still be feasible and beneficial. Resources for management, like resources for monitoring, are limited. Therefore, managers need to identify what areas will be most impacted, so we can optimally allocate our limited resources for management to these areas. Currently, impact is predicted solely by the abundance of the invasive species, so areas that have the highest density of the invader are expect to be most greatly impacted. While abundance has been shown to be positively correlated with impacts of invasive species, other factors might also be important and need to be incorporated to accurately determine what areas will be impacted. I hypothesize that injury may also be important in predicting the impact of invasive species as it can moderate their ability to forage efficiently on prey, including ecologically and economically important species. Injury as a predictor of impact of invasive species has been essentially ignored to date and therefore is the central focus of Chapter 4. If we can find factors that predict the injury of the species, this provides important information for researchers and resource managers as to what sites will be most ecologically and economically impacted by invasive species. To do this, I use the density data of Chapter 2 coupled with over eleven thousand records of injury for these species at 30 sites. This observational approach is complemented with experimental laboratory and field experiments that identify a possible mechanism for the observed patterns of injury and quantified exactly how injury affects consumption rates and therefore impact.

Chapter 4. Injury as a Moderator of Impacts of Invasive Species

Abstract

Predicting the impacts of an invasive species solely by its abundance is common, yet it ignores other potentially important moderating factors. One such factor is inter- or intraspecific aggression. Extreme aggression leads to mortality, which can directly reduce invader density. However, more moderate, sub-lethal levels of aggression can also temper the impact of invasive species via injury. Therefore, to predict impacts we need to examine not only abundance, but also moderating factors (e.g., injury) and predictors of these factors. We documented the density, injury (i.e., limb loss), and size of two conspicuous invaders, the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*), at thirty sites from Shinnecock County Park, New York to Lubec, Maine. We also conducted behavioral observation of crabs interacting under laboratory conditions to examine how the relative size of interacting individuals influenced the level of aggression, and thus the risk of injury. Finally, we used a field experiment to determine how injury influenced consumption rate of mussels (*Mytilus edulis*) by each crab species. We show that injury reduces consumption rates of both species on *M. edulis* and that size of crabs is positively correlated with both the level of aggression and the incidence of injury. Previous studies have highlighted the detrimental impacts of these two invaders on native bivalve prey. However, injury can

greatly reduce or even eliminate the ability of these predators to consume bivalves. Injury, therefore, may play an important role in moderating the impacts of these invaders and is an important but understudied predictor of impact.

Introduction

Introduced species are a current problem that is growing exponentially (Loop et al. 1988; Cohen and Carlton 1998; Ruiz et al. 2000) and are second only to habitat loss as a driver of species extinction (Miller et al. 1989; Wilcove et al. 1998; Dextrase and Mandrak 2006). While some introduced species are harmless, the subset designated as "invasive" can cause great ecological and economic impacts (Parker et al. 1999; Pimentel et al. 2000; Keller et al. 2007). Even though predicting the impact of an invader is a central focus in invasion biology, currently there are few approaches (Parker et al. 1999). The impact of invasive species is often predicted solely by their abundance. This type of approach has been extensively used to predict the impacts of both terrestrial (Medd et al. 1985; Bobbink and Willems 1987; Alvarez and Cushman 2002; Hester et al. 2006; Whittle et al. 2007) and aquatic invasive species (Crivelli 1983; Ricciardi et al. 1995; Chumchal et al. 2005; Driver et al. 2005; Finnoff et al. 2005).

While abundance is logically related to impact of an invader, other factors should also be related and could moderate the effects of abundance. Particularly, it is reasonable that as abundance (or density) increases, the number of inter- or intraspecific interactions should also increase, and if they are aggressive, to potentially cause injury to individuals (Griffen and Williamson 2008). This is particularly relevant, because in turn, injury has the potential to moderate both ecological and economic impacts by reducing mean per capita consumption rates of an invader. Further, we might expect that aggression relates to other attributes such as sex and size of organisms, which could likewise affect consumption and injury rates. Thus, moderating factors such as injury rates should be a consideration in predicting the impacts of invasive species. If we can identify predictors of injury, we can then identify sites within an invaded region where these predictors suggest that the impacts of introduced species are likely to be substantially modified from impacts predicted solely by species abundance.

Two conspicuous and very abundant marine invaders to North America with potentially large impacts are the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*). Currently, *C. maenas* can be found on the east coast from Virginia to Prince Edward Island and has recently been detected as far north as Newfoundland and Magdalen Islands (Klassen and Locke 2007; USGS 2009). On the west coast, its introduced range also spans over 10 degrees of latitude from California, USA to British Columbia, Canada (GCC 2002; Carlton and Cohen 2003; USGS 2009). Additionally, *C. maenas* is found on sections of all non-polar continents (Carlton and Cohen 2003), and often has large impacts by feeding on economically important species, such as blue mussels (*Mytilus edulis*) and other shellfish species (Grosholz and Ruiz 1996; Griffen and Delaney 2007). For example*, C. maenas* has severely damaged the soft-shell clam industry in New England and the Maritime Provinces of Canada (Smith and Chin 1951; Glude 1955; Moulton and Gustafson 1956; Ropes 1968; Miron et al. 2005). Much more recently*, H. sanguineus* also colonized the east coast of North America, but has not been as well studied*. H. sanguineus* was first detected in New Jersey in 1988, then spread north and south to create a distribution that already spans almost 10 degrees of latitude (Williams and McDermott 1990; Lohrer and Whitlatch 2002; USGS 2009) and is still currently expanding north in Maine (Delaney et al. 2008).

Latitude has been shown to be an important predictor of many aspects of an ecosystem and its biota. Examples of such gradients include latitudinal trends in biodiversity (Stevens 1989; Rohde 1992; Gaston 2000) as well as abundance and distribution of organisms (Fretwell 1972; Griffen and Delaney 2007). In addition, temperature, which varies greatly with latitude, can affect not only the distribution and density of a species (Helmuth et al. 2002), it can also regulate the activity rates of a species, such as feeding rates and aggression of species (Ropes 1968; Hill 1980; Taniguchi and Nakano 2000). We have previously demonstrated a strong inverse gradient in the density of *C. maenas* and *H. sanguineus* with latitude (Griffen and Delaney 2007). If latitudinal trends in injury also occur, these may further serve to modify the impacts of these invaders across sites. Given the importance of latitude (and confounding factors) as a predictor of ecological patterns and the wide range of latitudes invaded by these crabs, a latitudinal gradient in injury may exist. Therefore latitude could be an important predictor of injury and we will examine whether a relationship exists between latitude and the frequency of injury for these invasive species along the coast of New England and New York.

Given the potential importance of injury, determining the causal mechanisms that underlie and explain its prevalence may help in predicting how it moderates the impact of invasive species. Both crabs have been introduced to the same region, with the result that *H. sanguineus* has largely replaced *C. maenas* in the rocky intertidal zone of southern New England (Lohrer and Whitlatch 2002). This replacement appears to have resulted from aggressive interactions and we hypothesize that inter- and intraspecific aggression are the principle causes of injury. These agonistic acts likely occur more frequently between large individuals (e.g., due to pursuing and fighting for a mate), and this increased level of aggression should lead to higher risk of injury. Therefore we predict that injury will increase with crab size. We also predict that injury will increase with crab density due to higher frequency of interactions.

We take a three-pronged approach to examine injury and its effects on *C. maenas* and *H. sanguineus*. First, we observe the injury status of over eleven thousand crabs across 30 sites on the coast of New England and New York to assess the frequency of injury in nature and determine whether conspecific and heterospecific density and size are correlated with injury. Second, to identify a possible mechanism explaining patterns of injury found in nature, we use data from a laboratory behavioral study to determine how time spent in aggression varies between species and with individual size. Third, we use a field experiment to quantify the extent to which injury (in this case cheliped removal) reduces foraging efficiency. We then use these results to infer regions where the impacts of these two invaders are likely moderated substantially by injury.

Methods

Natural levels of crab injury

We quantified the density, injury, and size of *C. maenas* and *H. sanguineus* at 30 sites from Shinnecock County Park, New York (40.842N, -72.499W) to Lubec, Maine (44.815N, -66.950W) from late June to late August, 2006 (Table 4.1). Sampling of sites at different latitudes was interspersed throughout this time period to avoid confounding seasonal changes with latitudinal changes. To determine the average density of each introduced species at a site, we sampled 16 randomly placed 1 m^2 quadrats in the mid and low intertidal zone (i.e., from 0.5 m below to 3.5 m above mean lower low water line). Crabs collected from within these quadrats were also used for assessment of limb loss. If time permitted during the sampling day for that site, additional sampling was conducted outside the quadrats but within the study area in an attempt to increase sample size for the injury analysis rather than determine density. We searched, rock by rock, in an exhaustive manner to collect crabs from all size classes. For each crab, we recorded its carapace width (CW), sex, and whether the crab was injured. Following the protocol of Davis et al. (2005), regenerating limbs were considered intact. We performed two separate analyses on these data—an individual-level analysis to examine patterns of limb loss between individual crabs, and a regional-scale analysis to examine patterns of limb loss across sites.

We performed our individual-level analysis by pooling samples for each species separately across all 30 sites (4,721 *C. maenas* and 6,523 *H. sanguineus*). We then examined whether injury status (yes/no) varied with sex or with CW using a stepwise mixed model logistic ANCOVA with sex as a fixed factor, CW as a covariate, and site as a blocking (random) factor to control for variation between sites. We performed this analysis for each species separately. We performed our regional-scale analysis, using multiple regression separately for each species, where the data was pooled at each site. Given variation in density of each species from north to south (Lohrer and Whitlatch 2002; Griffen and Delaney 2007), we were unable to collect the same number of crabs at each site. We therefore used sample size of the focal crab species at each site as a weighting factor in the regression. We used the percent of crabs injured at a site as the response variable and latitude, average size of conspecifics and heterospecifics, and density of conspecifics and heterospecifics as predictor variables. For the analysis of *C. maenas*, we could not include average size of *H. sanguineus* because *H. sanguineus* was not present at many of the sites where *C. maenas* is established. Also, the average size of *C. maenas* was log-transformed to improve linearity.

Aggression experiment

We conducted a laboratory experiment to examine how aggression varied with conspecific density for *C. maenas* and *H. sanguineus*. The full methodological details of this experiment are given in Griffen and Williamson (2008). Here, we use data from the high density treatment of this experiment (8 crabs per tank) to determine how aggression varies with the relative size of interacting individuals. For each of three trials, eight crabs were placed together into a single polypropylene tank (0.5 × 0.4 m) with flowing seawater at the Shoals Marine Laboratory, Isles of Shoals, Maine. In the tank, we offered refugia in the form of a single 20 cm diameter rock placed in the center of each tank, resting on 2 cm of sediment. The sand allowed crabs to burrow (although shallowly), thus avoiding confrontations with aggressors. The density of these invasive species at a site ranged from 0.4 to 79.8 crabs/m^2 (Table 4.1), so the density (i.e., 40 crabs/m^2) used in this experiment is in the range for the density of invasive species along our study area (i.e., coast of New England and New York).

We monitored each crab's behavior every six minutes for two hours and recorded whether aggressive behavior occurred (defined as fighting, display of threat behavior with chelipeds, or displacement of one crab by another), yielding 20 observations for each crab. We then determined the proportion of these 20 observations where aggression occurred. Carapace width was determined for each crab and ranged from 30.8 - 70.1 mm for *C. maenas*, and 19.2 - 26.5 mm for the smaller species, *H. sanguineus*. We then determined the relative crab size within a trial by dividing each crab size by the largest crab in that trial. Finally, we used a separate linear regression for each species to examine the change in the proportion of time that individual crabs spent in aggressive behavior as a function of relative size, and we used a two-sided t-test to compare the overall level of aggression between the two species.

Changes in mussel consumption with crab injury

We conducted a field experiment at Odiorne Point State Park, New Hampshire to examine how injury influenced mussel consumption by *C. maenas* and *H. sanguineus*. A full description of the site is given in Griffen et al. (2008). Following methods described in Griffen and Delaney (2007), we placed individual *C. maenas* (CW = 52.7 ± 8.4 mm) or *H. sanguineus* (CW = 23.6 ± 2.2 mm) into field enclosures (0.5 × 0.6 × 0.3 m), which are constructed of lobster wire mesh lined with 0.25 cm plastic mesh, and filled with denuded small boulders. Crabs were either uninjured (i.e., no limbs missing) or injured (i.e., missing one cheliped) (n = 4). The loss of a cheliped (i.e., claw) is the most common form of injury for both *C. maenas* (McVean 1976; Abello et al. 1994) and *H. sanguineus* (Davis et al. 2005). We scattered 300 mussels into each cage 24 hours before introducing crabs to allow sufficient time for byssal thread attachment. We used mussel sizes that reflected the preference of each crab species (14 - 17 mm shell length for cages with *C. maenas*, and 7 - 10 mm shell length for cages with *H. sanguineus*) (Elner and Hughes 1978; DeGraaf and Tyrrell 2004). Crabs were allowed to forage for 3 days, after which the contents of each cage were removed and the number of mussels surviving was assessed. We determined mean daily mussel consumption as mussel mortality divided by 3 for each cage. We compared mean daily mussel consumption by injured and uninjured crabs for each species separately using one-sided t-tests.

Results

Natural levels of crab injury

We found that crab injury was influenced by both individual- and regional-level factors. At the individual-level, the frequency of injury for *C. maenas*, increased with its size ($F_{1,4607}$ = 53.46, P << 0.001), and differed between sites ($F_{29,4607}$ = 4.23, P << 0.001), and the interaction terms of its size and site ($F_{29,4607}$ = 2.01, P = 0.001) were all significant. Injury did not differ significantly by sex for *C. maenas* ($F_{1,4607}$ = 0.08, P = 0.77). For *H. sanguineus* the frequency of injury increased with crab size ($F_{1,6445}$ = 418.57, P << 0.001), differed between sites ($F_{19,6445}$ = 4.13, P << 0.001), and differed between males and females ($F_{1,6445}$ = 10.09, P = 0.001). There was also a significant interaction term between crab size and sex for *H. sanguineus* ($F_{1,6445}$ = 7.24, P = 0.007). Female *H. sanguineus* exhibited lower frequency of injury than males when smaller than 8.3 mm and more injury when larger than this size. Overall, 31.6% of all *C. maenas* (1,493 / 4,721) were injured and 30.7% of *H. sanguineus* (2,003 / 6,523) were injured. Of the crabs injured, 38.4% (573 / 1,493) and 30.5% (611 / 2,003) were missing cheliped(s) for *C. maenas* and *H. sanguineus*, respectively.

At the regional-scale, for *C. maenas,* the overall regression was significant ($F_{4,25}$ = 4.18, P = 0.010, R^2 = 0.305) and injury increased with the average size of *C. maenas* at a site (t = 3.28, df = 1, P = 0.003, Fig. 4.1) and decreased with latitude (t = -3.27, df = 1, P = 0.003), but was not influenced by density of conspecifics (t = -1.28, df = 1, P = 0.214) or *H. sanguineus* (t = -0.86, df = 1, P = 0.397). For *H. sanguineus* (overall regression: $F_{5,14}$ = 9.85, P < 0.001, R^2 = 0.699)*,* injury increased with the average size of *C. maenas* (t = 3.50, df = 1, P = 0.004, Fig. 4.2A) and conspecifics (t = 5.02, df = 1, P < 0.001, Fig. 4.2B) and was inversely related to conspecific density (t = -2.22, df = 1, P = 0.044). *H. sanguineus* injury was not influenced by *C. maenas* density (t = -1.38, df = 1, P = 0.190) or latitude (t = -1.35, df = 1, P = 0.198). Injury of both species was highly variable across sites, ranging from 0 - 80% and 15.2 - 50% percent for *C. maenas* and *H. sanguineus*, respectively (Table 4.1).

Aggression experiment

For *C. maenas*, aggressive behavior was positively associated with crab size ($F_{1,22} = 23.31$, $P < 0.001$, $R^2 = 0.51$, Fig. 4.3A). In contrast, the proportion of time *H. sanguineus* displayed aggressive behavior was not influenced by relative crab size ($F_{1,22} = 1.08$, $P = 0.31$, $R^2 = 0.05$, Fig. 4.3B). On average, *C. maenas* was approximately twice as aggressive as *H. sanguineus* (two-sided t-test, *C. maenas*: 35 ± 16% of time aggressive; *H. sanguineus*: 16 ± 12% of time aggressive; $t = 4.43$, df = 46, $P < 0.001$).

Changes in mussel consumption with crab injury

Our field experiment demonstrated that injury reduced mussel consumption by both crab species, though to different extents. Injured *C. maenas* consumed 21% fewer mussels than uninjured crabs (one-sided t-test, $t = 1.87$, df = 6, $P = 0.056$, Fig. 4.4), decreasing from 29.3 to 23.1 mussels per day. Injury completely eliminated mussel consumption by *H. sanguineus* (one-sided t-test, $t = 1.94$, df = 6, $P = 0.01$, Fig. 4.4).

Discussion

Factors affecting crab injury

Factors leading to high frequency of injury in these invasive species and in other crustaceans are unclear. Some argue that intraspecific interactions are highly ritualized and therefore rarely lead to limb loss (Hiatt 1948; Jachowski 1974; Sinclair 1977; Hyatt and Salmon 1978; Juanes and Smith 1995), while others argue that intraspecific aggression is among the most important factors for injury (McVean 1976; Shirley and Shirley 1988; Smith and Hines 1991; Davis et al. 2005). We provide evidence that aggression is size-dependent and that this relationship may explain patterns of injury on both an individual- and a regional-level. Our laboratory experiment demonstrates that intraspecific aggression is more intense for larger individuals and is more intense for *C. maenas* than for *H. sanguineus.* This aggression can have strong moderating impacts on predation rates independent of the effects of injury (Griffen 2006; Griffen and Delaney 2007). An extreme form of aggression, cannibalism, is also common within these species (Moksnes 2004), but is also more prevalent among *C. maenas* than *H. sanguineus* (Griffen and Byers 2009). Weaker aggression among *H. sanguineus* could be one of the reasons this species reaches historically high abundances where it is fully established (Lohrer and Whitlatch 2002; Griffen and Delaney 2007).

Contrary to our expectations, we found that crab density did not significantly influence injury for *C. maenas* and that *H. sanguineus* injury was actually negatively correlated with conspecific density. This is surprising given that density is correlated with aggression for both species in laboratory experiments (Griffen and Williamson 2008). This surprising result may potentially be explained by one or more of the following five factors.

First, the influence of density on crab injury may have been overshadowed by the influence of water temperature. Water temperature strongly influences the activity level of poikilotherms such as crabs, and may therefore alter the level of aggressive injury-causing interactions. Our sampling area throughout New England and New York has a steeply decreasing coastal water temperature gradient with latitude. This means that as one moves north throughout our sampling range, temperatures become colder at the same time that *C. maenas* densities increase and *H. sanguineus* densities decrease. We may therefore expect that temperature changes should counteract effects of increasing *C. maenas* densities and should exacerbate effects of increasing *H. sanguineus* densities.

Second, the influence of conspecific density on crab injury may have been complicated by the inverse densities of *C. maenas* and *H. sanguineus* across sites (Griffen and Delaney 2007). Aggressive interactions are common between these two species, but vary considerably in strength depending on density (Griffen and Williamson 2008), individual size (Lohrer and Whitlatch 2002; Griffen and Byers 2006a), and the availability of refuge habitat (Griffen and Byers 2006b), all of which varied across sites examined in this study.

Third, an implicit assumption of the expected relationship between injury and crab density is that sub-lethal injury is the most likely outcome of aggressive interactions. However, cannibalism and/or injury-related mortality are also likely outcomes. Cannibalism is prevalent in both of these species, particularly among *C. maenas*, and increases for both species with conspecific density (Griffen and Byers 2009), and is also influenced by population size structure (Moksness 2004). If injury is relatively uncommon as compared to cannibalism or other aggression-related mortality, then we may not in fact expect a strong relationship between crab density and injury.

Fourth, large *C. maenas* migrate from the subtidal into intertidal regions to forage at high tide (Hunter and Naylor 1993). Our low tide estimates of *C. maenas* density may therefore not accurately reflect the density of interacting crabs.

Fifth, other factors, such as sub-lethal predation from larger predators (e.g., fish and birds), may also be responsible for a substantial portion of the observed crab injury (Rome and Ellis 2004; Brousseau et al. 2008), which could obscure any relationship between injury and crab density.

From the above discussion it is clear that there are several factors that likely influence the incidence of injury simultaneously. Several of these vary across sites in ways that could have easily obscured any relationship between injury and conspecific density. We therefore have less confidence in our finding that density is an unimportant factor for crab injury.

Increased aggression with size may explain the positive relationship between size and injury that we document here and that have previously been documented (McVean 1976; Mathews et al. 1999; Davis et al. 2005). Alternatively, this pattern may be attributed to simple accumulation of injury with age. Younger individuals are better able to regenerate limbs, as regenerating limbs requires molting, and molt frequency decreases as a crab approaches sexual maturity (Bauchau 1961). Longer inter-molt intervals in older crabs thus provide longer periods for injury to occur with a reduced ability to regenerate the limb(s). In addition, older crabs lose the ability to regenerate limbs altogether after terminal anecdysis (Carlisle 1957). Yet, we also found that injury of *H. sanguineus* was positively related to the average size of *C. maenas* across sites. This suggests that injury is also therefore related to interspecific aggression. Increasing frequency of injury with crab size may therefore result from a combination of multiple mechanisms that require further investigation to disentangle.

Effect of injury on feeding rates and management implications

Exploiting knowledge on the effects of crab injury could increase the probability of successful management strategies. Both *C. maenas* and *H. sanguineus* show a high frequency of limb loss throughout their broad ranges (Mathews et al. 1999; Davis et al. 2005; Table 4.1). As we have shown, limb loss can reduce or even eliminate the consumption of ecologically and commercially important *M. edulis*. In addition, limb loss can induce prey shifts to smaller, more manageable prey or to alternative prey types (Bender 1971; Edgar 1990; Davis et al. 2005). In our study we found that when injured, *H. sanguineus* in field cages did not feed on mussels 7 mm or larger. Shellfish growers could possibly exploit this by increasing the size of seed stock beyond this threshold before seeding a shellfish farm to reduce predation by *H. sanguineus.* Delayed seeding strategies coupled with physical barriers to reduce predation pressure have previously been employed against *C. maenas* predation in their native range and have been successfully employed at aquaculture sites along the east and west coast of North America (Smith 1954; Beal 1998; Cigarría and Fernández 2000; GCC 2002). Our study suggests that these strategies may also be effective for minimizing predation by *H. sanguineus.*

Based on the results of this study, we can determine areas where injury may be expected to substantially reduce the impacts by these invasive species. For *C. maenas*, injury rates increased with its size and decreased with latitude. Therefore we predict that injury will have the greatest moderating effect on impact in southern sites that are composed of larger individuals (Fig. 4.5). We found that injury of *H. sanguineus* increased with its individual size and with the average size of conspecifics and *C. maenas*, but declined with the density of conspecifics. This corresponds to conditions commonly found in the northern part of *H. sanguineus'* range (Table 4.1; Fig. 4.5). This suggests that injury should more strongly restrict the impact of *H. sanguineus* in northern areas than in southern areas.

In conclusion, we have shown that injury is common among two widespread invasive predators throughout the Northwest Atlantic. The observed injury patterns across sites, together with our laboratory experimental observations, suggest that injury is largely a result of aggressive interactions between individual (particularly large) crabs. Our results also demonstrate that injury can substantially reduce or even eliminate the impacts of these invasive predators on ecologically and economically important native prey species. We therefore conclude that injury should be included when projecting the impacts of these and other invasive species rather than simply predicting impacts solely by abundance and per capita feeding rates.

Acknowledgements

This research was funded by NOAA's National Sea Grant Aquatic Invasive Species Research and Outreach Program (NA05OAR4171088). Field work was assisted by S. Trottier. We thank M.F. Delaney and H.R. Spence for offering comments on the manuscript.

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Tables

Table 4.1 The latitude and longitude of 30 sites from Shinnecock County Park, New York to Lubec, Maine with the % injury, mean size (mm), density (crabs/m^2) and sample size of *Carcinus maenas* and *Hemigrapsus sanguineus*. "% injury" is the percent of crabs at that site that were injured.

LAT	LON	Density *C. maenas*	% Injury *C. maenas*	Mean size *C. maenas*	*C. maenas* collected	Density *H. sanguineus*	% Injury *H. sanguineus*	Mean size *H. sanguineus*	*H. sanguineus* collected
40.842	-72.499	0.9	20.0	9.3	*15*	12.6	32.4	14.3	*339*
40.927	-73.311	5.3	14.1	5.2	*85*	20.0	23.8	14.6	*320*
40.966	-73.668	0.3	80.0	48.5	*5*	79.5	37.3	15.9	*635*
41.003	-72.298	0.1	25.0	28.1	*4*	6.5	43.6	19.2	*218*
41.364	-71.481	0.1	0.0	3.8	*2*	52.5	30.5	16.9	*840*
41.493	-71.039	0.9	55.6	27.7	*18*	14.6	45.6	17.6	*316*
41.505	-71.022	0.6	40.0	20.5	*10*	28.2	22.0	11.3	*451*
41.773	-70.500	2.8	4.5	5.4	*44*	18.9	15.2	10.0	*303*
42.092	-70.642	1.0	18.8	28.7	*16*	28.3	30.5	15.7	*453*
42.269	-70.848	2.3	22.2	7.1	*36*	25.1	26.4	15.3	*713*
42.280	-70.955	4.5	26.5	15.1	*181*	1.3	32.9	16.7	*231*
42.322	-70.930	2.8	35.7	13.4	*154*	2.8	29.7	15.4	*327*
42.326	-70.964	6.8	31.1	11.1	*177*	5.2	31.0	16.0	*352*
42.331	-70.955	6.4	36.3	12.6	*102*	14.2	26.9	12.1	*227*
42.420	-70.906	1.9	39.8	17.4	*118*	2.2	38.2	14.1	*170*
42.505	-70.832	2.6	43.3	24.6	*261*	6.9	32.5	15.2	*249*
43.002	-70.743	6.9	27.2	21.3	*206*	4.4	35.9	18.9	*145*
43.042	-70.715	7.9	26.6	19.4	*218*	0.7	31.0	20.8	*226*
43.648	-70.226	2.7	36.7	24.2	*245*	0.0	33.3	28.3	*6*
43.836	-69.507	1.9	39.1	33.5	*253*	0.1	50.0	31.0	*2*
43.926	-69.258	5.0	34.8	24.4	*342*	0.0			
44.093	-69.045	3.1	39.2	30.6	*260*	0.0			
44.292	-68.237	2.4	25.2	29.9	*238*	0.0			
44.338	-68.053	4.3	24.2	30.5	*244*	0.0			
44.425	-68.999	0.8	29.5	25.6	*278*	0.0			
44.439	-68.932	3.5	22.4	26.9	*366*	0.0			
44.455	-68.879	1.1	35.2	37.0	*321*	0.0			
44.470	-68.810	1.5	36.1	28.4	*252*	0.0			
44.535	-67.593	1.4	27.4	44.6	*212*	0.0			
44.815	-66.950	0.4	37.9	41.1	*58*	0.0			

Figures

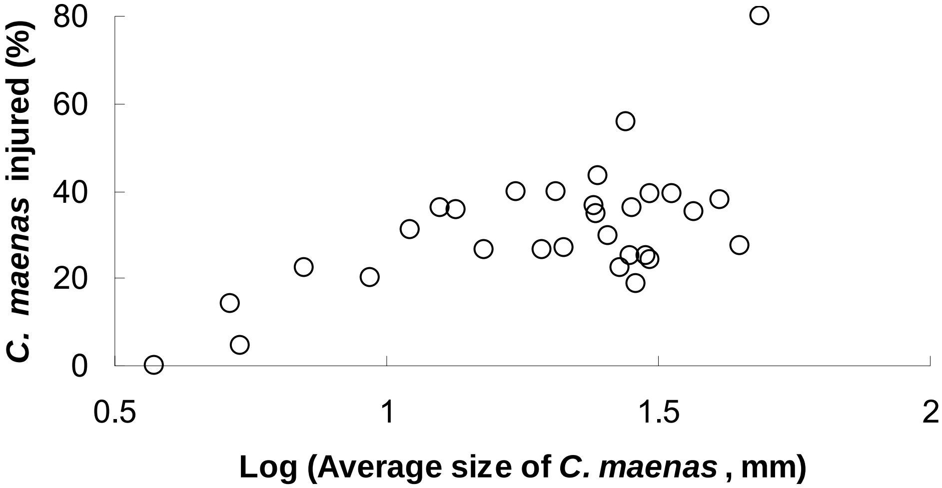
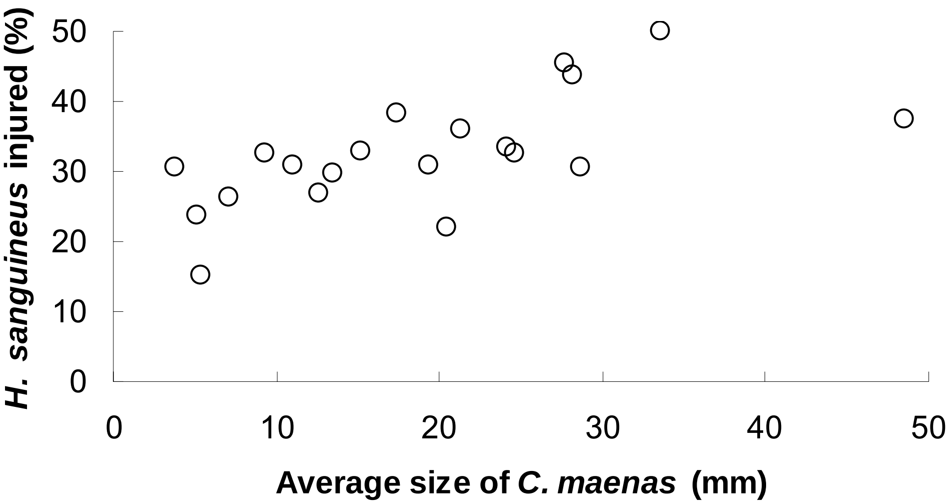


Figure 4.1 Incidence of *C. maenas* injury (%) at a site versus log-transformed value of its average carapace width (mm).

A)



B)

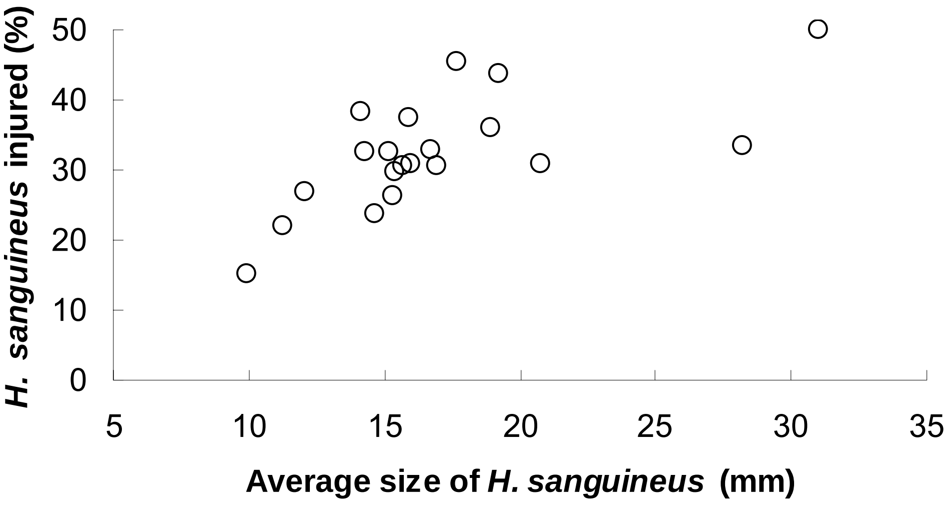


Figure 4.2 Incidence of injury (%) for *H. sanguineus* at a site versus average carapace width (mm) of *C. maenas* (A) or *H. sanguineus* (B).

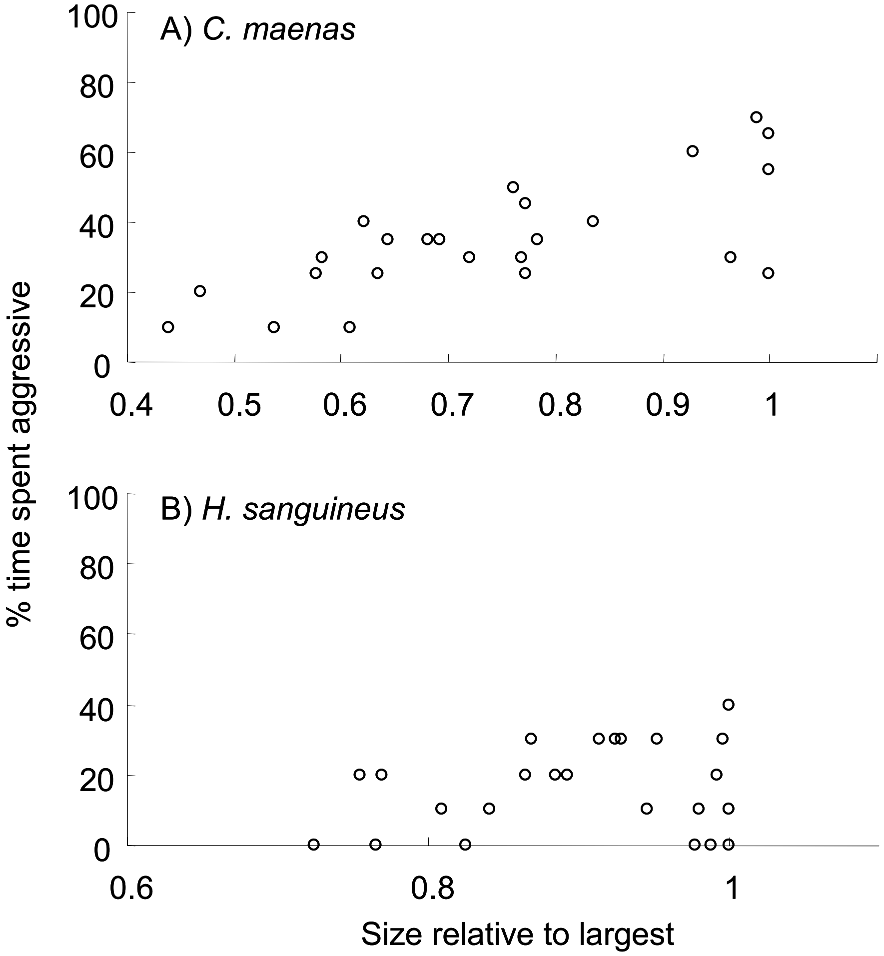


Figure 4.3 Percent of time exhibiting aggressive behavior in the presence of conspecifics versus relative crab size. The size of crab is relative to the largest crab in the tank. A: *C. maenas*. B: *H. sanguineus.*

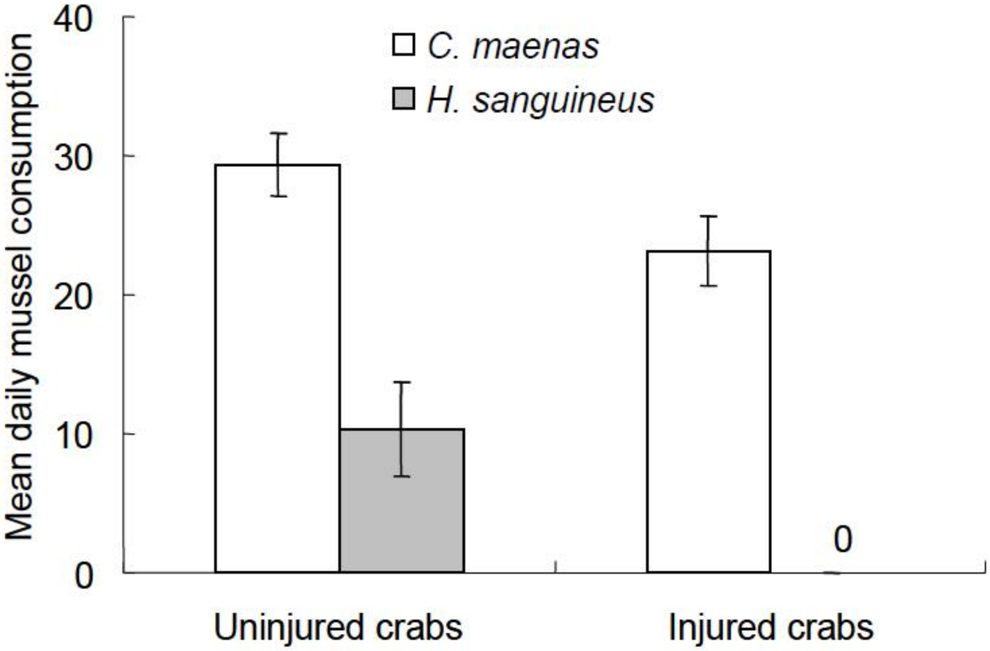


Figure 4.4 Effect of injury (loss of single cheliped) on mussel consumption by *C. maenas* and *H. sanguineus*. Values are means ± SE (n = 4 replicates).

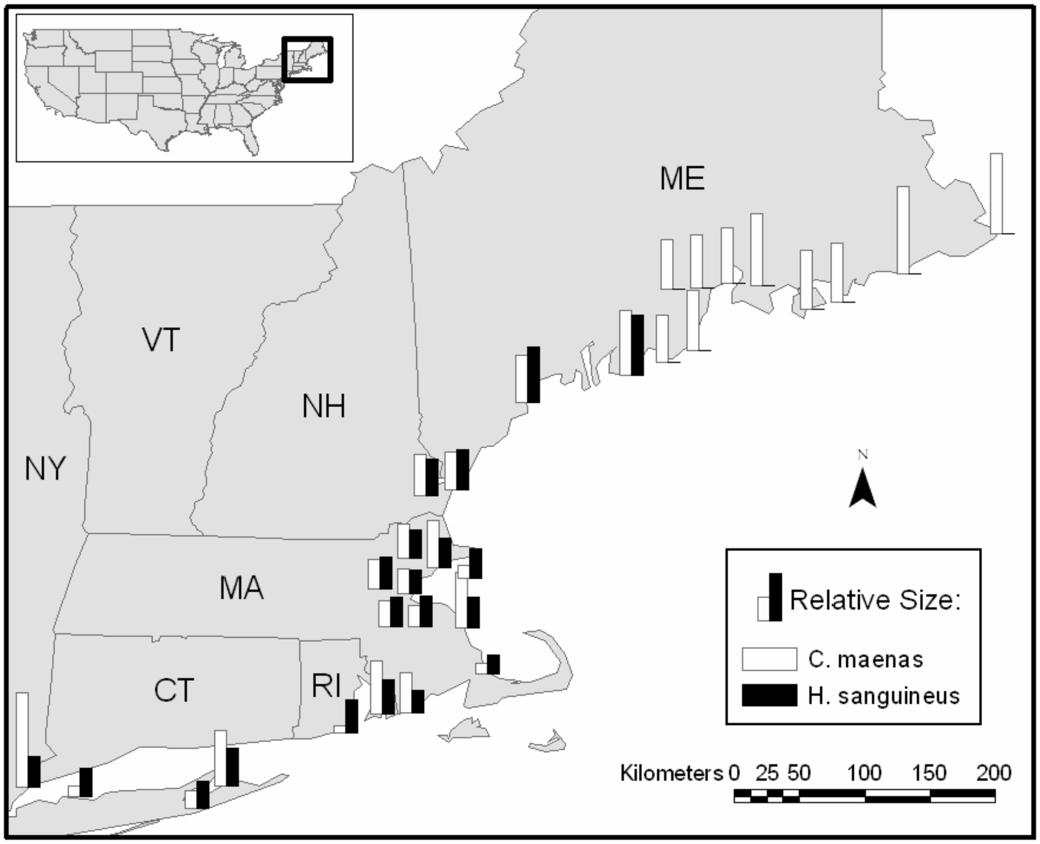


Figure 4.5 The average size of *C. maenas* (white bars) and *H. sanguineus* (black bars) at sites from Shinnecock County Park, NY to Lubec, ME. The size of the bar is proportional to the average carapace width of that species at that site.

General Conclusion

The overall goal of my research is more effective monitoring and management of invasive species to avoid significant economic, ecological, and/or human-health consequences. Progress to achieving this goal for marine introduced species, such as *C. maenas* and *H. sanguineus*, has been hampered by real-world limitations such as insufficient resources, limited data and an inability to detect organisms when they first colonize (Bax et al. 2001; Lodge et al. 2006). These problems are not ephemeral and in this thesis I have made progress to ameliorate these issues by improving our abilities to monitor more intensely, efficiently and effectively. Monitoring is an important precursor to effective invasive species management as early detection will maximize the probability of successful eradication, which is the most cost-effective management strategy.

In Chapter 1, I greatly increased the personnel to monitor for early detection. Nearly 1,000 volunteers sampled for native and invasive crabs at over 50 sites in 7 states. Given the increased personnel, we are better prepared to detect the next newly arriving species (e.g., *E. sinensis, H. takanoi*, and *H. penicillatus*). Even volunteers with limited education were quite accurate in correctly determining the sex and species of the marine organisms. From 2005, to the present, volunteers have been monitoring the coast of New England and New York. This citizen science monitoring network has not only increased the amount of personnel searching but also increased spatial coverage as volunteers monitor areas of the coast where scientists can not monitor themselves.

While no new marine introduced species were detected, they did detect a range expansion of *H. sanguineus* (Delaney et al. 2008).

What sampling approach is used for monitoring is critically important but an understudied area of research. In 2005 and 2006, the volunteers used both the TAS and random quadrat sampling approach. The TAS approach was more effective, increasing the probability of detecting species at low densities (Chapter 2), which is a prerequisite for eradication and fully capturing the entire distribution of a species. Therefore after comparing both sampling approaches (Chapter 2), the volunteer monitoring network subsequently used only the TAS approach given its increased ability for early detection, its simplicity, and lack of complicated sampling procedures (e.g., such as ensuring quadrats are randomly placed).

The regional survey of density conducted by volunteers (Chapter 1) and my field assistant and I (Chapter 2) coupled with drift card and recruitment studies provided datasets to test how well physical models coupled with larval behaviors can predict their secondary spread (Chapter 3). We found that while the model could predict passive particles, it could not consistently predict actual recruitment data. This indicates that larval behaviors are not fully documented and understood. Therefore more research is needed so the biology of the organisms can be successfully incorporated into the physical models to accurately and consistently predict the spread of marine invasive species as well as understand their distributions, abundance, spread rates, which has implications for pure and applied research. Finally, I examined injury as a novel predictor of impact so we can optimally allocate our limited effort for mitigating impacts and minimize the impacts of these invasive species (Chapter 4). The research techniques that I developed in this thesis will increase not only the available data but also the amount of resources (e.g., personnel) to manage future marine bioinvasions and allow us to optimally allocate limited resources for monitoring. Also the experiments and approaches that I developed can be used in other regions and are generalizable to other introduced species, which is a global and growing environmental problem that we need to address in spite of real-world limitations.

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Appendix A. Species Invasion Shifts the Importance of Predator Dependence

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2007 *Ecology* 88:3012–3021

Abstract

The strength of interference between foraging individuals can influence per capita consumption rates, with important consequences for predator and prey populations and system stability. Here we demonstrate how the replacement of a previously established invader, the predatory crab *Carcinus maenas*, by the recently invading predatory crab *Hemigrapsus sanguineus* shifts predation from a species that experiences strong predator interference (strong predator dependence) to one that experiences weak predator interference (weak predator dependence). We demonstrate using field experiments that differences in the strength of predator dependence persist for these species both when they forage on a single focal prey species only (the mussel *Mytilus edulis*) and when they forage more broadly across the entire prey community. This shift in predator dependence with species replacement may be altering the biomass across trophic levels, consistent with theoretical predictions, as we show that *H. sanguineus* populations are much larger than *C. maenas* populations throughout their invaded ranges. Our study highlights that predator dependence may differ among predator species, and demonstrates that different predatory impacts of two conspicuous

invasive predators may be explained at least in part by different strengths of predator dependence.

Introduction

Consumer-resource interactions are an integral part of natural communities and the rate of resource consumption can have important implications for population and community dynamics. Early predation theory assumed that predation rate was a function of prey density only, leading to prey dependent functional responses (Holling 1959). The influence of predator interference on predation rates was subsequently noted (Beddington 1975), and it has been suggested that prey and predator densities may be equally important so that predation rates are a function of the ratio between the two (Arditi and Ginzburg 1989). Under ratio dependent foraging, predation rates generally increase with prey density up to some maximum level and decrease with predator density.

Whether predator foraging is prey dependent or ratio dependent has ramifications for community and population dynamics. Predator-prey models based on prey dependent foraging predict that increased productivity of basal resources transfers through the food chain, alternately influencing the biomass of each trophic level depending on food chain length (Rosenzweig 1977; Oksanen et al. 1981; Arditi and Ginzburg 1989). In addition, these abundance changes are predicted to decrease the dynamic stability of the food web (i.e., the paradox of enrichment, Rosenzweig 1971). In contrast, models based on ratio dependent foraging predict that increasing productivity at the resource level will in turn increase abundance at each level of the food chain, including basal resources, prey, and predators, and will not affect food web stability (Arditi and Ginzburg 1989; Arditi and Akcakaya 1990; Arditi et al. 1991).

While considerable attention has been devoted to theoretical aspects of these predation strategies, and the relative merits of prey dependence vs. ratio dependence weighed, disagreement remains over which null model provides the appropriate starting point for ecological theory (reviewed by Abrams and Ginzburg 2000). However, these are two extremes of a continuum, and most species likely have varying levels of predator dependence and thus fall somewhere in between, depending on the level of conspecific interference among predators (Arditi and Akcakaya 1990; Abrams and Ginzburg 2000). Yet even if predation is not purely prey dependent or ratio dependent, the strength of predator interference has tremendous consequences for ecological systems, as interference stabilizes predator-prey dynamics and can lead to lower predator population sizes (Arditi et al. 2004). While theoretical aspects of this issue have been heavily debated, there have been few empirical tests of the competing theories, and the paucity of empirical evidence impedes determining where most organisms lie along the continuum (Abrams and Ginzburg 2000).

Because the strength of predator dependence likely varies with idiosyncrasies of predator species, changes in predator species composition or dominance within a system could potentially shift the importance of predator dependence. As a case in point, the introduction of nonnative predators has altered the species composition and dominance of predators in intertidal habitats along the northeast coast of North America. Until recently the dominant crab was the European green crab *Carcinus maenas*, an aggressive predator that was first noted in New York and New Jersey nearly two centuries ago (Say 1817). However, in 1988 a second species of exotic predatory crab, the Asian shore crab *Hemigrapsus sanguineus*, was documented in New Jersey

(Williams and McDermott 1990). *H. sanguineus* has spread rapidly along the Atlantic coast (McDermott 1998), largely eliminating *C. maenas* from rocky intertidal regions with its advancing invasion (Lohrer and Whitlatch 2002a). While *H. sanguineus* frequently consumes more plant material than *C. maenas*, both crabs are generalist predators that eat many of the same prey species (Ropes 1968; Elner 1981; Tyrrell and Harris 1999; Bourdeau and O'Connor 2003; Brousseau and Baglivo 2005). However, if the shift in dominant shore crabs from *C. maenas* to *H. sanguineus* has altered the importance of predator dependence for the dominant predator, then community implications may extend beyond slight differences in diet preferences.

Interference among predatory crabs is a widespread phenomenon (Mansour and Lipcius 1991; Clark et al. 1999; Taylor and Eggleston 2000; Sietz et al. 2001; Mistri 2003), and *C. maenas* and *H. sanguineus* are no exception (Jensen et al. 2002; Mistri 2003; Griffen 2006; Smallegange et al. 2006). Interference both between and within these species generally takes the form of aggressive interactions, resulting in reduced feeding rates (Griffen 2006; Griffen and Byers 2006a; Smallegange et al. 2006), injury (Davis et al. 2005), and predator mortality (Griffen and Byers 2006b). However, experimental evidence suggests that aggressive interactions among conspecifics are much stronger for *C. maenas* than for H. *sanguineus* (Griffen and Williamson in Review), and in fact conspecific aggression in the form of cannibalism can control *C. maenas* population size (Moksnes 2004). More aggression among conspecifics may thus translate into a greater influence of predator density on *C. maenas* predation than H. *sanguineus* predation. If this is the case, then based on theoretical predictions (Rosenzweig 1971; Arditi and Ginzburg 1989; Arditi et al. 2004), shifting from a *C.*

maenas-dominated system to an *H. sanguineus*-dominated system may alter the distribution of biomass across trophic levels in the invaded system, potentially resulting in greater predator abundance and lower system stability.

We investigated the strength of predator dependence for each of these species using field experiments in which we measure predation both on a single, favored prey species, and predation when the entire range of prey commonly used by these predators is available to them. We also conducted population sampling throughout the invaded regions of these two species along the New York and New England coasts in order to determine whether the shift in dominant species is altering population abundance (density and/or biomass) at the predator trophic level.

Methods

We conducted two separate experiments in June and July 2006 to determine the influence of predator density on foraging by *C. maenas* and *H. sanguineus*. Both were conducted in field enclosures (0.5×0.6×0.3 m) constructed of lobster wire, lined with 0.25 cm plastic mesh, and deployed 0.5 m above mean low water within an intertidal boulder field at south Odiorne Point, New Hampshire. This site is a moderately exposed site dominated by small boulders overlying a substrate of shell and sand. Crab density varies considerably throughout the site, but was relatively low in the area surrounding the enclosures (*C. maenas*: 2.8 ± 2.8 crabs/m^2, *H. sanguineus*: 1.5 ± 1.8 crabs/m^2, mean ± SD). Boulders from the surrounding area were placed inside experimental enclosures to provide the same structurally complex habitat as is found naturally at our field site.

Functional response experiment

The first experiment examined whether functional responses of *C. maenas* and *H. sanguineus* were best described by prey dependent or ratio dependent models. We measured predation by both of these predators independently while foraging at densities of 1, 2, or 4 predators per cage (C. *maenas* 40 - 60 mm carapace width [CW]; H. *sanguineus* 25-33 mm CW) on mussel prey (*Mytilus edulis*) at densities of 5, 10, 15, 20, 25, 30, 45, 60, or 90 mussels per cage. Crab densities used here (≈3 - 13 crabs / m^2), are similar to the range of densities observed during low tide sampling at our field site (0 - 12 crabs / m^2 of the sizes used here for both species, Griffen, unpubl. data). The range of mussel densities is also consistent with that observed at our field site (Tyrrell 2002). Predator and prey treatments listed above resulted in 27 different predator-prey combinations for each predator species. Four trials were conducted at each of these combinations. Our purpose in this experiment was to assess predation at specified levels of prey abundance. We therefore removed all other potential food items from experimental enclosures (i.e., boulders inside cages were denuded) so that the only prey available were the mussels we provided. Mussels were haphazardly scatted into cages 24 h before the addition of predators to allow time for byssal thread attachment. At the conclusion of each trial, the contents of each cage were removed and mussel survival was assessed.

Previous experiments in this system demonstrated that the per capita rate of mussel consumption by adult *C. maenas* is approximately twice that of *H. sanguineus* (Griffen 2006) and that these two species prefer different sizes of mussel prey (Elner and Hughes 1978; DeGraaf and Tyrrell 2004). These differences lead to very different levels of prey depletion when these species forage for the same length of time on the same sized mussels (Lohrer and Whitlatch 2002b; Griffen 2006). To avoid confounding our results by having different amounts of prey depletion (Abrams 1994), we approximately equalized total prey depletion by conducting experiments with *C. maenas* for 24 h and experiments with *H. sanguineus* for 48 h, and by presenting each species with its preferred mussel size (*C. maenas*: 14 - 17 mm shell length; *H. sanguineus*: 7-10 mm). We verified that the results reported here were not artifacts of these experimental differences by conducting a simplified supplementary experiment where both crab species were fed the same size mussels over the same experimental duration (Appendix B).

Data analysis for this experiment was a three step process and followed the procedures outlined by Juliano (2001). Analyses were conducted on per capita predation. We first determined the shape of the functional response curves for each of the three predator densities of each crab species (six curves total) using separate polynomial logistic regressions. Conclusions from these analyses were verified by visual inspection of plots of proportion of prey eaten vs. initial prey density.

We next estimated the parameters of the functional response equation (handling time and search efficiency) using nonlinear least squares regression for each of the six curves. This was done to understand how predator density influenced the mechanisms of predation for *C. maenas* and *H. sanguineus*. As logistic regression indicated type III functional responses for both predators at all three densities, we fit the data to a type III functional response model that accounts for prey depletion, as occurred in our experiments, and that incorporated the different experimental durations for the two crabs (Eqn. 10.5 from Juliano 2001). Estimates of handling time and search efficiency that were provided by fitting the data to this model were then compared between different predator density treatments using individual t-tests (Glantz and Slinker 1990; Juliano 2001; Fussmann et al. 2005).

Finally, our overarching goal was to determine whether *C. maenas'* and *H. sanguineus'* predation was explained better by the prey dependent or ratio dependent model. We developed the ratio dependent model by replacing initial prey density (N_0) in Juliano's Eqn. 10.5 (Juliano 2001), with the ratio of prey to predators: N_0 / P^m (Hassel and Varley 1969), where P is the number of predators in an enclosure, and m is an interference coefficient. When $m = 0$, the model reduces to the prey dependent form. Ratio dependence is modeled when $m = 1$. Intermediate values of m represent varying degrees of predator dependence. We fit the data for each predator species (across all predator densities simultaneously) to models ranging from prey dependence to ratio dependence at intervals of $m = 0.1$. We determined which of these models fit the data best by choosing the model with the smallest residual sum of squares (i.e., the one with the least amount of variability that was not explained by the model) (Fussmann et al. 2005). These statistical analyses are described in more detail in Appendix C.

Influence of omnivory

C. maenas and *H. sanguineus* are both omnivorous (Ropes 1968; Elner 1981; Tyrrell and Harris 1999; Lohrer et al. 2000). We conducted a second experiment to determine the effect of predator density when these predators had the choice of several different prey taxa that are available to them under natural conditions. Boulders that had a full compliment of naturally occurring flora and fauna, including barnacles, snails, limpets, urchins, mussels, and macroalgae were placed in field enclosures.

We allowed crabs to forage in enclosures for 24 h at one of 9 predator densities: 1, 2, 3, 4, 5, 6, 7, 8, or 10 crabs per cage. The experimental design was uneven (more replicates of lower predator densities were used) to approximately equalize the numbers of crabs used in the analysis from treatments at each of the predator densities (resulting in 7 - 12 crabs from each predator density). Since crabs forage predominantly during nighttime high tides (Lindberg 1980; Willason 1981; Batie 1983; Depledge 1984; Saigusa and Kawagoye 1997), experiments were terminated at dawn on ebbing tides to ensure that crabs had foraged as recently as possible. Upon termination of the experiment, crabs were immediately placed in 95% ethanol for later dissection. We determined the mass of material present in the gut of each crab by removing the cardiac stomach and passing its contents through a 6 - μm Ahlstrom filter. Filters were then dried at 70°C for 24 h, and then each was weighed. We corrected for differences in crab size by using the residual mass of the stomach contents for each crab after accounting for crab carapace width (i.e., the variance in stomach mass not explained by crab size) as the response variable in a regression analysis against the number of crabs in the cage for each species.

Population sampling

We sampled populations of *C. maenas* and *H. sanguineus* to determine whether the replacement of *C. maenas* by *H. sanguineus* has altered the overall abundance of predatory crabs throughout the invaded region. We used two metrics of abundance, density and biomass. Because *C. maenas* attains much larger maximum sizes than H. *sanguineus*, similar densities of these species may result in very different biomasses. Further, both metrics may influence and/or reflect the degree of interference. We therefore measured both.

We sampled crabs at 30 sites over a 700 kilometer transect from Rye, NY to West Quoddy Head, ME. Sampling was conducted from late June to late August, 2006. Sampling of sites at different latitudes was interspersed throughout this time period to avoid confounding seasonal changes with latitudinal changes. At each site we determined the number of crabs of each species, their carapace width, and gender within 16 randomly interspersed 1-m^2 quadrats throughout the mid and lower intertidal zones. We determined biomass of each crab species at each site using empirically derived relationships between carapace width and biomass for male and female *C. maenas* combined and for male and female *H. sanguineus* separately (because *H. sanguineus* is sexually dimorphic) ($R^2 \geq 0.99$ for each relationship, Griffen unpubl. data).

In comparing the abundance of *C. maenas* and *H. sanguineus* across our sampling range, it was necessary to control for latitudinal changes in environmental factors that exogenously influence crab abundance. While the use of ANCOVA with latitude as a covariate would have been ideal, the inverse gradient of the two species across our sampling range violated the assumption of homogenous slopes (Engqvist 2005). We therefore conducted an alternative analysis in which we converted latitude into a categorical variable, thus allowing us to compare *C. maenas* and *H. sanguineus* abundance in different parts of our sampling range (D'Alonzo 2004). To do this we divided our sampling range into three regions: sites from Cape Cod south where *H. sanguineus* has been present for more than a decade and has likely achieved maximum population abundance (Kraemer et al. In Press), sites within the Gulf of Maine where *H. sanguineus* has been present for less than a decade and is still increasing in abundance, and sites within the Gulf of Maine where *H. sanguineus* has not yet arrived. We then conducted separate two-way ANOVAs on log density and log biomass with species and sampling region as fixed factors, followed by planned linear contrasts to compare the abundance of *C. maenas* and *H. sanguineus* in each of the three regions.

Results

Functional response experiment

Maximum mussel consumption by C. *maenas* and H. *sanguineus* was similar over the duration of our experiment (Fig. A.1A,B), indicating that differences in the importance of predator density are not due to differences in the amount of prey depletion between predator species. Both *C. maenas* and *H. sanguineus* had type III functional responses at all three predator densities (significant positive linear term and negative quadratic term in the polynomial logistic regression). Statistical analyses were confirmed by plots of proportion of prey consumed vs. initial prey density (Fig. A.1C,D).

C. maenas' per capita daily mussel consumption decreased in a more consistent manner with increasing predator density than that of *H. sanguineus* (Fig. A.1E,F). The type III functional response model provided a highly significant fit to the data (nonlinear regression, $F_{2,34} > 34$, $P < 0.0001$ for all six predator combinations), and yielded estimates of handling times and searching efficiencies for each. Model parameters indicated that changes in foraging by *C. maenas* with predator density resulted both from increases in handling time and decreases in searching efficiency at higher predator densities (Fig. A.2). Whereas for *H. sanguineus*, prey handling time increased at higher predator densities, but there was no effect of predator density on searching efficiency (Fig. A.2).

These changes in handling time and searching efficiency with increasing predator density resulted in predator dependent foraging for both *C. maenas* and *H. sanguineus*, though to very different degrees. Foraging by *C. maenas* was strongly predator dependent, and was described best by the functional response model with an exponent (*m*) of 0.9 (i.e., this model explained the most variation in the data and thus had the lowest residual sum of squares, Table A.1). (The residual sum of squares was actually lowest using the purely ratio dependent model for *C. maenas*; however, confidence intervals for parameter estimates with this model included zero). In contrast, *H. sanguineus* foraging was influenced very little by predator density, and despite high variability in *H. sanguineus* predation rates (Fig. A.1F), its foraging was described best by the functional response model with an exponent of 0.1 (Table A.1). Thus, *C. maenas* and *H. sanguineus* forage on opposite ends of the ratio dependent – prey dependent continuum.

Influence of omnivory

The relative importance of predator density for *C. maenas* and *H. sanguineus* predation was unaffected by increasing the number of prey choices available. When all naturally available prey types were available to them, *C. maenas* consumed on average 45% mussels, the rest of the diet being comprised mainly of barnacles and red algae, while *H. sanguineus* consumed mainly red algae and mussels made up on average only 30% of their diet. Though variability was high, particularly at low predator densities, the amount of food consumed by individual *C. maenas* (gut content mass) decreased with increasing predator density (regression, $P = 0.05$, $R^2 = 0.04$, Fig. A.3A). Predator density had no impact on the amount of food consumed by individual H*. sanguineus* (regression, $P = 0.23$, $R^2 = 0.02$, Fig. A.3B).

Population sampling

The mean density of *H. sanguineus* was more variable across sites (0 - 79.5 crabs / m^2) than that of *C. maenas* (0.1 - 7.9 crabs / m^2), and the relative density of the two species differed by sampling region. Specifically, *H. sanguineus* was more dense than *C. maenas* in the region south of Cape Cod ($F_{1,54} = 50.65$, $P << 0.001$, region 1 in Fig. A.4). At sites within the Gulf of Maine where *H. sanguineus* has already invaded, but has been present for a relatively short time period, the density of the two species is similar ($F_{1,54}$ = 0.07, P = 0.79, region 2 in Fig. A.4). Pemaquid Point, ME represents the northernmost extent *of H. sanguineus'* invaded range, and only *C. maenas* was found at sites north of this ($F_{1,54}$ = 12.72, P < 0.001, region 3 in Fig. A.4). Averaging across all three of these regions, *H. sanguineus* population densities were nearly six times greater than those of *C. maenas* (Fig. A.4).

Despite the large body size of *C. maenas*, patterns in biomass were identical to those of density reported above. Specifically, the mean biomass of *H. sanguineus* was more variable (0 - 224.9 g / m^2) than that of *C. maenas* (0.004 - 35.2 g / m^2). *H. sanguineus* had higher biomass in the region south of Cape Cod ($F_{1,54}$ = 30.51, P << 0.001, region 1 in Fig. A.4). The two species were similar in biomass in southern Gulf of Maine sites ($F_{1,54}$ = 0.23, P = 0.63, region 2 in Fig. A.4). *C. maenas* biomass was higher by default in northern sites where *H. sanguineus* has not yet invaded ($F_{1,54}$ = 15.73, P < 0.001, region 3 in Fig. A.4). Qualitative results of these analyses were unchanged when the two sites with extremely high *H. sanguineus* abundance were excluded.

Discussion

Few studies have examined the strength of predator dependence in field settings (Reeve 1997; Vucetich et al. 2002; Schenk et al. 2005). We have shown that predator dependence was stronger for *C. maenas* than for *H. sanguineus* when each foraged in field enclosures in the same habitat and on the same prey resources. This is consistent with previous findings that *C. maenas* is more aggressive towards conspecifics than is

H. sanguineus (Griffen and Williamson In Review), and that prey handling times and searching efficiency of *C. maenas* are both negatively influenced at high predator densities (Smallegange et al. 2006). This study provides additional evidence that foraging may frequently fall short of either pure ratio dependence or pure prey dependence (Abrams and Ginzburg 2000; Hansson et al. 2001; Schenk et al. 2005); but rather, as was the case for both *C. maenas* and *H. sanguineus* (Table A.1), predation may often fall somewhere along the continuum between these extremes. The difference in predator dependence by two species of intertidal crabs also cautions that the strength of predator dependence is species-specific and that generalizations that apply across broad taxonomic groups (such as across all intertidal crabs) may not be possible.

Lower predator densities for C. *maenas* than for H. *sanguineus* are consistent with theoretical prediction that interference can reduce predator abundance (Arditi et al. 2004). Other factors besides conspecific interference may also influence maximum predator density, including the availability of prey, food conversion efficiency, and food-independent predator mortality (Arditi and Ginzburg 1989; Arditi et al. 2004). However, predator interference and aggression may also influence these factors. For example, interference that reduces consumption rates (Fig. A.1E, F) can lead to slower individual growth rates for both of these species (Griffen et al. In Review), and may thus indirectly increase predator mortality by increasing the time susceptible to size-dependent predation threats (deRivera et al. 2005). In addition, extreme conspecific aggression (i.e., cannibalism) is an important source of mortality for *C. maenas* and can directly limit population size for this species due to its density-dependent nature (Moksnes

2004). Predator interference and aggression may therefore act in multiple ways to differentially influence the densities of these two species, and may thus at least partially explain both the small size of current *C. maenas* populations at sites outside the invaded range of *H. sanguineus* (zone 3 in Fig. A.4), and the small historical *C. maenas* densities that were replaced by larger *H. sanguineus* densities at the same sites (Lohrer and Whitlatch 2002a, b and references therein).

Not only are these species influenced differently by intraspecific interference, but they are also influenced differently by interspecific interference. *C. maenas* eats less and alters its diet to consume less favorable food in the presence of *H. sanguineus*, while *H. sanguineus* predation is unaffected by interactions with *C. maenas* (Griffen et al. In Review). This implies that in regions of overlap when these two species forage together, predation by *C. maenas* is likely still heavily predator-dependent, but the important predator density is the combined density of *C. maenas* plus *H. sanguineus*; while predation by *H. sanguineus* is only weakly influenced by interactions with conspecifics or heterospecifics, and is thus still likely only weakly predator-dependent when foraging side-by-side with *C. maenas*.

The differential effect of predator interference for these two species may potentially contribute to the observed shift from a *C. maenas* to an *H. sanguineus* dominated system. When only *C. maenas* is present, interference decreases as predator density declines (Fig. A.1E). In contrast, when interference occurs with a heterospecific that is not influenced by the interaction (i.e., *H. sanguineus*) this inherent negative feedback is eliminated. Thus, from an interference perspective, *H. sanguineus* densities may increase because of low interference from *C. maenas* or from conspecifics, while *C. maenas* populations may be depressed by strong interference from both *H. sanguineus* and conspecifics, and this interference is not lessened as *C. maenas* densities decline because of concurrently increasing *H. sanguineus* densities.

H. sanguineus has only been present in the Gulf of Maine since the late 1990s (McDermott 1998). A previous report indicated that *H. sanguineus* densities on the New Hampshire coast were ten times lower than *C. maenas* densities for the first few years following its arrival (Tyrrell et al. 2006). Our study indicates *H. sanguineus* densities in this region are climbing, and are now similar to densities of *C. maenas*. Given the latitudinal range of native *H. sanguineus* populations in the western Pacific (McDermott 1998 and references therein), the continued spread of *H. sanguineus* is likely. However, as this new invader increases in abundance within the Gulf of Maine, it is uncertain whether it will reach high densities similar to those seen south of Cape Cod or whether it will displace *C. maenas* from rocky intertidal areas as it has in southern regions (Lohrer and Whitlatch 2002a). Current *C. maenas* densities for southern Gulf of Maine sites reported here are similar to historical densities before the arrival of *H. sanguineus* (Menge 1983), suggesting that displacement of *C. maenas* has not yet occurred.

While not strictly ratio dependent or prey dependent, the large differences in the importance of predator interference for *C. maenas* and *H. sanguineus* may have important consequences for the invaded community where *H. sanguineus* has displaced *C. maenas* to become the dominant predatory crab (Lohrer and Whitlatch 2002a). Much attention has been given to potential changes in community structure that may result from this species shift (Tyrrell and Harris 1999; Lohrer et al. 2000; Lohrer and

Whitlatch 2002b; Tyrrell et al. 2006). These studies have focused largely on diets of the two predators and how diet choice may affect predation pressure on various prey taxa. Our study highlights an additional mechanism by which a change in the dominance of these two predators in the invaded region may impact the native community. Even when predation is not strictly prey dependent, decreasing predator interference has a destabilizing influence in predator-prey systems (Arditi et al. 2004) that can lead to oscillatory predator-prey cycles of increasing amplitude (Hassell and May 1973). Thus, replacement of *C. maenas* (high predator dependence) with *H. sanguineus* (low predator dependence) may decrease system stability. This is consistent with drastic reductions in the abundance of mussel prey that have been reported in areas where *H. sanguineus* has achieved very high densities (Lohrer and Whitlatch 2002b), and with large effects of this species across the broader prey community (Tyrrell et al. 2006). Whether high densities of *H. sanguineus* will be able to persist in the face of depressed prey abundances, or whether a lack of food will eventually drive down *H. sanguineus* densities remains to be seen. However, given the open nature of both *H. sanguineus* and prey populations in intertidal habitats, increasing predator-prey oscillations that lead to local species extinction are unlikely.

We have demonstrated that while foraging by two predatory crabs is neither strictly prey dependent nor ratio dependent, their foraging falls at different ends of this continuum. Anthropogenic disturbance via the introduction *of H. sanguineus*, together with its subsequent displacement of *C. maenas*, has shifted the importance of predator dependence in our study system. Weaker predator dependence for *H. sanguineus* than for *C. maenas* may at least partially explain why this new invader has achieved higher population densities and can have greater impacts on the native community (Lohrer and Whitlatch 2002b; Tyrrell et al. 2006).

Acknowledgements

Portions of this work were funded by the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce We thank I. Altman, A. Blakeslee, J. Byers, M.F. Delaney, G.F. Fussmann, W.J. Lee, and L. Page for comments on the manuscript. We also thank A. Malek and S. Trottier for assistance in field work.

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Tables

Table A.1 Residual sum of squares from fit of different models to functional response data. The left-hand column represents the variable *m* in the functional response equation. *m* is zero in the prey dependent model and one in the ratio dependent model. Intermediate levels represent varying degrees of predator dependence.

m	C. *maenas*	H. *sanguineus*
0.0	26091.7	27393.8
0.1	20416.5	24292.7
0.2	16088.1	36053.7
0.3	12124.0	33404.0
0.4	10785.9	33398.9
0.5	6885.0	30001.7
0.6	6050.9	28851.1
0.7	6554.1	28362.2
0.8	4257.1	27785.1
0.9	4126.6	27975.1
1.0	961.5*	30049.6

*While this model yielded the lowest residual sum of squares, indicating that C. *maenas* predation may be strictly ratio dependent, parameter estimates (for handling times and searching efficiency) with this model were not significant. We therefore concluded that the model with the next lowest residual sum of squares (with *m* = 0.9) provided the best fit.

Figures

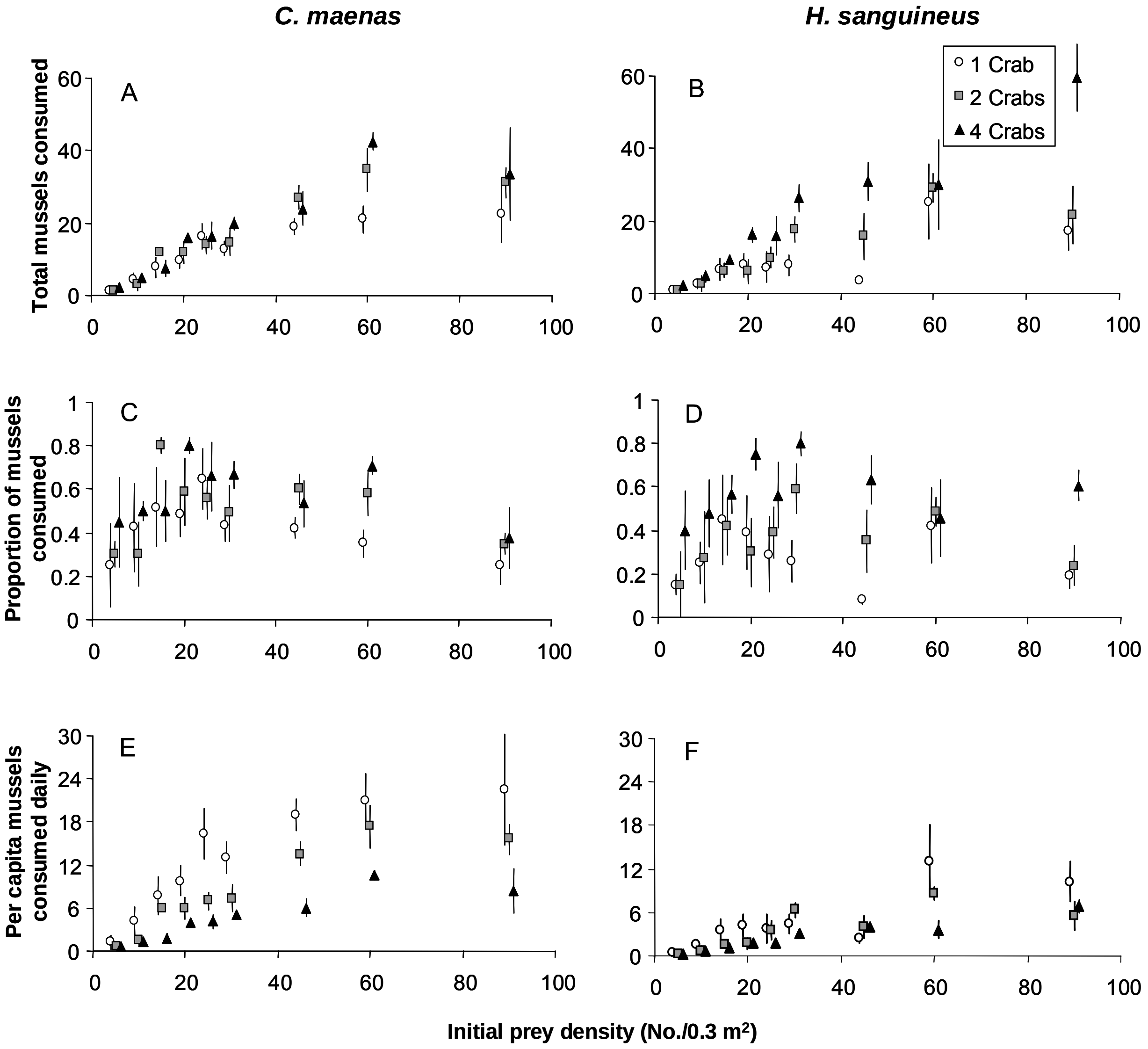

Figure A.1 Functional response of *Carcinus maenas* (parts A, C, and E) and *Hemigrapsus sanguineus* (parts B, D, and F) at different densities while foraging on mussel prey. Values are means ± SE (n = 4). A and B) Total number of prey consumed over the course of the experiment at different initial prey densities. C and D) Proportion of prey consumed at different initial prey densities. E and F) Per capita daily prey consumption at different initial prey densities.

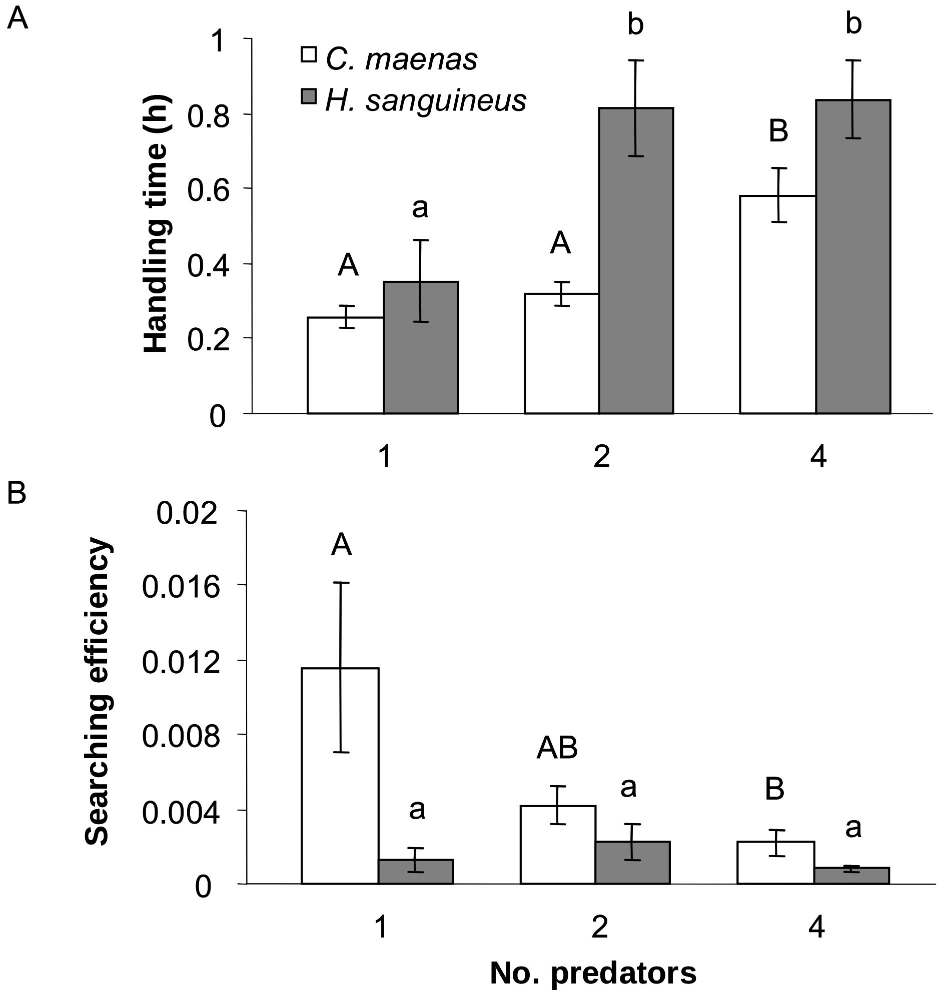

Figure A.2 Estimates (mean ± SE) of handling time and searching efficiency for *C. maenas* and *H. sanguineus* at different predator densities as determined by nonlinear least squares regression. Letters over bars indicate statistically significant differences based on individual t-tests (alpha = 0.05). Capital letters indicate comparisons among *C. maenas* only, and lowercase letters indicate comparisons among *H. sanguineus* only (*i.e.*, comparisons were not made between species).

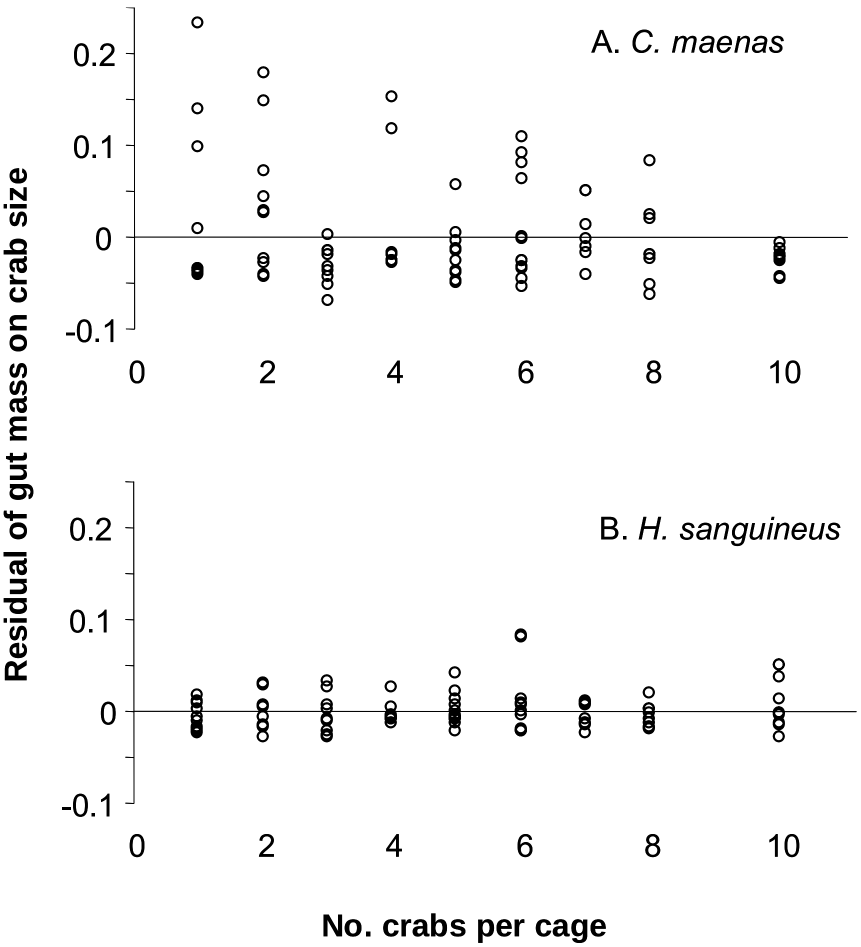

Figure A.3 Residual mass of stomach contents after crab size is accounted for at different predator densities. Values represent individual crabs.

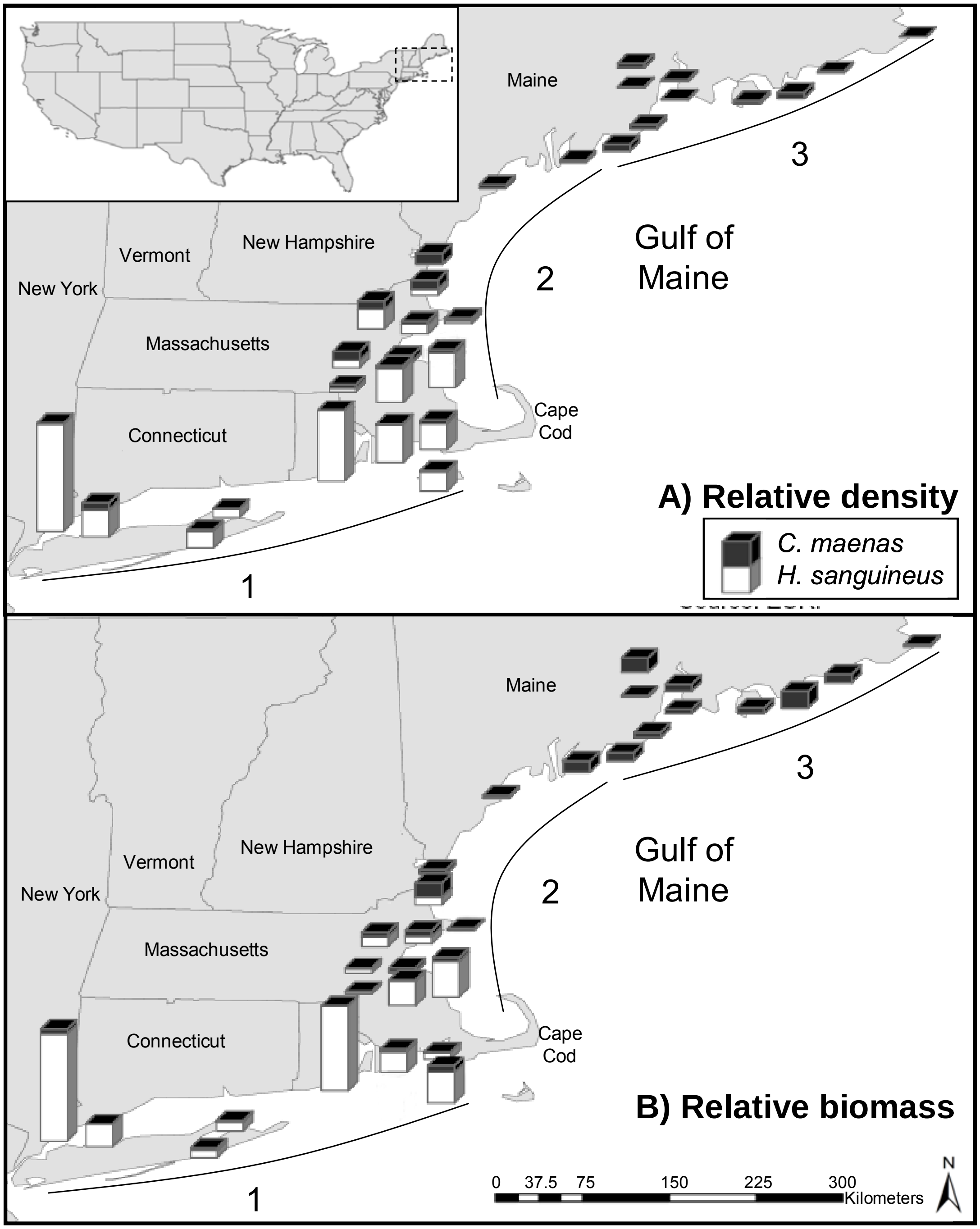

Figure A.4 Density (part A) and biomass (part B) of *C. maenas* and *H. sanguineus* at 30 sites throughout their invaded ranges. Heights of bars indicate relative mean values (n =16 per site). Lines drawn along the coast and corresponding numbers demonstrate three different regions for statistical analysis.

Appendix B. Experiment to Examine Potential Artifacts in Main Ratio Dependent Experiment

In our functional response experiment we used different experimental durations and mussel sizes for *C. maenas* and *H. sanguineus* in order to standardize prey depletion. We conducted a supplementary experiment to verify that results obtained in the functional response experiment were not an artifact of these experimental differences between predator species. In this experiment, we examined predation by *C. maenas* and *H. sanguineus* on mussel prey over a constant experimental duration (24 h) and on the same sized mussels (14 - 17 mm shell length) for each predator species. Our purpose was to capture the salient features of the functional response experiment (i.e., the relative importance of predator interference for *C. maenas* and *H. sanguineus*), but was not to determine the functional response, estimate parameters, or to compare between prey dependence and ratio dependence. In addition, we wanted to examine predation at a larger range of prey densities, consistent with the larger range of densities at our field site, to determine whether the effect of predator density differed at higher prey densities where competition for prey may not be as great. We therefore examined predation at four prey densities (10, 20, 100, and 200 prey per enclosure, using the same enclosures as described in the main text) and with two and four predators. Each of these eight predator-prey combinations was replicated four times for each species during separate trials.

I compared the effects of prey and predator density for each species separately using two-way ANOVAs on log transformed (to achieve homoscedasticty) per capita predation with prey density (four levels) and predator density (two levels) as fixed factors.

Results of this experiment indicated that *C. maenas* predation increased at higher prey densities (ANOVA, $F_{3,24} = 45.44$, $P < 0.0001$, Fig. B.1A), and that increasing predator density caused a decrease in *C. maenas* per capita predation (ANOVA, $F_{1,24} = 22.78$, $P < 0.0001$, Fig. B.1A) that was consistent across prey densities (predator density×prey density interaction $F_{3,24} = 0.38$, $P = 0.77$). In contrast, while increasing prey density also had a positive impact on *H. sanguineus* predation (ANOVA, $F_{3,24} = 11.66$, $P < 0.0001$, Fig. B.1B), increasing predator density had no influence on *H. sanguineus* predation (ANOVA, $F_{1,24} = 1.78$, $P < 0.20$, Fig. B.1B), and this was again consistent across prey densities (predator density×prey density interaction $F_{3,24} = 0.60$, $P = 0.62$).

These results are consistent with results in our main experiment where predation by both species increased asymptotically with prey density, and where predator density had a greater influence on predation by C. *maenas* than by *H. sanguineus*. Based on these results, we conclude that results of our functional response experiment given in the main text were not influenced by differences in experimental procedures with *C. maenas* and *H. sanguineus*, nor were they influenced by the range of experimental prey densities that we used.

Figures

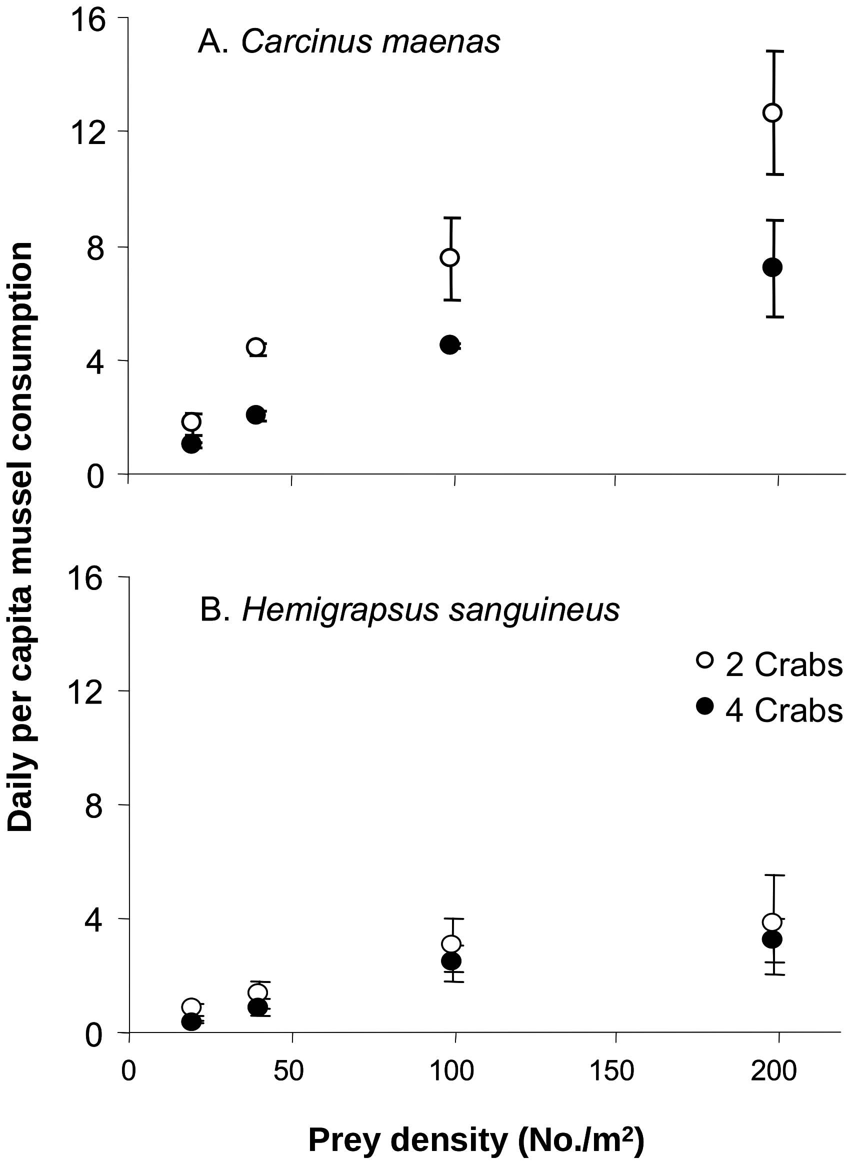

Figure B.1 Per capita mussel consumption rates of *C. maenas (*part A) and *H. sanguineus* (part B) when experiments were conducted using the same size mussel prey for both predator species and the same experimental duration. Values are means ± SE (n = 4).

Appendix C. Statistics Used for Functional Response Analysis

Data analysis for this experiment was a three step process and followed the procedures outlined by Juliano (2001). We first determined the shape of the functional response curves for each of the three predator densities of each crab species (six curves total) using separate polynomial logistic regressions. All six were saturating curves, indicating that predation followed either a type II or type III functional response. We fit a cubic model to each curve and observed the sign of the linear term in the polynomial equation to differentiate between type II and type III curves (a negative term indicates type II and a positive term together with a negative quadratic term indicates type III response). When the cubic term was not significant, it was removed and the analysis was repeated (there were no instances when quadratic polynomials had insignificant terms). Conclusions from these analyses were verified by visual inspection of plots of proportion of prey eaten vs. initial prey density.

We next estimated the parameters of the functional response equation using nonlinear least squares regression for each of the six curves. This was done to understand how predator density influenced the mechanisms of predation, specifically prey handling time and searching efficiency, for *C. maenas* and *H. sanguineus*. As logistic regression indicated type III functional responses for both predators at all three densities, we fit the data to a type III functional response model that accounts for prey depletion, as occurred in our experiments (this is the integrated form of the type III functional response equation given by Hassel 1978 where searching efficiency is a function of prey density, and is equation 10.5 from Juliano 2001):

$$N_e = N_0\{1 - \exp[(d + bN_0)(T_hN_e - T)/(1 + cN_0)]\} \qquad (1)$$

Where N_e and N_0 are the number of mussels consumed and the initial number of mussels offered, T is the duration of the experiment, T_h is the handling time (the time required to consume a single mussel), and *b, c,* and *d* are constants that relate the attack rate to prey density (i.e., the searching efficiency). The purpose of the analysis was to estimate values for T_h, *b, c*, and *d*.

Parameters values that were not significantly different from zero (based on 95% CI) were removed and the analysis was repeated. For each of the six functional response curves, *c* and *d* were not different from zero and were thus removed, resulting in the minimal form of the type III functional response equation. Nonlinear regression thus resulted in an estimate (mean and SE) of T_h and *b* for each curve.

Estimates of T_h and *b* were then compared between each pair of predator. Because we wanted to compare parameter estimates between three different predator densities for each species, an ANOVA would have been ideal. However, nonlinear regression analyses provide a single estimate and standard error for each of the parameters, rather than replicate estimates that are necessary to perform an ANOVA. We therefore made pair wise comparisons using individual t-tests (Glantz and Slinker 1990; Juliano 2001; Fussmann et al. 2005).

Finally, our overarching goal was to determine whether *C. maenas'* and *H. sanguineus'* predation was explained better by the prey dependent model or by the ratio dependent model. The model in Eqn. 1 represents the prey dependent model. The ratio dependent model was obtained by replacing N_0 with N_0 / P^m (Hassell and Varley 1969), where P is the number of predators in an enclosure, and m is an interference coefficient. When *m* = 0, the model reduces to the prey dependent form. Ratio dependence is modeled when *m* = 1. Intermediate values of *m* represent varying degrees of predator dependence. We fit the data for each predator species (across all predator densities simultaneously) to models ranging from prey dependence to ratio dependence at intervals of *m* = 0.1. We determined which of these models fit the data best by choosing the model with the smallest residual sum of squares (i.e., the one with the least amount of variability that was not explained by the model) (Fussmann et al. 2005).

All statistical analyses were conducted in SAS version 9.1. Program code for logistic and nonlinear regressions was modified from that given in Juliano (2001 supplementary material), and is available from the authors (Griffen) upon request.