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Population Decline of the Invasive Asian Shore Crab (*Hemigrapsus sanguineus*) and Dynamics of Associated Intertidal Invertebrates on Cape Cod, Massachusetts

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Abstract - A few moderately long-term studies have documented population dynamics of the invasive *Hemigrapsus sanguineus* (Asian Shore Crab) and species with which it interacts. One such study on Cape Cod reported exponential growth of the Asian Shore Crab through 2012, concurrent with declines in 2 resident species, but recent data at nearby sites suggest considerable geographic variation in population dynamics, with modest recovery of resident crab populations. We monitored the Cape Cod population for an additional 5 years to determine whether population growth of the Asian Shore Crab had slowed and whether there was any change in population dynamics of *Carcinus maenas* (Green Crab), *Littorina littorea* (Common Periwinkle), or *Mytilus edulis* (Blue Mussel). Asian Shore Crab density declined by nearly 90% since 2012. There was no evidence of recovery by the Green Crab, but the Blue Mussel experienced a brief but substantial increase in density in 2015, when both crab species displayed >70% reductions in density from the previous year. The pattern of population dynamics of the Asian Shore Crab from 2003 to 2017 is consistent with boom–bust dynamics, but it remains unclear whether the population will equilibrate near its current density or undergo recurrent boom–bust cycles.

Introduction

Recent studies have called for a long-term perspective on the impacts of introduced species (Kumschick et al. 2015, Strayer 2012, Strayer et al. 2017). This recommendation reflects the potential for community or ecosystem structure and function to respond to introduced species over long time periods (Strayer 2008) and in a context-dependent fashion (Ricciardi et al. 2013, Strayer et al. 2014). Although the number of medium- to long-term studies is increasing (e.g., Bahlai et al. 2015, Honek et al. 2016, Solomon et al. 2016), most studies of invasion biology have been short-term, failing to capture temporal dynamics to a meaningful extent (Strayer et al. 2006). This approach is problematic because multiple evolutionary and ecological processes, such as changes in phenotypes of invaders or resident species (Lankau 2010, Phillips and Shine 2004), community composition (Petrie and Knapton 1999), abiotic conditions (Tang et al. 2012), or the provision of ecosystem services (Mack et al. 2000) may mediate the ultimate consequences of species invasions.

Hemigrapsus sanguineus (De Haan) (Asian Shore Crab), since its introduction to the Atlantic coast of North America in the 1980s (Williams and McDermott

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1990), has colonized intertidal habitats from North Carolina to Maine (McDermott 1998, Stephenson et al. 2009). Declines in prey such as *Littorina littorea* (L.) (Common Periwinkle; e.g., Kraemer et al. 2007) and *Mytilus edulis* (L.) (Blue Mussel; e.g., Bloch et al. 2015), and competitors such as *Carcinus maenas* (L.) (Green Crab) and panopeid mud crabs (e.g., O'Connor 2014) have been attributed to its rapid population growth, efficiency as a predator (Brousseau et al. 2014, DeGraaf and Tyrrell 2004), diet breadth (Brousseau and Baglivo 2005, Ledesma and O'Connor 2001), tolerance of crowding by conspecifics (Hobbs et al. 2017), and competitive dominance over heterospecific crabs (Griffen 2016, Lohrer and Whitlatch 2002). The Asian Shore Crab is now the dominant brachyuran species in rocky intertidal habitats from New York through southern Maine (Ahl and Moss 1999, Kraemer 2019, Lord and Williams 2017, O'Connor 2018).

A few moderately long-term studies (10–15 y) have documented population dynamics of the Asian Shore Crab and species with which it interacts (Bloch et al. 2015, Kraemer 2019, O'Connor 2018). All reported a rapid increase in density of the Asian Shore Crab in the early to middle stages of the invasion, but later dynamics differed. At some sites, especially closer to the original site of invasion (near Cape May, NJ; Williams and McDermott 1990), density peaked and then declined (Kraemer 2019). No recovery of other crab species was observed (Kraemer 2019). In southern New England (Massachusetts and Rhode Island), population dynamics differed between an estuarine site, where density continued to rise until at least 2016, and 2 coastal sites, where density may have equilibrated or begun to decline, coincident with an increase in abundance of the Green Crab (O'Connor 2018). Therefore, additional observations are necessary to understand geographic variation in population dynamics and impacts of the Asian Shore Crab.

Bloch et al. (2015) conducted a 10-y study of densities of intertidal invertebrates at Sandwich, MA, a rocky intertidal site on the north side of Cape Cod that had a rapidly growing population of the Asian Shore Crab. As of 2012, population growth of the Asian Shore Crab showed no evidence of density-dependence, instead being consistent with exponential growth. Over the same time period, the Green Crab and the Blue Mussel declined substantially, but population size of the Common Periwinkle remained stable. The purpose of the current study was to continue monitoring populations of these species at this site to determine whether rapid population growth of the Asian Shore Crab has continued and whether there has been any recovery by competitors or prey during the ensuing 5 y.

Field-Site Description

The study was conducted at Town Neck Beach in Sandwich, MA (41°46.357′ N, 70°29.474′ W), on the north side of Cape Cod, just east of the Cape Cod Canal. This is a low-energy site with a broad, flat intertidal zone (slope = 0.5–2.5°). 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 cobbles and boulders decreases with increasing proximity to the mean high tide line (MHT). In the middle and lower intertidal zones, rock cover approaches 100%.

Methods

Field methods

Field methodology generally followed Bloch et al. (2015). We conducted annual surveys during a single daytime low tide each September from 2013 to 2017. Each year, we established a series of parallel transects perpendicular to the shore, running seaward from MHT. The number of transects varied from 21 to 33, depending on the assistance available for sampling in a given year. On each transect, we surveyed an area of 1.37 m^2 (comprising 3 contiguous circular quadrats of 76.2 cm diameter) in the upper intertidal zone, middle intertidal zone, and lower intertidal zone. Each quadrat was searched by 3–5 individuals. Cobbles and, when possible, boulders were removed and sandy substrate manually probed to facilitate capture of individuals of the 4 target species (Asian Shore Crab, Green Crab, Common Periwinkle, and Blue Mussel). We measured body size to the nearest 0.1 mm with a Vernier caliper for a subset of individuals of each species (up to 10 randomly selected individuals per zone, per transect). Body size measurements were carapace width for crabs, spire height for periwinkles, and greatest length of shell for mussels. At the completion of sampling, we returned rocks to the plots and released organisms at the location of capture.

Sampling in 2015 differed slightly. In that year, a dune restoration project caused the sampling site to be closed to the public during September. Consequently, sampling was more limited and occurred earlier (11 August). We haphazardly located 13 circular quadrats (76.2 cm diameter) throughout the intertidal zone for sampling as described above.

Statistical analyses

We estimated population density of each target species by averaging across all quadrats, irrespective of transect or tidal height. Although including data from the upper intertidal zone may reduce estimates of population density relative to those of previous studies that restricted sampling to the middle (e.g., Kraemer et al. 2007) or lower intertidal zone (e.g., O'Connor 2014, 2018), temporal patterns of population density of our focal species are similar across tidal heights (Bloch et al. 2015). Therefore, we did not conduct separate analyses for data from different tidal heights.

To characterize the pattern of population growth of the Asian Shore Crab, we fitted 3 different least-squares regression models (linear, exponential, and quadratic) to the time series of its population densities, including data from the current study and data reported by Bloch et al. (2015). We chose the first 2 models because they were consistent with the pattern of population growth during 2003–2012 (Bloch et al. 2015), and the quadratic to determine whether there was an inflection point in the time series. More complex models were not considered. We tested for significance of the regression models using analysis of variance (ANOVA). We then used Spearman's rank correlation coefficient to test for correlations in density between the Asian Shore Crab and each other focal 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. It is also less strongly influenced by extreme values.

To test for evidence of density-dependence in population growth of the Asian Shore Crab, we estimated per capita growth 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. These estimates included data collected for the current study (2013–2017) as well as previous data (2003–2012) reported by Bloch et al. (2015). This equation reflects the finite rate of growth - 1 (i.e., $\lambda - 1$); however, for notational simplicity and because the Asian Shore Crab exhibits overlapping generations and an extended breeding season, we treat it as an approximation of r, the intrinsic rate of increase. We used Spearman's rank correlation coefficient to evaluate the association between n and r at 3 different time lags: no lag (n_t versus r_t), 1 y (n_{t-1} versus r_t), and 2 y (n_{t-2} versus r_t). A negative correlation would indicate declining per capita growth with increasing population density (i.e., density-dependent population growth). Correlation with a 1- or 2-y lag would indicate delayed density-dependent effects.

We estimated mean body size for each target species, averaged across all quadrats, irrespective of transect or tidal height. Thereafter, we assessed temporal changes in body size for each species from 2013 to 2017 by using a Kruskal-Wallis test because data transformations were unable to normalize body size data for any species. We conducted post-hoc pairwise comparisons using Dunn's test (Dunn 1961). All analyses were conducted in IBM SPSS version 24.

Results

Density of the Asian Shore Crab generally increased through 2012 but declined thereafter, consistent with a quadratic regression model ($y = -0.40x^2 + 1616.56x - 1.6 \times 10^6$; $r^2 = 0.60$, $F_{2,12} = 8.99$, $P = 0.004$; Fig. 1A). Neither a linear ($F_{1,13} = 0.27$, $P = 0.611$) nor an exponential ($F_{1,13} = 0.47$, $P = 0.506$) model was statistically significant. Of the other 3 species, only the Blue Mussel exhibited densities that were significantly correlated with those of the Asian Shore Crab (Table 1, Fig. 1) for the entire study period. Densities of the Asian Shore Crab and the Green Crab were significantly correlated through 2014 ($\rho = 0.62$, $P = 0.033$), but the Green Crab declined each year thereafter, while density of the Asian Shore Crab also decreased in 2 of the 3 years, rendering the correlation nonsignificant for the complete time series (Table 1).

Table 1. Correlations (Spearman's rank correlation coefficient, ρ, and its significance, *P*) between mean densities of *Hemigrapsus sanguineus* (Asian Shore Crab) and those of 3 other species in the intertidal zone at Sandwich, MA, 2003–2017.

Species	ρ	*P*
Carcinus maenas (Green Crab)	-0.14	0.621
Littorina littorea (Common Periwinkle)	-0.01	0.980
Mytilus edulis (Blue Mussel)	-0.71	0.003

Since 2012, per capita growth (*r*) of the Asian Shore Crab was positive in only 1 year (2015–2016), after having been positive in 6 of the previous 9 years (Fig. 2). Nevertheless, *r* did not decline monotonically over time ($\rho = -0.25$, $P = 0.392$; Fig. 2A), nor was it associated with density in the same year (although the relationship approached significance; $\rho = -0.48$, $P = 0.085$) or with a 1-y lag ($\rho = -0.16$, $P = 0.603$). Instead, *r* was negatively associated with population density with a 2-y lag ($\rho = -0.59$, $P = 0.042$).

Body-size distributions of all 4 species varied significantly over time (Table 2). These differences were mostly, but not completely, attributable to changes in median body size over time. For the Asian Shore Crab, carapace width was greatest in 2014 and 2016, with significant declines in 2015 and 2017 (Fig. 3A). Carapace width of the Green Crab generally increased over time, with the exception of 2015 (Fig. 3B). Nevertheless, the inability to distinguish 2015 statistically from any of the other years is likely due to small sample size (*n* = 5 individuals observed in 2015, all juveniles). Median spire height of the Common Periwinkle declined until 2015 but remained stable thereafter (Fig. 3C). The greatest difference in length of the Blue Mussel was an increase between 2015 and 2016 (Fig. 3D); there was no significant difference in length of mussels among 2013, 2014, and 2017.

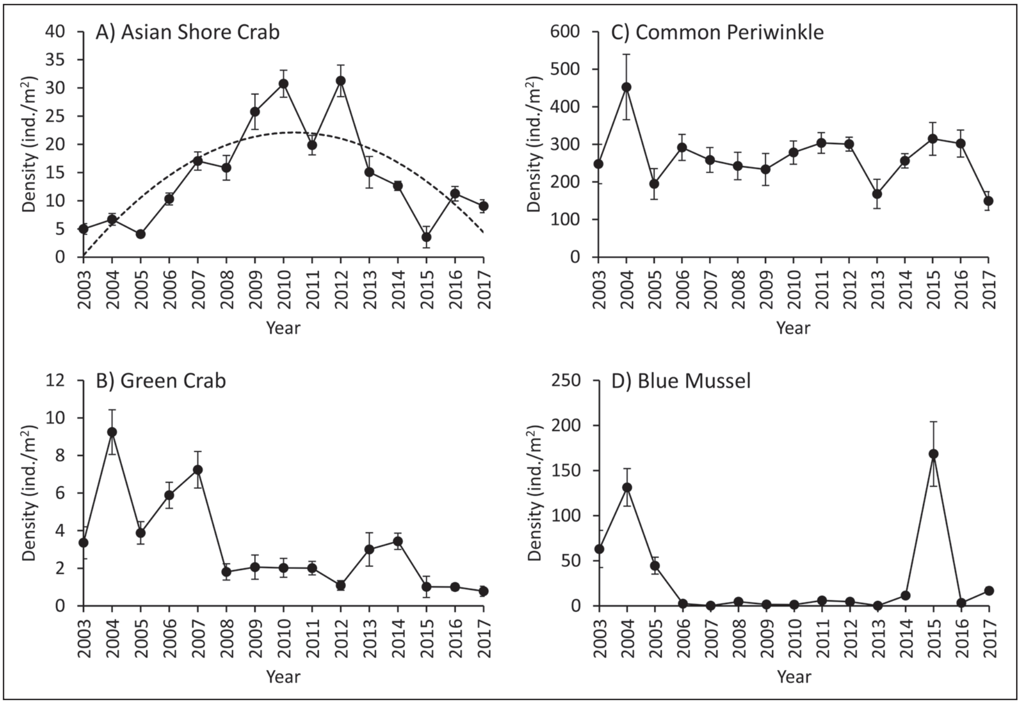

Figure 1. Annual estimates of population density (individuals/m^2, ± 1 SE) of 4 invertebrate species in the rocky intertidal zone at Town Neck Beach, Sandwich, Massachusetts. A: *Hemigrapsus sanguineus* (Asian Shore Crab), B: *Carcinus maenas* (Green Crab), C: *Littorina littorea* (Common Periwinkle), D: *Mytilus edulis* (Blue Mussel). The dashed line in A represents the quadratic least-squares regression model of Asian Shore Crab density. Density estimates prior to 2013 are from Bloch et al. (2015).

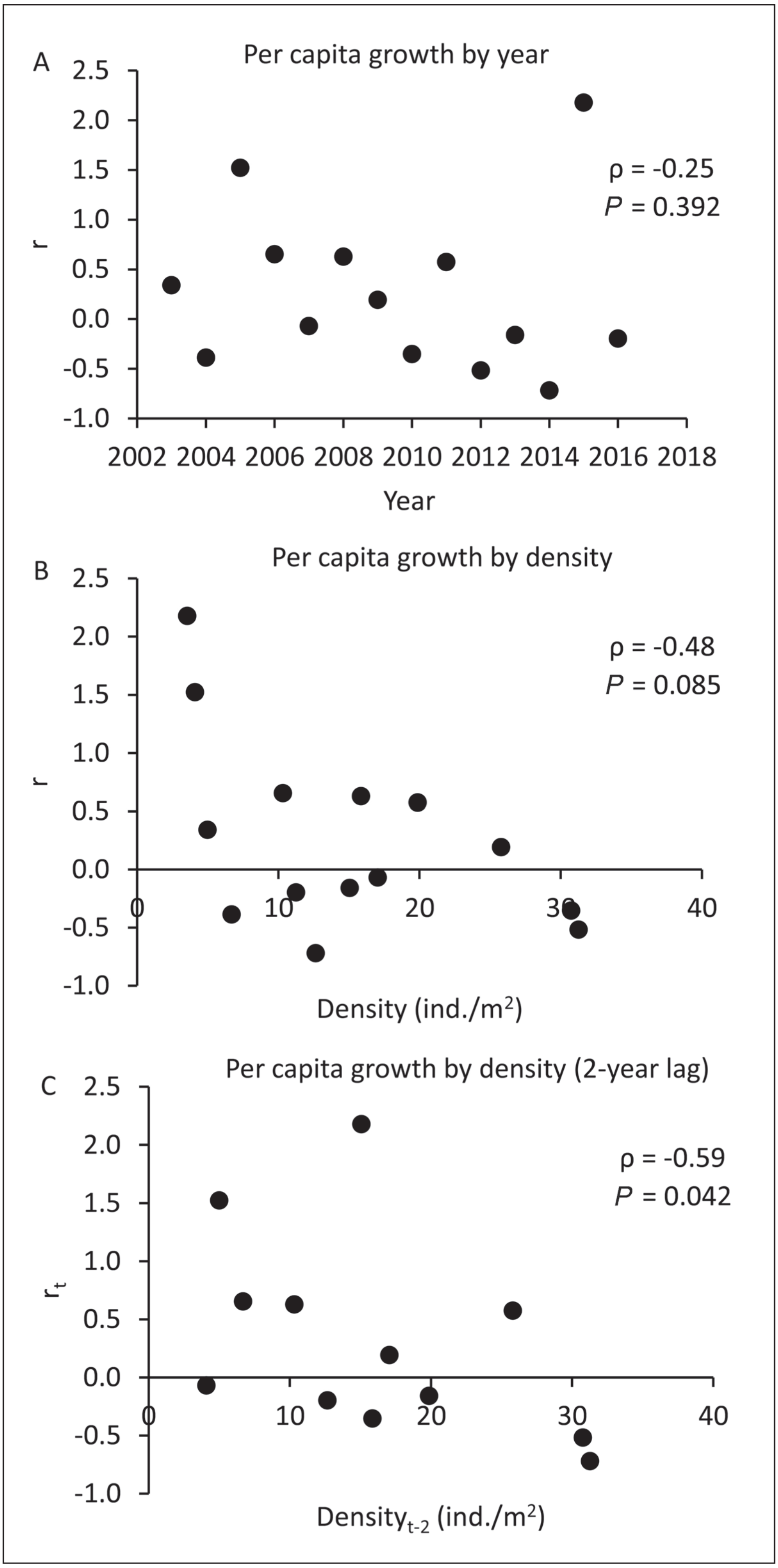

Figure 2. Per capita population growth (*r*) of *Hemigrapsus sanguineus* (Asian Shore Crab) (A) over time, (B) as a function of population density (individuals/m^2), and (C) as a function of population density with a 2-y time lag. Estimates prior to 2013 are from Bloch et al. (2015).

Discussion

Considerable geographic variation characterizes density and population dynamics of the Asian Shore Crab in North America. Near the northern extent of the crab's range, population densities are relatively low, but growing rapidly (Lord and Williams 2017), whereas closer to the original site of invasion (near Cape May, NJ; Williams and McDermott 1990), populations are more dense but at least one is in decline (Kraemer 2019). Southern New England lies between these regions, and is likewise characterized by geographic variation in population dynamics.

Table 2. Results of Kruskal-Wallis tests to compare body-size distributions among years (2013–2017) for four species of intertidal invertebrate at Town Neck Beach, Sandwich, MA.

Species	*n*	df	*H*	*P*
Hemigrapsus sanguineus (Asian Shore Crab)	3131	4	26.2	<0.001
Carcinus maenas (Green Crab)	920	4	72.7	<0.001
Littorina littorea (Common Periwinkle)	3417	4	546.6	<0.001
Mytilus edulis (Blue Mussel)	1263	4	23.4	<0.001

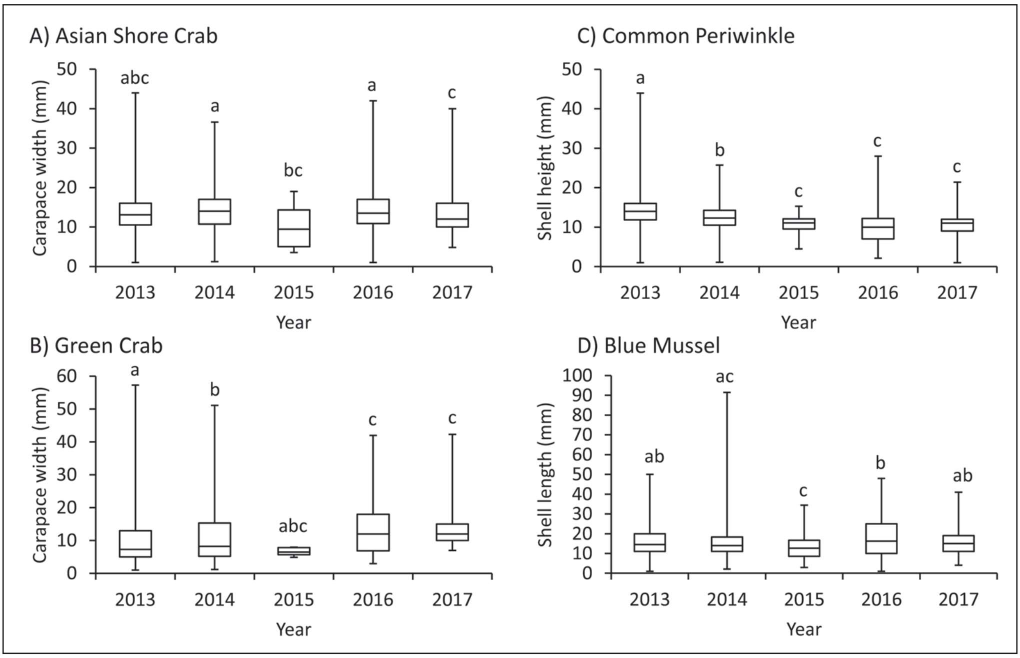

Figure 3. Annual estimates of body size of 4 invertebrate species in the rocky intertidal zone at Town Neck Beach, Sandwich, MA: (A) *Hemigrapsus sanguineus* (Asian Shore Crab), (B) *Carcinus maenas* (Green Crab), (C) *Littorina littorea* (Common Periwinkle), and (D) *Mytilus edulis* (Blue Mussel). Body-size measurements were carapace width for crabs, spire height for periwinkles, and greatest length of shell for mussels. Endpoints of error bars represent minimum and maximum values. Boxplots marked by different lowercase letters indicate years in which body size distributions differed significantly based on post-hoc comparisons following Kruskal-Wallis tests.

O'Connor (2018) reports evidence that densities at 2 coastal sites in Massachusetts north of Cape Cod have declined or approached equilibrium, whereas densities at an estuarine site in Rhode Island continued to grow through 2016. Our results were consistent with O'Connor's (2018) observations at the coastal sites, which were approximately 40 and 50 km north-northwest of Sandwich. Population growth, which had been nearly exponential from 2003 to 2012, exhibited density dependence (with a 2-y time lag) when 5 additional years were considered, and population density declined by nearly 90% from 2012 to 2015. This finding suggests that the Asian Shore Crab has reached the end of the initial growth phase of its invasion along the coast of Cape Cod Bay. Although the pattern of population dynamics was similar, our estimates of density were lower than those of O'Connor (2018), probably because of differences in sampling scheme; O'Connor (2018) focused solely on the lower intertidal zone, whereas our samples also included plots in the upper and middle intertidal zones, where densities would be expected to be lower (Bloch et al. 2015, O'Connor 2014).

Density of Green Crabs increased briefly from 2012 to 2014, but then decreased again, continuing an overall pattern of decline consistent with that reported by Bloch et al. (2015). Body size generally increased over time, suggesting that high juvenile mortality (possibly resulting from predation by Asian Shore Crabs; Lohrer and Whitlatch 2002) is largely driving the decline in Green Crab density, leaving fewer, larger individuals. It is unclear why these results differed from the observations of O'Connor (2018), who reported modest recovery of the Green Crab at all 3 of her sites, but our results are consistent with those of Kraemer (2019), who saw no recovery of other crab species during a decline in the Asian Shore Crab population in Long Island Sound.

From 2014 to 2015, both species of crab experienced a reduction in density of over 70% (Fig. 1A, B), leading to the lowest density of Asian Shore Crabs throughout the time series. The Asian Shore Crab also displayed reduced median body size (Fig. 3). This change may have resulted from high adult mortality during an unusually harsh winter, such that mostly new recruits were sampled in 2015 (e.g., all Green Crabs captured in 2015 were juveniles). At the same time, the Blue Mussel attained a density of nearly 170 individuals/m^2, the highest recorded from 2003–2017 (Fig. 1D; Bloch et al. 2015). Median body size of mussels was low in 2015 compared to other years (Fig. 3D). This finding may reflect a reduction in predation pressure that led to increased establishment and survival of juveniles. Nevertheless, population density declined again by 2016, as the Asian Shore Crab more than tripled in density. The Asian Shore Crab is responsible for a substantial proportion of mussel mortality (20–25% at Bridgeport, CT; Brousseau et al. 2014), so if density of the Asian Shore Crab remains low at Sandwich, some recovery of the Blue Mussel population is possible.

Sampling in 2015 differed from other years of the study (a few weeks earlier, and with smaller sample size). Nevertheless, we are confident that our observations in that year accurately reflect population dynamics of the target species, rather than a sampling artifact, for several reasons. First, the smaller team of researchers that sampled in 2015 was more experienced in field biology in general, and with the target species in particular, than were the student field workers in other years of the study. Therefore, the small number of crabs observed in 2015 is unlikely to reflect a sampling bias. Second, although the large number of Blue Mussels observed in 2015 may, to an extent, reflect greater sampling efficiency, Blue Mussel density was greater than in any other year of the study, suggesting that even naïve student researchers would find an increase in their abundance. Moreover, these mussels were significantly smaller than in other years (Fig. 3), reflecting the increased juvenile survival that would be expected in a year with low densities of crabs. Third, additional qualitative sampling confirmed that the unexpected observations in the sampling plots were consistent with conditions elsewhere in the intertidal zone, and not an artifact of plot placement.

Bloch et al. (2015) reported no significant correlation between densities of the Asian Shore Crab and the Common Periwinkle from 2003 to 2012. Our additional data are consistent with this observation, and with previous studies that found abiotic conditions to be most important in driving abundance of the Common Periwinkle (e.g., Carlson et al. 2006). Body size of the Common Periwinkle declined over time, probably reflecting increased proportional abundance of juveniles, but the reason for this is unclear. The lack of a strong effect of the Asian Shore Crab on the Common Periwinkle population is unsurprising, however, at least in part because bivalves appear to be more preferred prey than periwinkles (Bourdeau and O’Connor 2003). In a laboratory study, only large males successfully consumed periwinkles (Bourdeau and O’Connor 2003), probably because males have larger, stronger chelae than females (McDermott 1999, Payne and Kraemer 2013) and the shells of gastropods are more difficult to break than the shells of bivalves, possibly because of their coiled nature (Lawton and Hughes 1985) or the thickened lip that develops around the shell aperture in adults.

Once established in novel habitats that lack natural enemies or strong competitors, exotic species often exhibit rapid population growth and generate community-wide impacts through competition with or predation on resident species, and consequent modifications in habitat structure or ecosystem processes (Mack et al. 2000, O’Dowd et al. 2003). Alternatively, boom–bust dynamics, in which a population undergoes rapid growth, followed by a dramatic decline, may be common for invasive species (Aagaard and Lockwood 2016, Lester and Gruber 2016, Lockwood et al. 2013), but rigorous analyses of the phenomenon are rare (Strayer et al. 2017). This is similar to the concept of “parallel dynamics”, a phenomenon primarily observed in plant communities (McLane et al. 2012, Meiners 2007), in which population and community dynamics of introduced species resemble those of native species, such that population sizes initially increase with time and subsequently decline with no legacy effects (Rejmánek et al. 2013). The recent decline in Asian Shore Crab density at Sandwich, MA (nearly 90% in 3 years, the approximate lifespan of the species; Epifanio 2013, Fukui 1988), approximates boom–bust dynamics, and similar dynamics may be occurring at other sites (Kraemer 2019, O’Connor 2018, Schab et al. 2013). If so, this may lead to recovery by populations of resident species that have been impacted by the Asian Shore Crab, assuming these communities have not been shifted into an alternative stable state (but see Kraemer 2019). However, if these declines represent the "bust" phase of a boom–bust cycle, the mechanism driving them remains unknown. Kraemer (2019) observed a disproportionate decline in large individuals, resulting in a population-wide decrease in fecundity, but the cause of reduced adult survivorship is unclear.

It is difficult to attribute any single cause to the rapid population decline of an invasive species. Commonly hypothesized mechanisms include accumulation of natural enemies, parasites, or pathogens (Simberloff and Gibbons 2004, Faillace et al. 2017, Strayer et al. 2017); interactions with subsequent invaders (Jackson 2015, Lohrer and Whitlatch 2002); increased abiotic resistance (Dostál et al. 2013, Zenni and Nuñez 2013); and evolution of the invader or native species with which it interacts (Keller and Taylor 2008, Mooney and Cleeland 2001). Nevertheless, these are not necessarily mutually exclusive, and a lack of data on failed invasions (Zenni and Nuñez 2013) or declines in populations of well-established invasive species (Simberloff and Gibbons 2004, Strayer et al. 2017) precludes generalization.

While boom–bust dynamics largely stem from density-dependent population regulators, density-independent factors such as extreme climatic events could confound such observations. Although our study site experienced an unusually severe winter in 2014–2015, the population decline of Asian Shore Crabs was evident prior to 2015 (Fig. 1A). Thus, density-independent mortality driven by climate is unlikely to have caused the overall population dynamics described herein. Nevertheless, it is necessary to consider such confounding variables or alternative hypotheses when inferring mechanisms for a population decline. Moreover, it is unclear in any particular case whether densities will equilibrate following a solitary boom–bust episode or undergo recurrent boom–bust cycles (Strayer et al. 2017). Continued monitoring of populations of the Asian Shore Crab and its prey and competitors, including collection of data on demographic factors such as body-size distributions and reproductive activity, as well as abiotic conditions such as climate, will therefore be necessary to document and understand the dynamics and long-term impacts of this invader.

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