



2015

Long-Term Effects of an Invasive Shore Crab on Cape Cod, Massachusetts

Christopher P. Bloch

Bridgewater State University, cbloch@bridgew.edu

Kevin D. Curry

Bridgewater State University, kcurry@bridgew.edu

John C. Jahoda

Bridgewater State University, jjahoda@bridgew.edu

Follow this and additional works at: http://vc.bridgew.edu/biol_fac



Part of the [Ecology and Evolutionary Biology Commons](#)

Virtual Commons Citation

Bloch, Christopher P.; Curry, Kevin D.; and Jahoda, John C. (2015). Long-Term Effects of an Invasive Shore Crab on Cape Cod, Massachusetts. In *Biological Sciences Faculty Publications*. Paper 48.

Available at: http://vc.bridgew.edu/biol_fac/48

Long-term Effects of an Invasive Shore Crab on Cape Cod, Massachusetts

Christopher P. Bloch^{1,*}, Kevin D. Curry¹, and John C. Jahoda¹

Abstract - Invasive species can cause dramatic changes in the structure of intertidal communities. In some systems, however, abundance or impacts of invaders may peak 10–20 years after invasion and decline thereafter. *Hemigrapsus sanguineus* (Asian Shore Crab) has been established at Sandwich, MA, on the north side of Cape Cod, since the mid-1990s. This study documented population dynamics of the Asian Shore Crab and 3 species of prey or competitors (*Carcinus maenas* [Green Crab], *Mytilus edulis* [Blue Mussel], and *Littorina littorea* [Common Periwinkle]) over 10 years. An additional goal of the study was to determine whether population growth of the Asian Shore Crab has slowed since its initial establishment. Density of the Asian Shore Crab increased over time, with no evidence of a density-dependent decrease in per capita growth rates. Concurrently, density of the Green Crab and the Blue Mussel declined, but there was no significant temporal trend in density of the Common Periwinkle. If observations at Sandwich are representative of sites north of Cape Cod, populations of the Asian Shore Crab are growing rapidly, and dramatic changes in community structure may be widespread.

Introduction

Rapid global travel and the expansion of international commerce have dramatically increased the rate at which species are being introduced into established ecosystems (Mooney and Cleland 2001). In ballast water alone, thousands of species may be in transit during any particular day (Carlton 1999). Although most introduced species do not establish populations (Williamson 1996), those that do can have profound effects on native biota via multiple pathways, including competition and predation (Mooney and Cleland 2001). Such effects often result in reduced biodiversity of native species, impairment of ecosystem services (Bax et al. 2003), and, in extreme cases, disassembly of communities (Sanders et al. 2003). Hence, invasive species are a major concern in conservation biology, especially in marine systems where eradication of invaders is particularly difficult because of the ease with which planktonic or rafting larvae can disperse among sites (Thresher and Kuris 2004). Coastal ecosystems may be particularly susceptible to changes in community structure as a result of invasion (Grosholz et al. 2000, Raffa et al. 2014), especially on the northeast coast of North America, where biodiversity in intertidal ecosystems is generally low.

Hemigrapsus sanguineus (De Haan) (Asian Shore Crab) was first observed on the Atlantic coast of the United States at Cape May, NJ, in 1988 (Williams and

¹Department of Biological Sciences, Bridgewater State University, Bridgewater, MA 02325.*Corresponding author - cbloch@bridgew.edu.

McDermott 1990) and has since spread south to North Carolina and north to southern Maine (McDermott 1998a, Stephenson et al. 2009). This rapid range expansion was probably facilitated by a variety of physiological and behavioral traits including omnivorous dietary habits (Bourdeau and O'Connor 2003, Brousseau and Baglivo 2005), a high reproductive rate (a mean of approximately 15,000 eggs per brood, with multiple broods per year; Epifanio et al. 1998, Fukui 1988, McDermott 1998b), tolerance of a wide range of salinities (Gerard et al. 1999), and high mobility and low site fidelity (Brousseau et al. 2002). Moreover, adult Asian Shore Crabs produce chemical cues that promote settlement of larvae (Kopin et al. 2001), potentially accelerating establishment of populations at newly colonized sites. In many rocky intertidal habitats in New England, it has become the dominant brachyuran species (Ahl and Moss 1999), largely replacing *Carcinus maenas* (L.) (Green Crab; Lohrer and Whitlatch 2002a), which has been established in northeastern North America for over 200 years (Grosholz and Ruiz 1996).

In both laboratory and field situations, the Asian Shore Crab readily consumes other invertebrate species, including *Mytilus edulis* (L.) (Blue Mussel; Bourdeau and O'Connor 2003, DeGraaf and Tyrrell 2004, Gerard et al. 1999), and *Littorina littorea* (L.) (Common Periwinkle; Gerard et al. 1999, Kraemer et al. 2007). Both of these species are important in rocky intertidal communities in New England. The Blue Mussel is a dominant competitor for space (Seed 1976), and littorinid snails, as common grazers, play key roles in controlling the abundance, composition, and density of algal communities (Bertness et al. 1983, Lubchenco 1983, Mak and Williams 1999), as well as the settlement and survival of sessile invertebrates (Holmes et al. 2005) in rocky intertidal zones. Indeed, it has been argued that no introduced marine mollusk has had a greater effect on intertidal ecosystems in North America than the Common Periwinkle (Carlton 1999). Consequently, predation by the Asian Shore Crab has the potential to markedly alter community structure on North American rocky shores.

Considerable research has been conducted in an effort to understand potential and realized effects of the Asian Shore Crab on coastal communities in the northeastern US. Most of these studies, however, have been short-term or experimental; long-term field observations have been less common (but see Kraemer et al. 2007, O'Connor 2014, Payne and Kraemer 2013). This lack of long-term data is problematic for 2 reasons. First, several species that are preyed upon by the Asian Shore Crab are most vulnerable as larvae or juveniles; therefore, the full effects of invasion by the Asian Shore Crab may not be clear until individuals that were adults at the time of invasion die (Gerard et al. 1999). Second, in some systems, abundance or impacts of invaders may peak 10–20 years after invasion and decline thereafter (Creed and Sheldon 1995, Lohrer and Whitlatch 2002a, Phelps 1994). For example, populations of native *Panopeus herbstii* H. Milne-Edwards (Common Mud Crab) in the Delaware Bay appear to have rebounded from initial declines following invasion by the Asian Shore Crab circa 1988 (Schab et al. 2013). Thus, long-term observations of invaded communities are important for a full understanding of the effects of the Asian Shore Crab.

The objective of this study was to document changes in abundance of the Asian Shore Crab and 1 native (Blue Mussel) and 2 established (Green Crab and Common Periwinkle) species over 10 years in a rocky intertidal community on Cape Cod, MA. Each of these other species is subject to predation or competition in the presence of the Asian Shore Crab (Gerard et al. 1999, Jensen et al. 2002, Kraemer et al. 2007). A second objective was to determine whether the Asian Shore Crab displayed evidence of reduced population growth approximately 20 years after invading Cape Cod.

Field-Site Description

The study was conducted at Town Neck Beach in Sandwich, MA ($41^{\circ}46.357'N$, $70^{\circ}29.474'W$), on the north side of Cape Cod, just east of the Cape Cod Canal (Fig. 1). This is a low-energy site with a broad, flat intertidal zone (slope = $0.5\text{--}2.5^{\circ}$). Substrate in the intertidal zone is primarily comprised of boulders and cobbles overlaying a mixture of pebbles and sand. In the upper intertidal zone, sand is more prominent, and the number of rocks decreases with increasing proximity to the mean high-tide line (MHT).

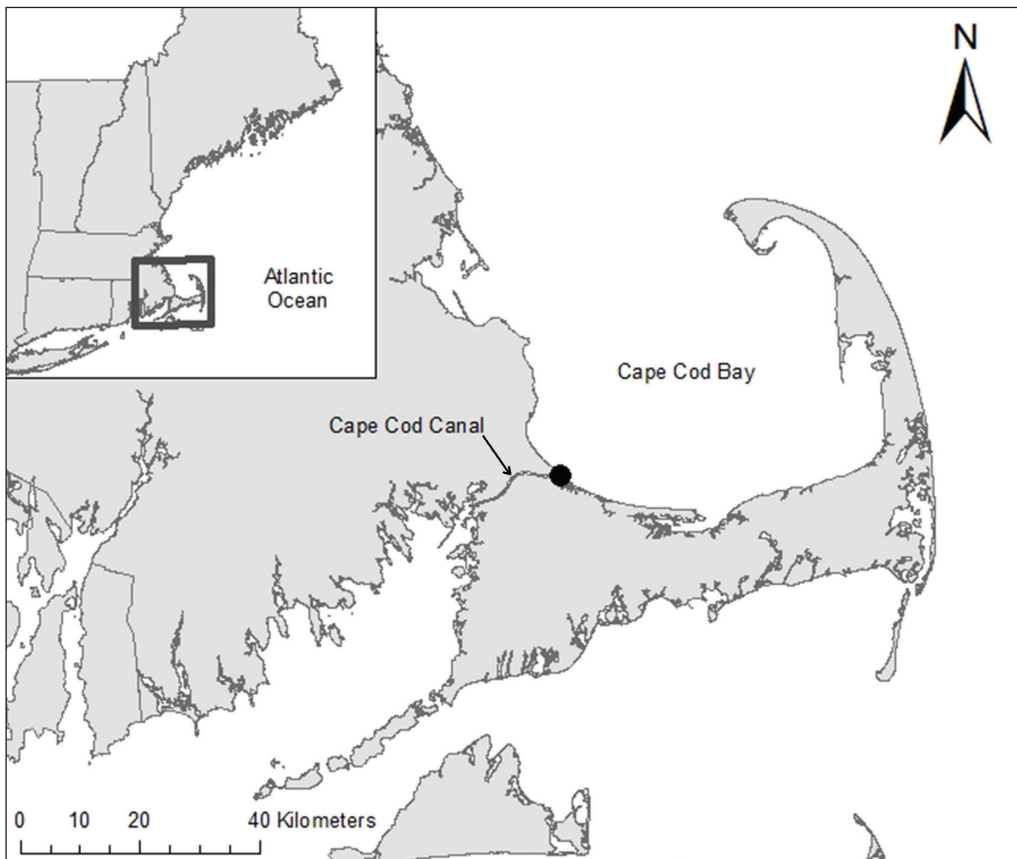


Figure 1. Map of southeastern Massachusetts, indicating the location of the study site (black circle). Inset displays the location of Massachusetts in relation to other New England states.

Methods

Field methods

We sampled 4 species of intertidal invertebrate (Asian Shore Crab, Green Crab, Common Periwinkle, Blue Mussel) annually from 2003 to 2012. Although the exact date of sampling differed each year, sampling always occurred during low tide on a Saturday in September. Each year, we laid out from 14 to 33 transects perpendicular to the shore, beginning at MHT. In general, the number of transects increased over time. We established 3 circular quadrats of 76.2 cm diameter at each of 3 locations along each transect. From 2003 to 2008, these locations were 15 m from MHT, 30 m from MHT, and 45 m from MHT; from 2009–2012, distances were 20 m, 30 m, and 50 m from MHT. These sampling locations (hereafter, the upper, middle, and lower intertidal zones, respectively) corresponded to general habitat characteristics. The lower intertidal zone remained wet throughout low tide and exhibited extensive cover of *Semibalanus balanoides* (L.) (Acorn Barnacle) and occasional patches of algae. The middle intertidal zone remained moist at the time of sampling and featured lower densities of algae and barnacles. Whereas the substrate of the lower and middle zones was almost entirely rocky, sand was more prominent in the upper intertidal zone, with cobbles, boulders, and pebbles interspersed. This zone was dry at the time of sampling and contained no algae or barnacles.

Within each quadrat, we collected and counted all individuals of the 4 target species. We removed large rocks within each quadrat to facilitate capture of crabs and mussels. After sampling was complete, we returned rocks to their original positions and released all organisms at the location of capture.

Statistical analyses

When the same plots or individuals are sampled multiple times, a repeated-measures design provides greater statistical power than a factorial ANOVA (Sokal and Rohlf 2012). However, the number of transects and their exact locations differed among years, so this study was not a true repeated-measures design and could not be analyzed as such. Consequently, for each species, we used analysis of covariance (ANCOVA) to compare density among regions of the intertidal zone and to test for linear trends in population density over time. Because the 3 quadrats at a given location on a transect abutted one another, they were not treated as independent samples. Instead, we pooled counts from each set of 3 quadrats to generate a single sample covering an area of 1.37 m², and sample size for each year was equal to the number of transects.

We used Spearman's rank correlation coefficient to test for correlations in population density between the Asian Shore Crab and each of the 3 other species. Unlike parametric correlation analysis, Spearman's rank correlation coefficient does not assume a linear association between variables (Sokal and Rohlf 2012) and can therefore detect a monotonic relationship between variables regardless of the exact form of the relationship. To account for effects of vertical zonation on interactions between species, we estimated population density of each species in each year in 2 ways: averaged among all samples within each region of the intertidal zone, and averaged among all samples regardless of region.

To test for evidence of density-dependence in population growth of the Asian Shore Crab, the per capita growth rate (r) was estimated for each year t as:

$$r_t = (n_t - n_{t-1}) / n_{t-1},$$

where n = estimated population density, averaged among all samples for a particular year. No estimate of r was calculated for 2012 because n was unavailable for 2013. We used Spearman's rank correlation coefficient to evaluate the association between n and r at 3 different time lags: no lag (r_t versus n_t), 1 year (r_t versus n_{t-1}), and 2 years (r_t versus n_{t-2}). A negative correlation would indicate declining per capita growth with increasing population density (i.e., density-dependent population growth). To confirm the appropriateness of using r as a measure of per capita growth, we fitted an exponential model to the 10-year time series of population densities of the Asian Shore Crab via least-squares regression. All analyses were conducted using SPSS version 19.

Results

Population density of the Asian Shore Crab increased over time (Table 1, Fig. 2A). From 2003–2005, density remained <7 individuals/m², but by 2012 density had increased to 31.3 individuals/m². This pattern of increase was consistent among regions of the intertidal zone (non-significant zone × year interaction: $P = 0.338$). There was no significant difference in density among regions of the intertidal zone, irrespective of year.

The Green Crab was present at low abundances throughout the study (<10 individuals/m² in all 10 years, and <5 individuals/m² in 7 years; Fig. 2B). Nevertheless, density declined over time (Table 1) in a consistent fashion in all regions (non-significant zone × year interaction: $P = 0.292$). Density of the Green Crab did not differ significantly among regions of the intertidal zone.

Table 1. Results of analyses of covariance to compare mean densities of each species among regions of the intertidal zone at Sandwich, MA, and over time. Year is treated as a covariate. The number of error degrees of freedom was 561 for each species. * indicates statistically significant results.

Species	Source of variation	df	<i>F</i>	<i>P</i>
Asian Shore Crab	Zone	2	1.08	0.342
	Year	1	151.14	<0.001*
	Zone × year	2	1.09	0.338
Green Crab	Zone	2	1.24	0.291
	Year	1	80.78	<0.001*
	Zone × year	2	1.23	0.292
Common Periwinkle	Zone	2	5.86	0.003*
	Year	1	0.50	0.822
	Zone × year	2	5.79	0.003*
Blue Mussel	Zone	2	25.40	<0.001*
	Year	1	108.85	<0.001*
	Zone × year	2	25.34	<0.001*

The Common Periwinkle was the most abundant of the 4 study species (Fig. 2C), with a maximum population density of 452.5 individuals/m² (in 2004) and a minimum of 233.4 individuals/m² (in 2009). Density of periwinkles was generally greatest in the lower intertidal zone and least in the upper intertidal zone, but the degree of difference between the lower and middle zones changed over time (zone × year interaction: $P = 0.003$; Table 1). Overall, there was no significant linear trend in density of periwinkles.

From 2003 to 2004, the Blue Mussel was second in abundance to the Common Periwinkle. Maximum density of Blue Mussels was 131.3 individuals/m² (in 2004). Thereafter, however, abundance dramatically declined (Fig. 2D), such that density of Blue Mussels exceeded 5 individuals/m² only once after 2005 (5.9 individuals/m² in 2011). The slope of the decline was significantly steeper in the lower and mid-intertidal zones than in the upper intertidal zone (zone × year interaction: $P < 0.001$; Table 1).

Overall, mean population density of the Asian Shore Crab in a particular year was not significantly correlated with that of any of the other 3 species (Table 2), although negative correlations with the Green Crab and the Blue Mussel approached significance ($0.05 < P < 0.10$). Results were similar when analyses were restricted to the lower or middle intertidal zones, except that the negative correlation with the Blue Mussel in the middle intertidal zone was significant. A positive correlation between the Asian Shore Crab and the Common Periwinkle in the upper intertidal

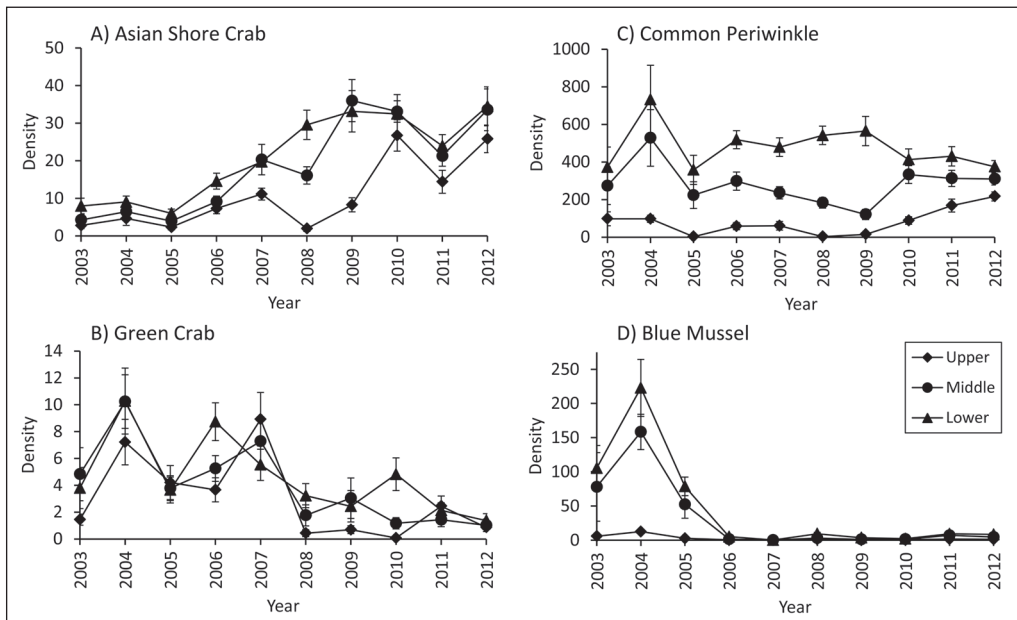


Figure 2. Annual estimates of population density (individuals/m², ± 1 SE) of 4 species of intertidal invertebrate at 3 regions of a rocky intertidal zone (diamonds: upper intertidal, circles: mid-intertidal, triangles: lower intertidal) at Town Neck Beach, Sandwich, MA. A: Asian Shore Crab (*Hemigrapsus sanguineus*), B: Green Crab (*Carcinus maenas*), C: Common Periwinkle (*Littorina littorea*), and D: Blue Mussel (*Mytilus edulis*).

zone approached significance. There was no correlation in density between the Common Periwinkle and the Green Crab or the Blue Mussel.

There was no evidence of density-dependent population growth of the Asian Shore Crab (Fig. 3A). The correlation between r and n was non-significant ($\rho = -0.43$, $P = 0.244$). Results were consistent for analyses incorporating a 1-year lag ($\rho = -0.17$, $P = 0.693$) and a 2-year lag ($\rho = -0.25$, $P = 0.589$). Moreover, r did not exhibit a significant trend over time ($\rho = -0.07$, $P = 0.865$; Fig. 3B). Per capita growth was positive in all except 3 years (2004–2005, 2007–2008, and 2010–2011). The observed pattern of population growth was consistent with an exponential growth model ($r^2 = 0.82$, $P < 0.001$; Fig. 3C), although a linear model ($y = 3.1x - 6155.6$; $r^2 = 0.83$, $P < 0.001$) fit the data equally well.

Discussion

In August and September of 1996, mean population density of the Asian Shore Crab at Sandwich, MA, varied from 2–4 individuals/m² in the lower intertidal zone, and few individuals were observed in the middle or upper regions of the intertidal zone (Ledesma and O'Connor 2001). By 2003, when the present study began, density had reached 8.0 individuals/m² in the lower intertidal zone and 5.0 individuals/m² overall. Density continued to increase thereafter (more than six-fold from 2003 to 2012), and growth does not yet appear to be slowing (Fig. 3). It is unclear to what extent this pattern reflects in situ reproduction relative to settlement of larvae dispersing from other sites (e.g., through the Cape Cod Canal).

Despite the steady population growth observed since 2003, density of Asian Shore Crabs at Sandwich remains less than half that reported from several other sites in southern New England (Kraemer et al. 2007, Lohrer and Whitlatch 2002a). Sandwich is located on the north side of Cape Cod, which historically may have served as a biogeographic barrier, as densities of Asian Shore Crabs reported

Table 2. Correlations (Spearman's rank correlation coefficient [ρ] and its significance [P]) between mean densities of the Asian Shore Crab and 3 other species in 3 regions of the intertidal zone (upper, middle, and lower), as well as overall, at Town Neck Beach, Sandwich, MA. * indicates statistically significant results. † indicates results that approach significance.

Species	Location	ρ	P
Green Crab	Upper	-0.20	0.580
	Middle	-0.61	0.060†
	Lower	-0.56	0.090†
	Overall	-0.61	0.060†
Common Periwinkle	Upper	0.60	0.067†
	Middle	-0.01	0.987
	Lower	0.24	0.511
	Overall	0.27	0.446
Blue Mussel	Upper	-0.37	0.293
	Middle	-0.64	0.048*
	Lower	-0.58	0.082†
	Overall	-0.59	0.074†

from sites north of Cape Cod (Griffen and Byers 2006) have generally been lower than those from south of Cape Cod (Kraemer et al. 2007). More recent sampling indicates that some sites north of Cape Cod are approaching similar densities to more southerly sites (O'Connor 2014). Nevertheless, habitat characteristics and prey abundance could also explain spatial variability in density. Abundance of the Asian Shore Crab is strongly associated with rock cover and structural complexity (Ledesma and O'Connor 2001, Lohrer et al. 2000a), but more comprehensive studies of habitat quality are lacking.

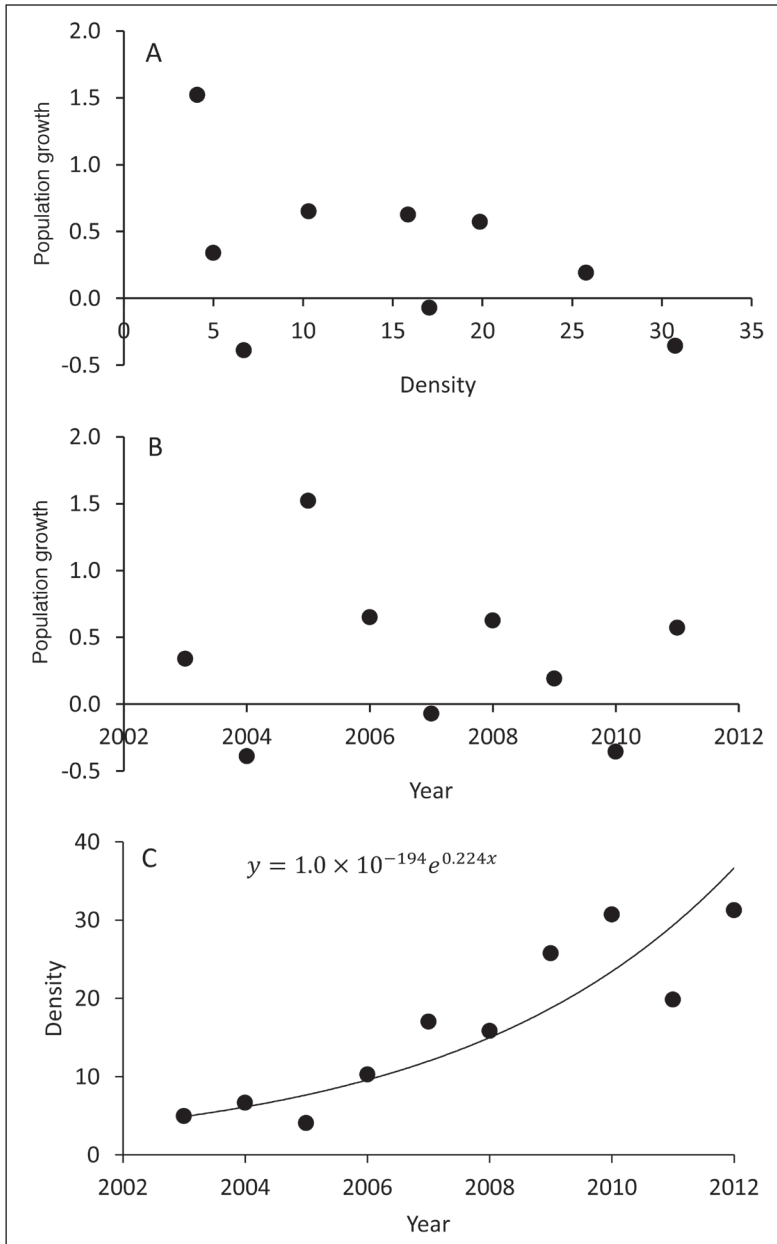


Figure 3. Per capita population growth (r) of the Asian Shore Crab (*Hemigrapsus sanguineus*) (A) as a function of population density (individuals/m²) and (B) over time, and (C) population density as a function of time, illustrating the fit of an exponential model.

Coincident with the increase in density of the Asian Shore Crab, there was a decline in densities of Green Crabs and Blue Mussels (Fig. 2). Negative correlations of densities of these species with those of Asian Shore Crabs were not strong, but for Blue Mussels this is probably artifactual. Because zero places a natural lower bound on abundance, mussel density was not free to decline throughout the study. Instead, after a precipitous decline from 2004 to 2006, density remained low. Although the source of this recruitment has not been documented, it is likely that they dispersed as larvae to the intertidal zone at Sandwich, rather than originating in situ, given that adult mussels were scarce after 2005. The observed population dynamics do not conclusively demonstrate a causal link between the Asian Shore Crab and the decline of the Green Crab or the Blue Mussel. Rather, the Asian Shore Crab could be an ecological “passenger” (*sensu* MacDougall and Turkington 2005) that benefits directly or indirectly from conditions that adversely affect other species. Direct interactions between the Asian Shore Crab and both the Green Crab and the Blue Mussel are well documented, however.

In laboratory experiments, the Asian Shore Crab dominates competition with the Green Crab for food and shelter (Jensen et al. 2002). This dominance extends to field settings; in the presence of the Asian Shore Crab, the Green Crab shifts its habitat use, abandoning otherwise preferred shelter under rocks (Jensen et al. 2002). In contrast, the Asian Shore Crab displays little difference in niche between its native and introduced ranges (Lohrer et al. 2000b), suggesting that competition from resident crabs in North America has only minor effects. Intraguild predation may also help explain declines in Green Crab abundance after invasion by the Asian Shore Crab. Juveniles of both species are consumed by larger crabs, but juvenile Green Crabs are more vulnerable to cannibalism and predation than are juvenile Asian Shore Crabs, possibly because their defense mechanism (camouflage) is more effective against visual predators (e.g., gulls, fish) than against other crabs (Lohrer and Whitlatch 2002a). Thus, even if the Asian Shore Crab was initially an ecological passenger, establishing itself during a period of reduced recruitment of Green Crabs, its greater competitive ability and lower susceptibility to predation on juveniles will likely enable it to prevent resurgence of the Green Crab. Moreover, O’Connor (2014) demonstrated that the Asian Shore Crab can successfully invade communities that have high densities of Green Crabs.

Although the Green Crab is a voracious predator of the Blue Mussel and other bivalves (Ropes 1968), its replacement by the Asian Shore Crab has not relieved predation pressure. Most studies suggest that the Green Crab consumes more mussels per capita than does the Asian Shore Crab (Griffen 2006; Lohrer and Whitlatch 2002a, b), although DeGraaf and Tyrrell (2004) observed similar feeding rates between the two species except for predation on large mussels, which were consumed more readily by the Asian Shore Crab. Regardless, overall rates of predation on Blue Mussels are as great or greater for the Asian Shore Crab than the Green Crab because the Asian Shore Crab is far more abundant throughout the introduced ranges of the 2 crab species (Griffen and Delaney 2007; Lohrer and Whitlatch 2002a, b). Increased conspecific density may cause Asian Shore Crabs to increase diet breadth

and reduce feeding rates (Brousseau and Baglivo 2005), but foraging of the Green Crab is more strongly affected by density of conspecifics than is that of the Asian Shore Crab (Griffen and Delaney 2007). Therefore, predation pressure on the Blue Mussel has probably increased at Sandwich as density of the Asian Shore Crab has increased, a conclusion that is consistent with the rapid decline in density of the Blue Mussel between 2004 and 2006. Predation rates are likely greatest on larvae and juveniles, but large male Asian Shore Crabs can open mussels up to 31 mm in length (Bourdeau and O'Connor 2003). In 2011, no mussels observed at Sandwich exceeded this length (J. Jahoda, K. Curry, and C. Bloch, Bridgewater State University, Bridgewater, MA, unpubl. data). However, 53 out of 386 individuals measured in 2012 (14%) were >31 mm in length. It is difficult to draw substantive conclusions about the importance of this observation based on this small and short-term sample. Small mussels from populations in southern New England produce thicker shells in the presence of chemical cues from the Asian Shore Crab (Freeman and Byers 2006). If the evolution of such inducible defenses increases survival through the 4 to 12 months during which juvenile Blue Mussels remain small enough to be vulnerable to predation (Gerard et al. 1999), this may facilitate recovery of the mussel population at Sandwich. It is unclear whether the increased abundance of larger mussels at Sandwich in 2012 presages such a recovery. Further observation is warranted to evaluate this possibility.

With increasing density of the Asian Shore Crab and a dramatic decline in bivalve prey (Fig. 2), an increase in predation pressure on other species would be expected. Because the Asian Shore Crab feeds on both invertebrates and algae (Bourdeau and O'Connor 2003, Brousseau and Baglivo 2005, Gerard et al. 1999), it could negatively affect populations of grazing mollusks (e.g., the Common Periwinkle) via two mechanisms: predation and competition for algae. The latter has not been documented, but Asian Shore Crabs at central Long Island Sound in 1997–1998 ate periwinkles up to 13 mm in shell height (Gerard et al. 1999). Abundance of the Common Periwinkle at Rye, NY (another site on Long Island Sound) declined by approximately 80% over the next several years, coincident with an increase in abundance of the Asian Shore Crab (Kraemer et al. 2007). No such decline occurred at Sandwich, however, during our study. The strength of competition between the Asian Shore Crab and the Common Periwinkle, if any, remains unknown, but predation pressure on the Common Periwinkle by Asian Shore Crabs may not be strong at all sites where they coexist. In laboratory experiments, few periwinkles were eaten by Asian Shore Crabs, and these were consumed only by large males (Bourdeau and O'Connor 2003). Many damaged shells, probably indicating unsuccessful attempts at predation, were observed, however. The coiled geometry of snail shells may make the Common Periwinkle more resistant than the Blue Mussel to predation by crabs (Lawton and Hughes 1985). The high abundance of the Common Periwinkle at Sandwich throughout our study was not just a function of persistence of adults. Many small individuals were present in 2011 and 2012; indeed, in 2011 only 34% of individuals exceeded 13 mm in shell height (J. Jahoda, K. Curry, and C. Bloch, unpubl. data). Thus, it is not clear whether recruitment of the Common

Periwinkle at Sandwich simply outpaces predation or whether predation is somehow limited. Acorn Barnacles are common at Sandwich, but their abundance was not monitored during this study. As they are consumed by the Asian Shore Crab in laboratory settings (Brousseau and Baglivo 2005, Gerard et al. 1999, Tyrrell et al. 2006) and in eastern Long Island Sound (Lohrer et al. 2000b), it is possible that Acorn Barnacles, rather than Common Periwinkles, are the secondary prey for the Asian Shore Crab at Sandwich.

Long-term data from the present study and others (Kraemer et al. 2007, O'Connor 2014), coupled with extensive experimental evidence (e.g., Brousseau and Baglivo 2005, Jensen et al. 2002, Tyrrell et al. 2006), clearly demonstrate strong effects of the Asian Shore Crab on the structure of rocky intertidal communities on the northeast coast of North America. These effects probably differ geographically, however (as observed for population dynamics of the Common Periwinkle at Sandwich versus at Rye). Unlike at some sites in the Delaware Bay (Schab et al. 2013), the Asian Shore Crab population at Sandwich continued to grow from 2003 to 2012, and there is little evidence of numerical recovery by affected species, although abundance and body-size distributions of the Blue Mussel warrant further observation. Historically, populations of the Asian Shore Crab north of Cape Cod have been smaller than those to its south. However, like Sandwich, two other sites in Massachusetts north of Cape Cod supported rapidly growing populations of the Asian Shore Crab from 2004–2012 (O'Connor 2014). If these observations are representative of sites north of Cape Cod, dramatic changes in community structure (similar to the decline in the Common Periwinkle at Rye or the Blue Mussel at Sandwich) may be widespread and may intensify as populations of the Asian Shore Crab continue to grow. Data on long-term effects of the Asian Shore Crab on resident species other than the Green Crab remain limited, however. Additional field studies are necessary to document interactions between the Asian Shore Crab and other intertidal species and to identify environmental conditions (e.g., temperature; Stephenson et al. 2009) that mediate the strength of these interactions.

Acknowledgments

Support for this study was provided by the Department of Biological Sciences at Bridgewater State University. Additional support was provided for C.P. Bloch by a Summer Grant from the Center for the Advancement of Research and Scholarship at Bridgewater State University. We thank E. Chappuis and M. Armour for logistic support. Many students and colleagues assisted with data collection; without their efforts, this study would have been impossible. D. Padgett provided helpful information about invasion biology. This manuscript benefited from the thoughtful comments of K. Boyd, D. Padgett, M. Penella, and 2 anonymous reviewers.

Literature Cited

- Ahl, R.S., and S.P. Moss. 1999. Status of the nonindigenous crab *Hemigrapsus sanguineus* at Greenwich Point, Connecticut. *Northeastern Naturalist* 6:221–224.
- Bax, N., A. Williamson, M. Aguero, E. Gonzalez, and W. Geeves. 2003. Marine invasive alien species: A threat to global biodiversity. *Marine Policy* 27:313–323.

- Bertness, M.D., P.O. Yund, and A.F. Brown. 1983. Snail grazing and the abundance of algal crusts on a sheltered New England rocky beach. *Journal of Experimental Marine Biology and Ecology* 71:147–164.
- Bourdeau, P.E., and N.J. O'Connor. 2003. Predation by the nonindigenous Asian Shore Crab, *Hemigrapsus sanguineus*, on macroalgae and molluscs. *Northeastern Naturalist* 10:319–334.
- Brousseau, D.J., and J.A. Baglivo. 2005. Laboratory investigations of food selection by the Asian Shore Crab, *Hemigrapsus sanguineus*: Algal versus animal preference. *Journal of Crustacean Biology* 25:130–134.
- Brousseau, D.J., J.A. Baglivo, A. Filipowicz, L. Segó, and C. Alt. 2002. An experimental field study of site fidelity and mobility in the Asian Shore Crab, *Hemigrapsus sanguineus*. *Northeastern Naturalist* 9:381–390.
- Carlton, J.T. 1999. The scale and ecological consequences of biological invasions in the world's oceans. Pp. 195–212, *In* O.T. Sandlund, P.J. Schei, and Å. Viken, (Eds.). *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Dordrecht, Netherlands. 431 pp.
- Creed, R.P., Jr., and S.P. Sheldon. 1995. Weevils and watermilfoil: Did a North American herbivore cause the decline of an exotic plant? *Ecological Applications* 5:1113–1121.
- DeGraaf, J.D., and M.C. Tyrrell. 2004. Comparison of the feeding rates of two introduced crab species, *Carcinus maenas* and *Hemigrapsus sanguineus*, on the Blue Mussel, *Mytilus edulis*. *Northeastern Naturalist* 11:163–167.
- Epifanio, C.E., A.I. Dittel, S. Park, S. Schwalm, and A. Fouts. 1998. Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA). *Marine Ecology Progress Series* 170:231–238.
- Freeman, A.S., and J.E. Byers. 2006. Divergent induced responses to an invasive predator in marine mussel populations. *Science* 313:831–833.
- Fukui, Y. 1988. Comparative studies on the life history of the grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. *Publications of the Seto Marine Biological Laboratory* 33:121–162.
- Gerard, V.A., R.M. Cerrato, and A.A. Larson. 1999. Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. *Biological Invasions* 1:353–361.
- Griffen, B.D. 2006. Detecting emergent effects of multiple predator species. *Oecologia* 148:702–709.
- Griffen, B.D., and J.E. Byers. 2006. Partitioning mechanisms of predator interference in different habitats. *Oecologia* 146:608–614.
- Griffen, B.D., and D.G. Delaney. 2007. Species invasion shifts the importance of predator dependence. *Ecology* 88:3012–3021.
- Grosholz, E.D., and G.M. Ruiz. 1996. Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European Green Crab, *Carcinus maenas*. *Biological Conservation* 78:59–66.
- Grosholz, E.D., G.M. Ruiz, C.A. Dean, K.A. Shirley, J.L. Maron, and P.G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81:1206–1224.
- Holmes, S.P., G. Walker, and J. van der Meer. 2005. Barnacles, limpets, and periwinkles: The effects of direct and indirect interactions on cyprid settlement and success. *Journal of Sea Research* 53:181–204.

- Jensen, G.C., P.S. McDonald, and D.A. Armstrong. 2002. East meets west: Competitive interactions between the Green Crab, *Carcinus maenas*, and native and introduced shore crabs, *Hemigrapsus* spp. *Marine Ecology Progress Series* 225:251–262.
- Kopin, C.Y., C.E. Epifanio, S. Nelson, and M. Stratton. 2001. Effects of chemical cues on metamorphosis of the Asian Shore Crab, *Hemigrapsus sanguineus*, an invasive species on the Atlantic Coast of North America. *Journal of Experimental Marine Biology and Ecology* 265:141–151.
- Kraemer, G.P., M. Sellberg, A. Gordon, and J. Main. 2007. Eight-year record of *Hemigrapsus sanguineus* (Asian Shore Crab) invasion in western Long Island Sound estuary. *Northeastern Naturalist* 14:207–224.
- Lawton, P., and R.N. Hughes. 1985. Foraging behavior of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: Comparisons with optimal-foraging theory. *Marine Ecology Progress Series* 27:143–154.
- Ledesma, M.E., and N.J. O'Connor. 2001. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England. *Northeastern Naturalist* 8:63–78.
- Lohrer, A.M., and R.B. Whitlatch. 2002a. Interactions among aliens: Apparent replacement of one exotic species by another. *Ecology* 83:719–732.
- Lohrer, A.M., and R.B. Whitlatch. 2002b. Relative impacts of two exotic brachyuran species on Blue Mussel populations in Long Island Sound. *Marine Ecology Progress Series* 227:135–144.
- Lohrer, A.M., Y. Fukui, K. Wada, and R.B. Whitlatch. 2000a. Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian Shore Crab, *Hemigrapsus sanguineus* (de Haan). *Journal of Experimental Marine Biology and Ecology* 244:203–217.
- Lohrer, A.M., R.B. Whitlatch, K. Wada, and Y. Fukui. 2000b. Home and away: Comparisons of resource utilization by a marine species in native and invaded habitats. *Biological Invasions* 2:41–57.
- Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123.
- MacDougall, A.S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55.
- Mak, Y.M., and G.A. Williams. 1999. Littorinids control high-intertidal biofilm abundance on tropical, Hong Kong rocky shores. *Journal of Experimental Marine Biology and Ecology* 233:81–94.
- McDermott, J.J. 1998a. The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: Geographic distribution and ecology. *ICES Journal of Marine Science* 55:289–298.
- McDermott, J.J. 1998b. The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: Reproduction. *Journal of Crustacean Biology* 18:308–316.
- Mooney, H.A., and E.E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* 98:5446–5451.
- O'Connor, N.J. 2014. Invasion dynamics on a temperate rocky shore: From early invasion to establishment of a marine invader. *Biological Invasions* 16:73–87.
- Payne, A., and G.P. Kraemer. 2013. Morphometry and claw strength of the non-native Asian Shore Crab, *Hemigrapsus sanguineus*. *Northeastern Naturalist* 20:478–492.
- Phelps, H.L. 1994. The Asiatic Clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River estuary near Washington, DC. *Estuaries* 17:614–621.

- Raffo, M.P., V. Lo Russo, and E. Schwindt. 2014. Introduced and native species on rocky shore macroalgal assemblages: Zonation patterns, composition, and diversity. *Aquatic Botany* 112:57–65.
- Ropes, J.W. 1968. The feeding habits of the Green Crab, *Carcinus maenas* (L). *Fishery Bulletin* 67:183–203.
- Sanders, N.J., N.J. Gotelli, N.E. Heller, and D.M. Gordon. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences* 100:2474–2477.
- Schab, C.M., S. Park, L.A. Waidner, and C.E. Epifanio. 2013. Return of the native: Historical comparison of invasive and indigenous crab populations near the mouth of Delaware Bay. *Journal of Shellfish Research* 32:751–758.
- Seed, R. 1976. Ecology. Pp. 13–65, *In* B.L. Bayne, (Ed.). *Marine Mussels: Their Ecology and Physiology*. Cambridge University Press, New York, NY. 506 pp.
- Sokal, R.R., and F.J. Rohlf. 2012. *Biometry: The Principles and Practice of Statistics in Biological Research*. 4th Edition. W.H. Freeman and Company, New York, NY. 937 pp.
- Stephenson, E.H., R.S. Steneck, and R.H. Seeley. 2009. Possible temperature limits to range expansion of non-native Asian Shore Crabs in Maine. *Journal of Experimental Marine Biology and Ecology* 375:21–31.
- Thresher, R.E., and A.M. Kuris. 2004. Options for managing invasive marine species. *Biological Invasions* 6:295–300.
- Tyrrell, M.C., P.A. Guarino, and L.G. Harris. 2006. Predatory impacts of two introduced crab species: Inferences from microcosms. *Northeastern Naturalist* 13:375–390.
- Williams, A.B., and J.J. McDermott. 1990. An eastern United States record for the Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). *Proceedings of the Biological Society of Washington* 103:108–109.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall, London, UK. 244 pp.