

BIOTIC RESISTANCE TO INVASION: NATIVE PREDATOR LIMITS ABUNDANCE AND DISTRIBUTION OF AN INTRODUCED CRAB

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Abstract. Introduced species frequently escape the natural enemies (predators, competitors, and parasites) that limit their distribution and abundance in the native range. This reduction in native predators, competitors, and parasites may result in ecological release in the introduced range. However, biological interactions also can limit the establishment and spread of nonnative populations. The extent to which such biotic resistance occurs is poorly resolved, especially for marine ecosystems. Here we test whether a native predator, the blue crab *Callinectes sapidus*, affects the abundance and geographic range of the introduced European green crab *Carcinus maenas* in eastern North America. Both crab species occur in shallow, soft-sediment habitats of bays and estuaries, and their ranges overlap in eastern North America. First, we tested for a negative relationship in the abundances of the two species from trap samples across a 640-km (5.78° latitude) coastal transect. Second, we estimated variation in predation pressure on tethered *Carcinus maenas* across latitude and as a function of *Callinectes sapidus* abundance. Third, we measured predation rates on *Carcinus maenas* by *Callinectes sapidus* in field and laboratory experiments. Our results support the hypothesis that the native predator *Callinectes sapidus* provides biotic resistance to invasion and prevents the southward spread and establishment of *Carcinus maenas*. Within and across bays, *Carcinus maenas* were significantly less abundant at sites and depths with *Callinectes sapidus* compared with areas lacking *Callinectes sapidus*. Moreover, no *Carcinus maenas* were found in Chesapeake Bay, where *Callinectes sapidus* were most abundant. Predation of tethered *Carcinus maenas* increased with *Callinectes sapidus* abundance. In laboratory and field experiments, *Callinectes sapidus* preyed readily on *Carcinus maenas*. Thus, we conclude the predation by *Callinectes sapidus*, alone or in combination with other factors, limits the abundance and geographic range of an invasive marine species.

Key words: biological invasion; biotic resistance; blue crab; *Callinectes sapidus*; *Carcinus maenas*; European green crab; geographic range; nonindigenous species; predation.

INTRODUCTION

Biological invasions result from the arrival of propagules and the establishment of self-sustaining populations beyond the species' historical distribution. Invasions have occurred for millions of years and are a central component of ecology, biogeography, and the evolution of diversity. In recent times, however, the observed rates and effects of invasion have increased dramatically across many geographic regions, habitats, and taxonomic groups (Ruiz and Carlton 2003 and references therein). Such increases are attributed to human activities, adding a new dimension and urgency to questions about the factors controlling the establishment, geographic range, and abundance of species.

Many fundamental questions remain about mechanisms that underlie invasion patterns and processes. Colonization may often be limited by propagule supply, including both the density and frequency of inoculation

(Underwood and Denley 1984, Roughgarden et al. 1988, Kolar and Lodge 2001). The likelihood that an introduced species survives in and spreads beyond an area also depends on the interaction of multiple factors in the recipient environment (Lonsdale 1999). Environmental conditions alone can prevent an introduced species from establishing or spreading (Ford 1996). Alternatively, when environmental conditions are tolerable, biotic resistance may operate alone or in concert with environmental conditions to determine the local success of an invader (Pimm 1989). Biotic resistance can stem from community diversity (e.g., Case 1990, 1991, Stachowicz et al. 1999, Tilman 1999) or from abundant native predators or strong competitors independent of diversity (Herbold and Moyle 1986, Baltz and Moyle 1993, Crawley et al. 1999). The relative importance and interaction of these various factors in shaping the establishment, spread, abundance, and demography of nonindigenous species is unresolved.

Recently, considerable attention has focused on the role of natural enemies, especially predators and parasites, in invasion processes. Introduced species escape

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many species of predators and parasites that occur in their native ranges (Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003). Such ecological release may strongly affect the characteristics of nonnative populations (Torchin et al. 2001, Grosholz and Ruiz 2003, Maron et al. 2004). However, predators and parasites in the recipient range may affect introduced species. For example, nonindigenous fishes may be prevented from invading some California streams by native fish predation combined with unfavorable abiotic conditions (Baltz and Moyle 1993). In addition, several studies have shown predators limit local population size or habitat use of invaders (von Suter 1982, Robinson and Wellborn 1988, Reusch 1998, Byers 2002). To our knowledge, however, no studies have demonstrated that a native predator or parasite operates to limit the geographic range of an introduced species.

In this study, we explore the role of predation in limiting the abundance and distribution of the introduced European green crab, *Carcinus maenas*, along eastern North America. Native to the Atlantic coast of Europe, *Carcinus maenas* has colonized many different global regions, including both coasts of North America, Australia, and South Africa (Carlton and Cohen 2003, Thresher et al. 2003). *Carcinus maenas* became established along eastern North America in the 1800s and now occurs from Nova Scotia to Maryland. Expansion and contraction of the northern limit along the western Atlantic has coincided with short-term temperature changes, suggesting that cold water temperature determines the northernmost limit (Glude 1955, Welch 1968; see also Beukema [1991] for discussion of a similar pattern in the native range). In contrast, the southern range limits for the northwestern Atlantic have been stable for over a century and appear to be more restricted than expected, based upon temperature distribution reported in its native range (Carlton and Cohen 2003). The native portunid crab *Callinectes sapidus* occurs in high abundance at the southern range limit of *Carcinus maenas* and declines northward. Both crabs occur in shallow-water habitats of bays and estuaries and broadly overlap in habitat utilization and diet (Williams 1984). Moreover, the native *Callinectes sapidus* grows to more than twice the size of adult *Carcinus maenas* (Williams 1984). *Callinectes sapidus* is a voracious predator of smaller crabs (Hines et al. 1990, Clark et al. 1999), and its larger size than *Carcinus maenas* suggests it may be an important predator on this introduced species.

Here, we explicitly tested the hypothesis that predation by the native crab *Callinectes sapidus* operates to prevent the southern range expansion of *Carcinus maenas* in eastern North America. We examined whether (a) *Carcinus maenas* and *Callinectes sapidus* have reciprocal abundances along a latitudinal gradient, (b) predation rates are higher in the southern part of the range of *Carcinus maenas* and in areas of high *Callinectes sapidus* abundance, and (c) *Callinectes sapidus*

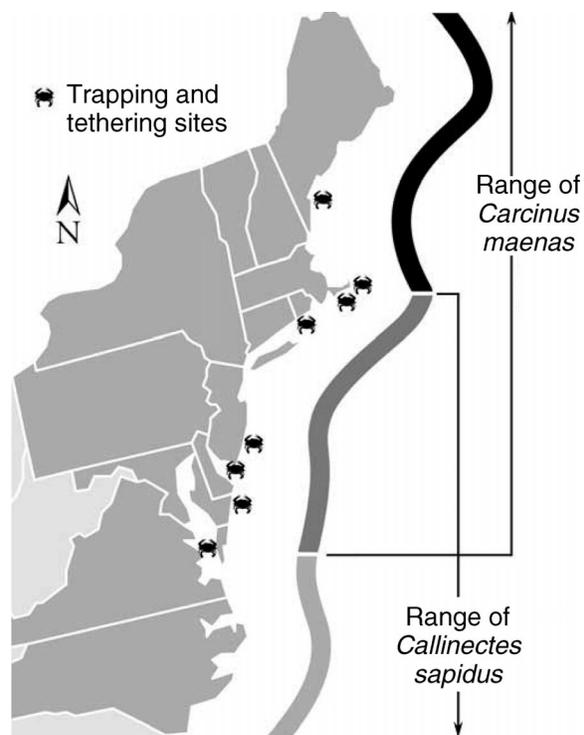


FIG. 1. Map of study sites and crab geographic distribution along the East Coast of the United States.

routinely prey upon *Carcinus maenas* in laboratory and field experiments. Several factors may covary with predation pressure across this latitudinal gradient, including a southward increase in temperature, decrease in amount of rocky coastline, and decrease in area of the intertidal zone, which can provide an important refuge from predation (Connell 1970, Menge and Lubchenco 1981). To control for these other variables, we also tested the effect of *Callinectes sapidus* on the abundance and mortality of *Carcinus maenas* within a single bay in which both species occurred and exhibited spatial variation in abundance.

METHODS

Study sites

From June to August 2001 and 2002, we studied *Carcinus maenas* and *Callinectes sapidus* at multiple ($N = 64$) sites across eight bays. These bays spanned 640 km within and south of *Carcinus maenas*' range in eastern North America (Fig. 1, Table 1). Each site within a bay was at least 0.5 km, by water, from every other site.

We used Waquoit Bay, Massachusetts, USA, to test whether predation and abundance patterns found across latitudes persisted within a single bay. We examined *Carcinus maenas* abundance and predation in multiple areas of Waquoit Bay with and without *Callinectes sapidus*. Waquoit Bay, a shallow bay on the south side of Cape Cod, Massachusetts, is near the northern limit of

TABLE 1. The coordinates of the eight bays studied, the number of sites, traps, and tethers in each, and the abbreviation used for each bay.

Bay	Coordinates	No. trap sites	No. trap sets	No. retrieved traps	No. tether sites	No. tether sets	No. retrieved tethers	Abbreviation
Casco Bay (Biddeford Pool and Portland), Maine	43.45° N, 70.35° W	7	21	59	7	21	142	CBME
Nauset Marsh, Massachusetts	41.81° N, 69.96° W	7	21	59	7	21	138	NMMA
Waquoit Bay, Massachusetts	41.57° N, 70.53° W	11	31	87	11	31	211	WBMA
Long Island Sound, Connecticut and Point Judith Pond, Rhode Island	41.40° N, 71.51° W	6	18	47	6	18	124	CTRI
Great Bay, New Jersey	39.53° N, 74.33° W	8	22	56	7	18	121	GBNJ
Cape May and adjacent Delaware Bay, New Jersey	39.03° N, 74.82° W	8	23	57	6	16	95	CMNJ
Chincoteague and Sinepuxent Bays, Maryland	38.13° N, 75.28° W	9	23	64	9	23	156	CBMD
Chesapeake Bay, Virginia	37.67° N, 75.86° W	8	20	55	8	20	128	CBVA
Total		64	179	484	61	168	1115	

Note: A set refers to a set of traps or tethers at one depth at one site.

Callinectes sapidus but well within *Carcinus maenas*' western Atlantic range (Fig. 1, Table 1).

Crab abundance

To estimate the abundance of *Callinectes sapidus* and *Carcinus maenas* and to test for reciprocal abundance of species across sites, we trapped crabs at 64 study sites in eight bays (Fig. 1, Table 1). The crab traps (0.11 m³) were covered with plastic mesh (1.27 cm openings) so small crabs could not walk out except through the entrances. For each site, three baited crab traps were deployed at each of three depths (0.0, -0.5, and -1.5 m relative to mean lower low water [MLLW]). Every trap was deployed at least 20 m from its neighbors to ensure independent catches. We retrieved traps 24 ± 1 h after deployment. We recorded species, sex, and maximum carapace width (in millimeters) of all trapped crabs. We also identified trapped fish before releasing them.

Traps were lost or damaged at several sites. We calculated the mean number of crabs per trap from the remaining traps at these sites and depths. For trapping sets where all three traps were missing, we excluded the data from that depth at that site. We did not retrieve any traps at 0.0 m at five sites (three at Chincoteague Bay sites, two at Great Bay), at 1.5 m at two sites (one at Chincoteague Bay, one at Cape May), and at neither 0.0 m nor -1.5 m at three sites (two at Chesapeake Bay, one at Waquoit Bay). Therefore, we retrieved traps from a total of 179 trapping sets (set of traps per depth per site).

Environmental measurements and tidal amplitude

At each site we recorded several environmental variables that could influence the density and types of crabs in an area. We measured temperature (in degrees Celsius), salinity (parts per thousand [ppt]), and oxygen (in milligrams per liter) with a meter at the time of trapping. We took readings 0.1 m just below the surface

and just above the substrate at depths of 0.5 m and 1.5 m below MLLW. We used the surface reading from the 0.5-m depths as an estimate of the 0.0 m values. We measured sediment particle size by collecting two sediment samples from each site then sieving them for grain size analysis following Buchanan (1984). We used a standard set of sieves for sediment analysis using the Wentworth scale. Data from each pair of sediment samples were averaged to yield one result per site. We report the proportion of the sample that was fine-grained sand or coarser (>62 µm). To estimate the tidal amplitude and the extent of the intertidal zone for each area, we obtained the values for the mean range of tide for the nearest National Oceanic and Atmospheric Administration benchmark site to each of our study bays. We used mean tidal ranges from the observed water levels for 1983–2001.

Predation

We estimated the relative risk of predation for *Carcinus maenas* across latitude and as a function of *Callinectes sapidus* abundance. We used tethered crabs to assess relative predation pressure among sites in the field (e.g., Heck and Thoman 1981, Wilson et al. 1987, Everett and Ruiz 1993, Hines and Ruiz 1995). Risk faced by tethered crabs is typically higher than natural risk, and tethering may include other artifacts (Peterson and Black 1994, Zimmer-Faust et al. 1994). Thus, we further evaluated the predation by using field enclosure experiments and laboratory experiments. This dual approach helped balance the uncontrolled variables inherent in fieldwork with the artificiality of laboratory experiments and helped evaluate predation risk.

Tethering

We measured mortality rates of tethered *Carcinus maenas* in each of the eight bays under study. We trapped and hand-caught crabs for tethering and, in Chincoteague and Great Bays, supplemented our sup-

ply with *Carcinus maenas* sold at bait shops. We only tethered active, intermolt 30–52 mm carapace width *Carcinus maenas* that had at least one cheliped and seven limbs total. Each tethered crab was secured by a 0.5-m length of flexible 13.6-kg test steel leader, which was attached to the crab and to a 0.5- or 1.4-kg lead weight. We used a single piece of leader for both the halter and the leash: we looped one end around the crab's cephalothorax, crimped it tightly, then glued it to the carapace. The tethers did not restrict movement of crab limbs (see Hines and Ruiz [1995] for further discussion of the general method). Tethered crabs were assigned randomly by size and by sex to each site and depth; the exception was Virginia, where only males were used to prevent transfer of any reproductive females.

For each of the 64 sites, we set out a set of seven tethered crabs at each depth, using the same depths as the traps (0.0, -0.5, and -1.5 m MLLW). Each tether was deployed at least 2 m from its neighbors and away from aquatic vegetation. Tethers were set for 24 ± 1 h starting the day before or two days after trapping at a site. We retrieved tethered crabs from 61 of the trapping sites and 168 of the tether sets (number of depths \times sites), but did not successfully retrieve from the other sites and sets, ones with strong currents (Fig. 1, Table 1).

We categorized retrieved tethers according to the presence of a live crab, a newly injured crab, a carapace (or pieces), or just a harness. Carapace fragments, dead crabs with punctures, and limb loss are diagnostic of predation by *Callinectes sapidus* (Hines and Ruiz 1995). Entire removal of the crab also has been attributed to *Callinectes sapidus* predation and was common in previous studies (Dittel et al. 1995, Hines and Ruiz 1995). We did not attribute empty tethers to escape because no crabs escaped from their tethers overnight before they were deployed in the field ($N = 805$) and no crabs escaped from their tethers when left in aquaria for 7 d ($N = 50$). The two aquaria housing these tethered crabs had a flow-through seawater system and were aerated. Similarly, no *Carcinus maenas* ($N = 30$) escaped monofilament halters when kept in large tanks overnight (C. A. Scheuerman and P. Jivoff, unpublished data). In addition, no crabs tethered with steel leader escaped after 24 h ($N = 56$) or 72 h ($N = 7$) in 2004 in Bodega Harbor where they could bury themselves under rocks or in mud (C. E. deRivera, unpublished data). Therefore, we considered limb loss, carapace remains, or an empty harness to represent predation on the crab. We calculated the proportion of eaten crabs out of the number of remaining tethers.

Laboratory aquarium and enclosure experiments

We paired *Carcinus maenas* and *Callinectes sapidus* in aquaria with an alternative food source, a live clam, *Macoma balthica* (25–30 mm), to measure predation of one crab on the other, prey preference, and com-

petition between crabs for the clam. *Macoma balthica* are eaten in the wild by both species (Raffaelli et al. 1989, Hines et al. 1990). Crabs were obtained from traps, seining, and trawling. Prior to use in the experiment, they were kept in large tanks with conspecifics and fed shrimp pellets every other day and frozen squid weekly.

We followed a standardized protocol for the laboratory experiment. We used 120-L aquaria with a 7.5-cm sand layer at the bottom covered by aerated, filtered estuarine water that was adjusted to 25 ppt salinity with sea salts. The afternoon before an experiment started, we divided each experimental aquarium with plexiglass and placed a *Callinectes sapidus* on one side of the divider and a *Carcinus maenas* on the other side. The next morning, after 14 h acclimation, we started the 48-h experiment by pulling out the divider and adding a clam. We observed each tank for four 0.5-h periods and scanned tanks every 2 h each day to check for crab or clam predation. To identify which crab ate the clam, we marked clams with nontoxic zinc oxide that rubbed off on predators, and we also videotaped a subset of the tanks. We ran four experimental tanks simultaneously, randomizing treatments, for a total of 36 pairs of crabs. Only experimentally naive crabs were used for each replicate. We paired male or female crabs in all size class combinations, matching small (7–22 g wet mass, 30–47 mm carapace width, $N = 22$) and large (32–51 g, 50–60 mm, $N = 14$) *Carcinus maenas* with small (35–56 g, 80–95 mm including spines, $N = 13$), medium (58–77 g, 90–104 mm, $N = 16$), and large (92–214 g, 120–165 mm, $N = 7$) *Callinectes sapidus* (replication = 10 small : small [*Carcinus maenas* : *Callinectes sapidus*], seven small : medium; five small : large; three large : small; nine large : medium; two large : large).

We conducted a field enclosure experiment to determine whether *Callinectes sapidus* or *Carcinus maenas* avoided traps holding heterospecifics, to measure predation rates when these species were together, and to identify escape rates from the traps. The experiment was conducted in Sinepuxent Bay, Maryland, in August 2001 at 0.5 m below MLLW. We used four treatments, two controls with single-species additions and two treatments with mixed-species additions. For each control, we placed a baited trap (0.11 m³: 0.61 \times 0.61 \times 0.30 m) containing no crabs within a mesh enclosure (0.55 m³: 1.22 \times 1.22 \times 0.37 m) and added either 10 *Carcinus maenas* or five *Callinectes sapidus* to the enclosure. Replicates of one experimental treatment started with two *Callinectes sapidus* in the enclosed, baited trap and 10 *Carcinus maenas* outside of the trap but in the surrounding enclosure. The second experimental treatment had seven *Carcinus maenas* in the trap and five *Callinectes sapidus* outside of the trap in the surrounding enclosure. When a trial ended, 24 h after the crabs were introduced into the enclosures, we recorded the number and condition of each species in each trap.

We used two experimental treatments and two controls, each with eight replicates interspersed across three trials. We did not use data from two of the *Callinectes sapidus* control replicates because they were vandalized and missing crabs. New crabs were used for each replicate. The *Callinectes sapidus* ranged from 69 to 125 mm carapace width, with a median of 97 mm for each treatment; the *Carcinus maenas* ranged from 40 to 50 mm width. Crabs were fed the day before they were used and had baitfish available in the traps throughout the experiment.

Statistics

We examined abundance and predation data using univariate and multivariate two-tailed analyses. Statview version 5.0.1 (SAS Institute, Cary, North Carolina, USA) was used for the Student's *t* tests and G^2 contingency table analyses, and JMP version 4.0.4 (SAS Institute) was used for analyses of variance (ANOVA) and covariance (ANCOVA) logistic regression and χ^2 contingency table analyses. We report the likelihood ratio χ^2 value for the logistic regressions. Variables used in parametric tests were transformed to meet test assumptions such as normality and homoscedasticity; we checked residuals from the statistical tests for normality to verify that the test assumptions had been met.

Trapping and environmental statistics.—First, we examined whether the number of *Carcinus maenas* (ln) and *Callinectes sapidus* (ln) varied across all eight bays studied. We then tested for reciprocal abundance of these two crabs in the five bays studied within their overlapping range, Chincoteague and Sinupuxent Bays, Maryland, to Waquoit Bay, Massachusetts. This analysis included bay, site nested within bay as a blocking factor, depth, and the interaction between bay and depth. All independent factors other than site were fixed effects, while site was a random effect. We also included several covariates: the mean number of *Callinectes sapidus* (ln) trapped at each site and depth, temperature (square root) (a possible contributor to the latitudinal abundance patterns observed in both species), salinity (ln), and dissolved oxygen. We used the mean number of *Callinectes sapidus* caught per site per depth (trap set) rather than including data per trap (sub-samples) because the mean should give a more accurate and representative estimate of *Callinectes sapidus* abundance for each depth \times site location than the sub-samples (traps). Most covariates were not strongly correlated across the overlapping range of these crabs ($r = 0.69$ for temperature and dissolved oxygen, $r < 0.26$ for all other combinations).

In Waquoit Bay, crab abundances were not normally distributed. Therefore we used presence/absence data for both crab species from each site and depth and used a G^2 contingency table to test for the reciprocal relationship between the two species. Including depth as a third factor decreased the numbers per cell to the

point that the three-way table violated the assumptions of both χ^2 and G^2 tests. Environmental variables also were not normally distributed, even after transformation, within Waquoit Bay, so were excluded in the analysis.

Because we rarely caught other crab species, the effect of other crabs on *Carcinus maenas*' distribution was examined using a two-way χ^2 contingency table with presence/absence data of all other crab species and of *Carcinus maenas* for the bays with multiple sites with *Carcinus maenas*, from Cape May, New Jersey, to Casco Bay, Maine. This was repeated for *Callinectes sapidus* and the other crab species for the bays within *Callinectes sapidus*' range.

Tests identifying the differences in environmental variables across bays only used the values from -0.5 m MLLW because the within-site readings at the three different depths were highly correlated and the 0.5 m readings were representative of the entire site. One-way ANOVAs were used to examine whether these factors varied across the eight bays in our study.

Predation statistics.—As with the trapping data, we examined whether the proportion of tethered *Carcinus maenas* that were depredated (arcsine square-root transformed) varied across all eight bays studied. We then tested for the effect of *Callinectes sapidus* on depredated tethered *Carcinus maenas* proportions in the six bays where we trapped *Callinectes sapidus*, Chesapeake Bay, Virginia, to Waquoit Bay, Massachusetts. This analysis included bay, site nested within bay as a blocking factor, depth, and the interaction between bay and depth. All independent factors other than site were fixed effects, while site was a random effect. We also included the mean number of *Callinectes sapidus* (ln) trapped at each tethering site and depth as a covariate. Tethered crabs varied by bay with respect to size, so we also included the mean width of the tethered crabs as a covariate in this analysis. The sex of the tethered crabs did not significantly affect the likelihood of predation (χ^2 contingency table excluding Virginia sites: $\chi^2 = 0.64$, $N = 1081$, $df = 1$, $P = 0.4247$) so was therefore excluded from this analysis.

In Waquoit Bay, *Callinectes sapidus* abundance was highly skewed. Therefore we used *Callinectes sapidus* presence/absence information in an ANOVA with depth and the interaction between these two factors to test for the effect of *Callinectes sapidus* presence on tether predation.

We also examined the effect of predatory fish presence or absence on the predation of tethered *Carcinus maenas* across the eight bays with a one-way ANOVA.

To determine prey preference in aquaria, we excluded all the cases in which *Carcinus maenas* ate the clam, the cases in which clam predator was unknown, and the cases in which neither or both were eaten, then conducted a two-tailed binomial test on *Callinectes sapidus*' choice of *Carcinus maenas* or *M. balthica* ($N = 12$). We used a logistic regression to determine

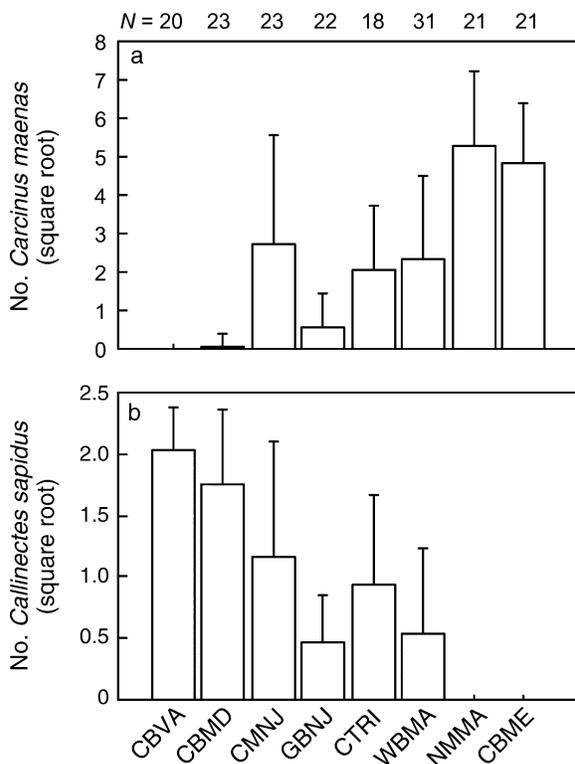


FIG. 2. Catch size (square-root transformed) for (a) *Carcinus maenas* and (b) *Callinectes sapidus* in eight bays (left to right, from south to north) along a latitudinal gradient (mean + SD); sample sizes, the number of trapping sets (depth \times site) per bay, are given along the top. Mean catch refers to the number of crabs per set divided by the number of traps in the set (usually three; a set refers to the traps at one depth at one site). See Table 1 for site abbreviations.

whether size difference (ratio of *Callinectes sapidus* mass to *Carcinus maenas* mass, continuous) and hunger level (fed 1 d or 2 d prior to the start of the experiment, nominal) affected predation on *Carcinus maenas* (eaten, not, nominal). We did not include an interaction between the independent variables because there were no cases of "no predation" when *Callinectes sapidus* had not eaten for 2 d prior to the experiment. We included all 36 replicates in this analysis.

To determine whether *Callinectes sapidus* outcompeted *Carcinus maenas* for the clam, we conducted a two-tailed binomial test ($N = 19$). We could not determine which species ate the clam in three trials, so we excluded these from the analysis.

RESULTS

Pattern of *Carcinus* and *Callinectes* distribution across latitudes

The number of trapped *Carcinus maenas* decreased from north to south in eight bays along eastern North America (Fig. 2, $F_{7,171} = 36.43$, $r^2 = 0.60$, $P < 0.0001$), while also exhibiting considerable variation within and among bays. The two northernmost bays averaged 31.3

± 22.8 *Carcinus maenas* (mean \pm SD, $N = 21$ trap sets, the mean catch for the set of traps at a depth \times site combination) and 25.7 ± 15.4 *Carcinus maenas* ($N = 21$ trap sets), whereas the two southernmost bays in our study averaged 0.1 ± 0.5 *Carcinus maenas* ($N = 23$) and 0.0 ± 0.0 *Carcinus maenas* ($N = 20$ trap sets). No small (< 50 mm) *Carcinus maenas* were found in the southern part of the range (south of Sinepuxent Bay, Maryland) and no *Carcinus maenas* were found in Chesapeake Bay, Virginia.

In contrast, the number of trapped *Callinectes sapidus* decreased significantly with increasing latitude, from a mean of 4.3 ± 1.4 individuals per trap set ($N = 20$ trap sets) in Chesapeake Bay to 0.8 ± 1.3 individuals ($N = 31$ trap sets) in Waquoit Bay (Fig. 2, $F_{7,171} = 40.68$, $r^2 = 0.62$, $P < 0.0001$). We did not trap or find any *Callinectes sapidus* in the two northernmost bays, although they live in Nauset Marsh, Massachusetts (J. McGrath, personal communication).

Environmental gradients across latitudes

Tidal range, temperature, salinity, dissolved oxygen, and sediment composition all varied across the sampled bays (Fig. 3). Tidal range decreased with decreasing latitude, but there was some variation due to local bathymetry (Fig. 3a). Temperature varied by bay (Fig. 3b, $F_{7,55} = 31.59$, $r^2 = 0.80$, $P < 0.0001$): Chesapeake Bay, Virginia, had the warmest water and Maine had the coolest; however, two northern shallow bays, Point Judith Pond, Rhode Island, and Waquoit Bay, Massachusetts, were warm, while Great Bay, New Jersey, was deeper and had cool water. Salinity in these bays generally increased with latitude, but the saltiest waters were in Cape May, New Jersey (Fig. 3c, $F_{7,55} = 11.65$, $r^2 = 0.60$, $P < 0.0001$). Dissolved oxygen varied by bay but did not show a latitudinal pattern (Fig. 3d, $F_{7,55} = 15.18$, $r^2 = 0.66$, $P < 0.0001$). A larger proportion of sediment mass was composed of sand, particles > 62 μ m diameter, in the northern bays, though Chesapeake Bay sites also were sandy (Fig. 3e, $F_{7,53} = 5.83$, $r^2 = 0.43$, $P < 0.0001$).

The effects of *Callinectes* and other variables on the distribution of *Carcinus*

Callinectes sapidus abundance alone explained a significant amount of the variation in *Carcinus maenas* abundance throughout the overlapping ranges of these crabs along eastern North America. *Carcinus maenas* were less abundant in areas with than without *Callinectes sapidus* (Fig. 4; Appendix A, Table A1). Across our study sites, *Carcinus maenas* abundance was not significantly affected by temperature, salinity, or dissolved oxygen (Appendix A, Table A1).

Even across sites within a bay, the reciprocal abundance of *Carcinus maenas* and *Callinectes sapidus* was evident. In Waquoit Bay, Massachusetts, *Carcinus maenas* were present where *Callinectes sapidus* were

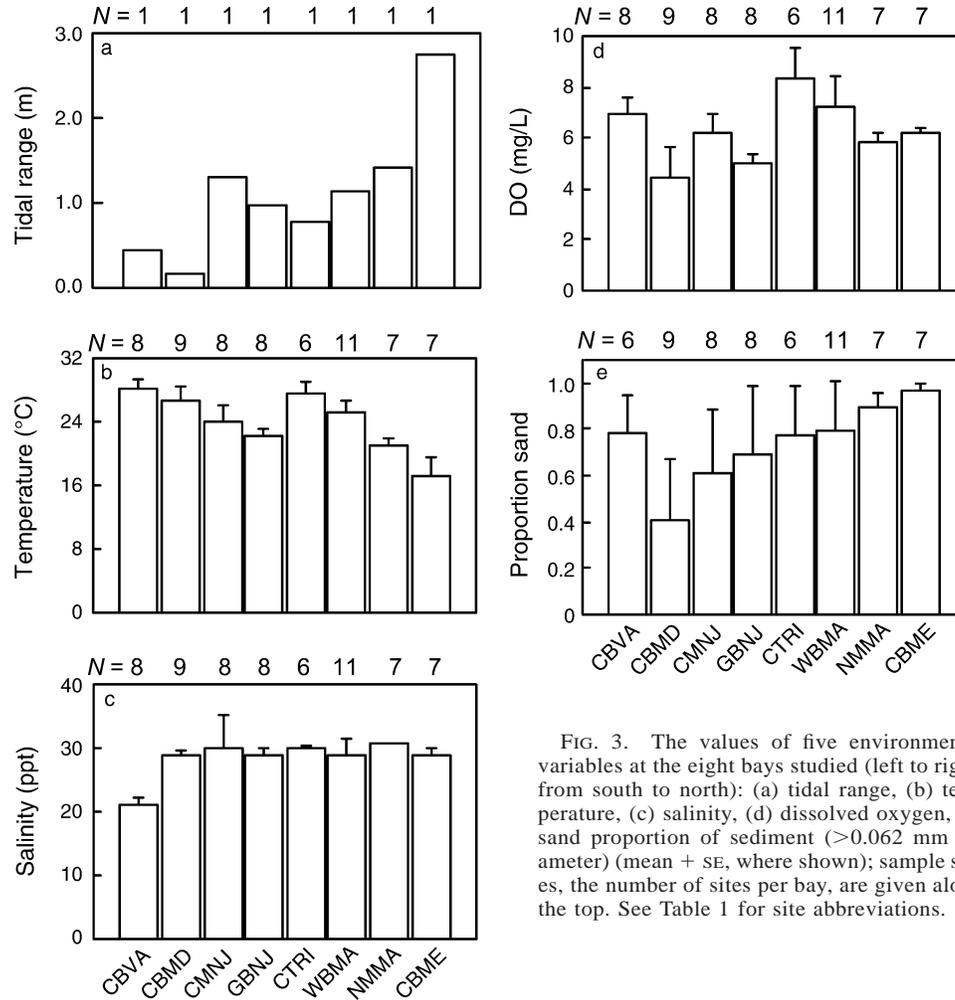


FIG. 3. The values of five environmental variables at the eight bays studied (left to right, from south to north): (a) tidal range, (b) temperature, (c) salinity, (d) dissolved oxygen, (e) sand proportion of sediment (>0.062 mm diameter) (mean + SE, where shown); sample sizes, the number of sites per bay, are given along the top. See Table 1 for site abbreviations.

absent and vice versa (Fig. 4b, $G^2 = 6.39$, $N = 31$, $df = 1$, $P = 0.0115$).

The presence of *Carcinus maenas* was not dependent on other crab species, spider crabs (*Libinia emarginata* and *L. dubia*), lady crabs (*Ovalipes ocellatus*), speckled crabs (*Arenaeus cribrarius*), and rock crabs (*Cancer irroratus*), within *Carcinus maenas*' range (χ^2 contingency for presence/absence of other crab species vs. presence/absence *Carcinus maenas*: $\chi^2 = 0.06$, $r^2 < 0.01$, $N = 136$, $df = 1$, $P = 0.8097$). In contrast, these other crabs were rare where *Callinectes sapidus* was present throughout *Callinectes sapidus*' range ($\chi^2 = 8.68$, $r^2 = 0.06$, $N = 137$, $df = 1$, $P = 0.0032$).

Callinectes predation upon *Carcinus*

Predation of tethered green crabs.—There was a significant difference among bays in the predation rate on tethered crabs, whereby more *Carcinus maenas* were eaten in the two southernmost bays than in New Jersey and New England bays (Fig. 5a, ANOVA $F_{7,160} =$

18.00, $r^2 = 0.44$, $P < 0.0001$; Tukey-Kramer post-hoc tests indicate the southernmost two bays had significantly higher predation than all other bays and that there were no other significant differences between bays). Moreover, the proportion of depredated *Carcinus maenas* increased significantly with the abundance of *Callinectes sapidus* within *Callinectes sapidus*' range (Fig. 5b; Appendix A, Table A2). Similarly, in Waquoit Bay, predation on tethered *Carcinus maenas* was much higher in areas with *Callinectes sapidus* than those without (Fig. 5c, ANOVA $F_{1,29} = 28.52$, $r^2 = 0.50$, $P < 0.0001$).

Across bays, water depth affected predation risk. Fewer crabs were eaten when tethered at 0.0 m MLLW (predation = 3.3 ± 0.6 crabs at 0 m [mean \pm SE], $N = 39$) than subtidally (5.7 ± 0.6 crabs at -0.5 m, $N = 46$ and 5.4 ± 0.5 crabs at -1.5 m, $N = 41$; Appendix A, Table A2). Furthermore, there was a significant interaction between depth and bay, most likely due to the variation in *Callinectes sapidus* abundance between

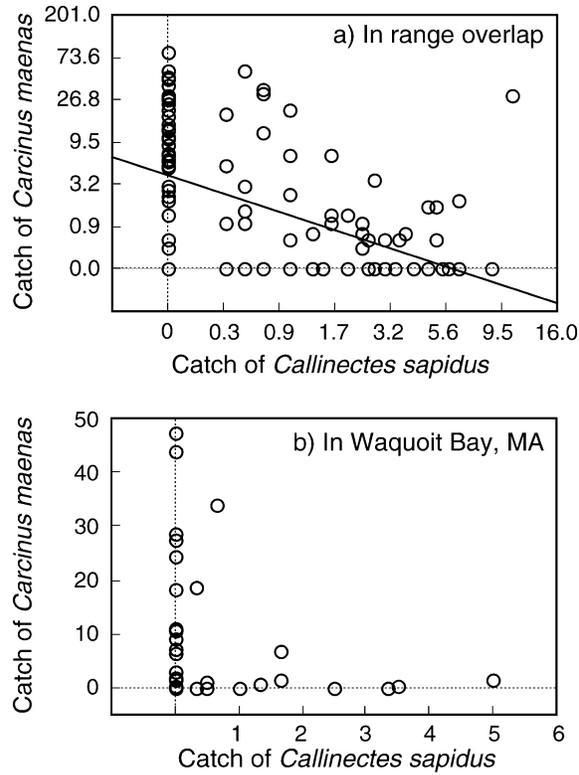


FIG. 4. Mean number of *Carcinus maenas* vs. mean number of *Callinectes sapidus* per trap set (depth × site): (a) across the five bays within the overlapping ranges of these crabs ($N = 117$ trap sets [per depth, per site], $y = 2.24 - 0.87x$, $r^2 = 0.24$) (data were ln transformed; axis labels were back-transformed for ease of interpretation); and (b) at 11 sites within Waquoit Bay, Massachusetts ($N = 31$ trap sets).

bays (Appendix A, Table A2). For example, Casco Bay, Maine, is the only site where predation was higher on crabs tethered at 0.0 m than at -0.5 m MLLW.

The mean width of the tethered crabs explained a significant amount of the variation in survivorship (Appendix A, Table A2), with smaller crabs more likely to be eaten than larger crabs. However, the largest tethered crabs were eaten at sites with *Callinectes sapidus*. For example, the size of a tethered crab did not predict its likelihood of predation in Chesapeake Bay, which has many *Callinectes sapidus*, despite the fact that most of our largest tethered crabs were deployed there (logistic regression for size: $\chi^2 = 0.14$, $r^2 = 0.002$, $N = 128$, $df = 1$, $P = 0.7082$).

We observed a *Callinectes sapidus* feeding upon a tethered, live *Carcinus maenas* in Chesapeake Bay. In addition, of the 447 tethered crabs that were categorized as preyed upon, 38.5% showed direct evidence of predation by *Callinectes sapidus*: the tethered crab was partially eaten, all or bits of the carapace remained, and/or the carapace was punctured with a pinch mark ($N = 91$); the crab was missing its claw(s) and/or multiple legs ($N = 25$); or the crab was missing and the leader had pinch marks on it in a place unreachable by

the tethered crab ($N = 56$). In 259 additional cases the crab was removed entirely from its tether, which could be attributable to *Callinectes sapidus* or other predators.

Callinectes sapidus were not the only predators of tethered *Carcinus maenas*. In Maine, beyond *Callinectes sapidus*' range, 14.3% (median, range = 0.0–42.9%) of tethered crabs were eaten. In addition, a crab in Maryland had a turtle bite (*Malaclimys terrapin*) and a carapace in Maine was covered with thick mucus; in

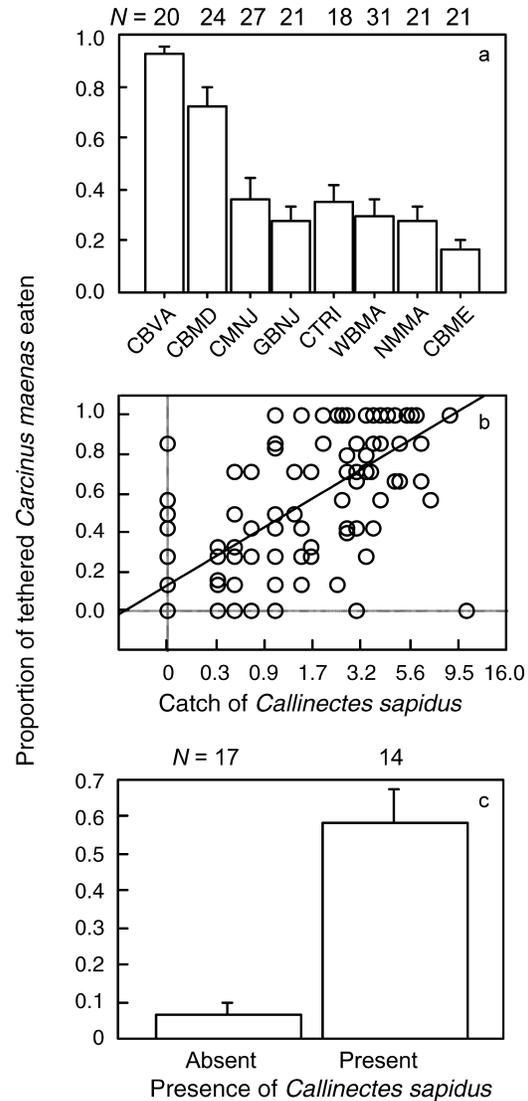


FIG. 5. Proportion (mean + SE) of tethered *Carcinus maenas* that were preyed upon (a) along a latitudinal gradient; sample sizes (numbers of tether sets [per depth, site]) are given along the top; (b) vs. *Callinectes sapidus* abundance in studied bays within the *Callinectes sapidus* range, from Chesapeake Bay, Virginia, to Waquoit Bay, Massachusetts ($N = 126$ tether sets, $y = 0.12 - 0.30x$, $r^2 = 0.55$); and (c) separately *Callinectes sapidus* presence or absence in Waquoit Bay (mean + SE; sample sizes, number of tether sets, are given along the top). See Table 1 for site abbreviations.

15 cases, a harness or leader was missing, suggesting a larger predator; and an oyster toadfish (*Opsanus tau*) in Waquoit Bay was still attached to the leader of a tethered crab. In addition, we observed a gull (*Larus argentatus*) in Cape May consume a tethered crab. Other tethered crabs fought gulls and remained unharmed ($N = 3$). Gulls (*Larus* spp.) were prevalent throughout the bays we studied but could only eat the crabs tethered at 0 m MLLW and only when the tide was out. We trapped potential *Carcinus maenas* predators, oyster toadfish, dogfish (*Squalus acanthia* and *Mustelus canis*), or eels (*Anguilla rostrata*), in all the bays we studied. Predation rates on tethered crabs were not higher at sites where we caught predatory fish (across eight bays, $F_{1,166} = 0.12$, $r^2 < 0.01$, $P = 0.7310$).

Laboratory and enclosure experiments

In laboratory experiments, *Callinectes sapidus* ate 18 of the 36 *Carcinus maenas*: 3/14 (21.4%) of the large (>32 g, 50 mm) and 15/22 (68.2%) of the small *Carcinus maenas*. Moreover, *Callinectes sapidus* ate *Carcinus maenas* (10 cases) significantly more often than *M. balthica* (two cases) when one of these two prey species was consumed (binomial test: $N = 12$, $P = 0.0386$). *Callinectes sapidus* ate both prey species in four additional cases. *Callinectes sapidus* preyed upon *Carcinus maenas* significantly more often when they were much larger than *Carcinus maenas* and when they had not eaten for 2 d prior to the start of the experiment (mass ratio for *Carcinus maenas* eaten after 1 d without food = 6.43 ± 0.76 , mean \pm SE, $N = 10$; *Carcinus maenas* eaten after 2 d = 5.67 ± 0.77 , $N = 8$; *Carcinus maenas* not eaten, 1 d = 2.57 ± 0.43 , $N = 18$; logistic regression for predation, whole model = $R^2 = 0.56$, $N = 36$, $\chi^2 = 28.14$, $P < 0.0001$; mass ratio $\chi^2 = 14.72$, df = 1, $P = 0.0001$; days without food [nominal, 1 or 2 d] $\chi^2 = 9.75$, df = 1, $P = 0.0018$). *Callinectes sapidus* ate the *Carcinus maenas* in all eight trials in which they had not eaten for 2 d prior to the experiment.

Callinectes sapidus did not eat the clam more often than *Carcinus maenas* did (binomial test, $N = 19$, $P = 0.1671$); in fact, *Carcinus maenas* consumed the clam (13 times) more often than *Callinectes sapidus* did (six times). *Callinectes sapidus* ate *Carcinus maenas* in 10 of the 14 cases of no clam predation, and in half of these cases they ate *Carcinus maenas* before the mean *Carcinus maenas* clam consumption time.

In field enclosures, 11 of 95 (11.6%) *Carcinus maenas* were eaten by *Callinectes sapidus* within 24 h, though the crabs had baitfish provided to them the previous day and throughout the experiment. Neither *Callinectes sapidus* nor *Carcinus maenas* avoided entering traps that housed the heterospecific (see Appendix B).

DISCUSSION

The role of native predators

Our results indicate that predation on the introduced crab *Carcinus maenas* by the native blue crab, *Calli-*

nectes sapidus, increases dramatically from north to south along eastern North America and operates alone or in combination with other factors to set the southern range limit of the introduced crab. *Callinectes sapidus* abundance increased from Massachusetts to Virginia, while *Carcinus maenas* abundance and survivorship decreased. The predator-prey relationship observed in laboratory and field experiments further suggests predation by *Callinectes sapidus* directly affects the abundance, distribution, and mortality patterns of *Carcinus maenas* in the northwestern Atlantic.

Both across this geographic range and within a bay, the abundance of *Callinectes sapidus* explained a significant amount of the variation in observed *Carcinus maenas* abundance and mortality patterns. Across bays, *Callinectes sapidus* abundance more strongly predicted *Carcinus maenas* abundance than did other variables, despite the overlapping habitat utilization of these species. We observed a similar result in Waquoit Bay, Massachusetts, which suggests the result is not due to spurious correlation with factors that may covary with *Callinectes sapidus* abundance from north to south. *Carcinus maenas* were abundant in Waquoit Bay except at the sites with *Callinectes sapidus*. A similar inverse pattern of abundance between these species also has been observed among small bays on the island of Martha's Vineyard, Massachusetts (W. Walton and D. Ber-rin, unpublished data).

We observed high predation rates by *Callinectes sapidus* on *Carcinus maenas* throughout our study. In field and laboratory experiments >10% and 50% *Carcinus maenas* were consumed despite other available food. Moreover, *Callinectes sapidus* preferentially consumed *Carcinus maenas* over *M. balthica* in aquaria trials. Furthermore, predation rates on tethered *Carcinus maenas* increased dramatically with increasing *Callinectes sapidus* abundance both across bays and within Waquoit Bay.

The observed predation rates appear to be sufficiently high for the peripheral southern *Carcinus maenas* populations to be kept at low density or extirpated. In Chesapeake Bay, where most sites had many *Callinectes sapidus*, predation of tethered crabs exceeded 90% in 24 h, six times higher than in Maine. Although our tethering data suggest a high relative predation pressure at the southern range of *Carcinus maenas*, predation risk for free-ranging crabs is difficult to estimate. Predation rates on tethered animals can be much higher than actual rates and may also interact with other differences among sites (Zimmer-Faust et al. 1994). We attempted to control for variation in habitat type and depth by standardizing among sites. In addition, predator-specific mortality characteristics attributed many predation events to *Callinectes sapidus* and increased confidence in the source of mortality for tethered *Carcinus maenas*.

Comparison of our tethering results to previous *Callinectes sapidus* tethering studies further supports the

hypothesis that *Callinectes sapidus* limits the distribution and abundance of *Carcinus maenas*. Tethered *Carcinus maenas* in Chesapeake Bay suffered higher predation rates than tethered *Callinectes sapidus* of equivalent mass in similar studies that suggest *Callinectes sapidus* cannibalism is high enough to regulate its population dynamics (Pile 1993, Ruiz et al. 1993, Hines and Ruiz 1995). Not only is predation pressure on *Carcinus maenas* higher than that reported for *Callinectes sapidus* of comparable sizes, but also it takes longer for *Carcinus maenas* to achieve a size-based refuge, if any exists given the relative adult sizes of the two species. Even the largest tethered *Carcinus maenas* (45–52 mm) were eaten where *Callinectes sapidus* were abundant, so *Carcinus maenas* would not reach a size-based refuge until after their second winter (Berrill 1982), if at all.

Fewer tethered crabs were eaten at 0 m MLLW than subtidally, suggesting that, similar to blue crab juveniles, shrimp, and small fish (e.g., Harvey et al. 1988, Posey and Hines 1991, Ruiz et al. 1993, Dittel et al. 1995), *Carcinus maenas* gain a partial refuge in shallow water. High tidal amplitude in the central part of *Carcinus maenas*' range creates a large intertidal refuge from *Callinectes sapidus* and other swimming predators. However, tidal amplitude, and perhaps intertidal refuge, diminishes in the southern part of *Carcinus maenas*' range where predation by *Callinectes sapidus* was highest.

Though other predators contributed to the high mortality of our tethered crabs, we think it unlikely that other predators strongly impact *Carcinus maenas* distribution in the western Atlantic. All elements of our data suggest that the predation pressure exerted by *Callinectes sapidus* was the key variable contributing to the patterns, including: the strong relationship between mortality and *Callinectes sapidus* abundance; the high predation rate in experiments involving *Callinectes sapidus* as the only potential predator; the great success of *Carcinus maenas* in New England; and the one-time-only observation of an oyster toadfish attached to the leader, as is typical of this species (Wilson et al. 1987, Hines and Ruiz 1995).

The role of temperature

Temperature may play an important role in the distribution and abundance of *Carcinus maenas* with latitude. We did not test this hypothesis directly, but four lines of evidence suggest that the direct effects of temperature (thermal stress) on *Carcinus maenas* are not sufficient to explain the observed patterns. First, temperatures beyond the range boundary fall within the reported temperature distribution observed elsewhere in the world (Carlton and Cohen 2003). Second, the dramatic drop-off (step function) in abundance seen between Cape May, New Jersey, and Chincoteague Bay, Maryland, only 0°85' south of New Jersey, suggests that climate, which should cause a more gradual

change in density, is not the only contributing factor (Caughley et al. 1988). Moreover, the southern boundary, which has been stable for a century, stands in sharp contrast to the fluctuating northern range limits observed on both sides of the North Atlantic (Glude 1955, Welch 1968, Beukema 1991). Third, the variation in abundance of *Carcinus maenas* within the overlapping ranges of these two species was explained by *Callinectes sapidus* abundance, not temperature (Appendix A, Table A1). Fourth, a similar result was observed in Waquoit Bay, Massachusetts, which controlled for broader-scale differences across bays.

We hypothesize that temperature operates synergistically with predation to establish a southern limit to *Carcinus maenas* distribution. Predation pressure on *Carcinus maenas* may vary across latitudes due to temperature-dependent changes in *Callinectes sapidus* abundance and activity levels, such as feeding behavior and rate (Williams 1984, Bergman 1987, Hines et al. 1990, Rome et al. 2005). Thus, per capita feeding rate of *Callinectes sapidus* and the portion of a year with relatively high feeding rates should increase from north to south. The combination of high temperature and predation may affect *Carcinus maenas* distribution due to prey behavior as well. Escaping *Callinectes sapidus* or foraging in less productive patches to avoid this crab could decrease the energy budget available to *Carcinus maenas* for tolerating suboptimal conditions such as warm water.

Overall, we suggest that predation is the most important factor but that the combination of temperature and predation pressure also may be important to establishing the geographic distribution and abundance of *Carcinus maenas* in the northeastern Atlantic. Further resolution requires experimental analyses to explicitly test the direct and indirect effects of temperature on *Carcinus maenas* reproduction, growth, behavior, and predation risk.

Potential roles of other factors

Several factors not addressed in our analyses may contribute to the distribution pattern of *Carcinus maenas* along eastern North America. The primary goal of our study was to test whether predation was a viable hypothesis. Although strong evidence exists for the importance of predation, it does not preclude the potential influence of other factors.

Ocean currents affect larval recruitment and could present a hard barrier to dispersal (Underwood and Denley 1984, Roughgarden et al. 1988). However, the distribution of *Carcinus maenas* stops well north of Cape Hatteras, a recognized biogeographic boundary with shifts in currents that may prevent recruitment. Other introduced species, such as the crab *Hemigrapsus sanguineus*, have successfully colonized Chesapeake Bay and North Carolina from the north. It is similarly unlikely that flow-induced dispersal barriers (Gaylord

and Gaines 2000) would generate the across- and within-bay abundance patterns observed.

Rocky substrate is common along the New England coast but is rare south of Long Island. Structure provided by rocks is used by *Carcinus maenas*, especially new recruits, to escape predation. Therefore, the geographic shift in rock availability and hence the decreased availability of suitable recruitment grounds south of New York could be responsible for the southern range limit of *Carcinus maenas*. However, we found a large population of *Carcinus maenas* in southern New Jersey marshes that did not have natural rocky substrate nearby (none within 2° latitude). Similarly, the strong reciprocal relationship between *Carcinus maenas* and *Callinectes sapidus* in Waquoit Bay cannot be attributed to this latitudinal change in rocky substrate.

Torchin et al. (2002) have shown that introduced species have fewer parasite species and a lower prevalence than conspecifics in their native regions. However, Torchin et al. (2001) found a striking paucity of metazoan parasites, native or nonnative, from *Carcinus maenas* along eastern North America. Thus, there is no evidence for an effect of parasites on the observed distribution pattern.

Carcinus maenas competes with other decapods for food or structure (Crothers 1970, McDonald et al. 2001, Jensen et al. 2002), and resource competition could affect their geographic distribution. While the recently introduced crab *Hemigrapsus sanguineus* (McDermott 1991) has competitively displaced *Carcinus maenas* from rocky habitats in New England (Lohrer and Whitlatch 2001, Jensen et al. 2002), the stable southern range boundary of *Carcinus maenas* predates the *H. sanguineus* introduction. Furthermore, *Carcinus maenas* remained numerically dominant in soft-sediment areas throughout their overlapping ranges (Walton 2003). Despite the high potential for *Callinectes sapidus* to compete with *Carcinus maenas* for food, *Callinectes sapidus* did not outcompete *Carcinus maenas* for *M. balthica* clams in our laboratory experiment.

We do not mean to refute these alternative hypotheses, as we did not collect data to test them. Instead, we simply wish to indicate that a clear mechanism between these other factors and the observed distribution patterns for *Carcinus maenas* is not presently evident to us.

Conclusions

The southern distribution of the European green crab *Carcinus maenas* along the eastern United States appears to be affected strongly by predation. More specifically, our results support the hypothesis that predation by the native crab *Callinectes sapidus* has a significant effect on the abundance of *Carcinus maenas*, with increasing effects at the southern end of the range. We expect that several other factors may influence the abundance of *Carcinus maenas* in this region,

as in other studies (Case and Taper 2000, Gross and Price 2000). However, in this case, it appears that these other factors may operate interactively to reinforce a key role of predation in setting the southern range limits. To our knowledge, there are no other documented examples of biotic resistance whereby a native species limits the geographic range of an introduced species, in coastal ecosystems or elsewhere.

Analysis of temporal changes in temperature and in *Callinectes sapidus* abundance and range may further illuminate the effects of temperature and predation on *Carcinus maenas*. The abundance and range of many marine species fluctuate with cyclic changes in sea temperature (e.g., Southward et al. 1988, Sauriau 1991), and the range and impact of *Callinectes sapidus* should also vary with climate. Our data predict that an increase in sea surface temperature and a corresponding expansion of the *Callinectes sapidus* range would decrease *Carcinus maenas* abundance in the southern part of its range. In contrast, a decrease in *Callinectes sapidus* abundance, such as a continuation of the documented recent declines in Chesapeake Bay (Abbe and Stagg 1996, Lipcius and Stockhausen 2002), could allow range expansion of *Carcinus maenas* and a consequent trophic cascade in this bay.

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LITERATURE CITED

- Abbe, G. R., and C. Stagg. 1996. Trends in blue crab (*Callinectes sapidus* Rathbun) catches near Calvert Cliffs, Maryland, from 1968 to 1995 and their relationship to the Maryland commercial fishery. *Journal of Shellfish Research* 15:751–758.
- Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* 3:246–255.
- Bergman, E. 1987. Temperature-dependent differences in foraging ability of two percids *Perca fluviatilis* and *Gymnocephalus cernuus*. *Environmental Biology of Fishes* 19:45–54.
- Berrill, M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *Journal of Crustacean Biology* 2:31–39.
- Beukema, J. J. 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold

- and mild winters. *Journal of Experimental Marine Biology and Ecology* **153**:97–113.
- Buchanan, J. B. 1984. Sediment analysis. Pages 41–65 in N. A. Holme and A. D. McIntyre, editors. *Methods for the study of marine benthos*. Blackwell Scientific, Boston, Massachusetts, USA.
- Byers, J. E. 2002. Physical habitat attribute mediates biotic resistance. *Oecologia* **130**:146–156.
- Carlton, J. T., and A. N. Cohen. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography* **30**:1809–1820.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA* **87**:9610–9614.
- Case, T. J. 1991. Invasion resistance, species build-up, and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* **42**:239–266.
- Case, T. J., and M. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *American Naturalist* **155**:583–605.
- Caughley, G., D. Grice, R. Barker, and B. Brown. 1988. The edge of the range. *Journal of Animal Ecology* **57**:771–785.
- Clark, M. E., T. G. Wolcott, D. L. Wolcott, and A. H. Hines. 1999. Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology* **233**:143–160.
- Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* **40**:49–78.
- Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion resistance in experimental grassland: species richness or species identity. *Ecology Letters* **2**:140–148.
- Crothers, J. 1970. The distribution of crabs on rocky shores around the Dale Peninsula. *Field Studies* **3**:263–274.
- Dittel, A. I., A. H. Hines, G. M. Ruiz, and K. K. Ruffin. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science* **57**:902–916.
- Everett, R. A., and G. M. Ruiz. 1993. Coarse woody debris as refuge from predation in aquatic communities: an experimental test. *Oecologia* **93**:475–486.
- Ford, S. D. 1996. Range extension by the oyster parasite *Perkinsus marinus* into northeastern United States: Response to climate change? *Journal of Shellfish Research* **15**:45–56.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* **155**:769–789.
- Glude, J. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *Transactions of the American Fisheries Society* **84**:13–26.
- Grosholz, E. D., and G. M. Ruiz. 2003. Biological invasions drive size increases in marine and estuarine invertebrates. *Ecology Letters* **6**:700–705.
- Gross, S., and T. K. Price. 2000. Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography* **27**:869–878.
- Harvey, B. C., R. C. Cashner, and W. J. Matthews. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *Journal of Fish Biology* **33**:481–487.
- Heck, K. L. J., and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* **53**:125–134.
- Herbold, B., and P. B. Moyle. 1986. Introduced species and vacant niches. *American Naturalist* **119**:751–760.
- Hines, A. H., A. M. Haddon, and L. A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series* **67**:105–126.
- Hines, A. H., and G. M. Ruiz. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bulletin of Marine Science* **57**:884–901.
- Jensen, G. C., P. S. McDonald, and D. A. Armstrong. 2002. East meets west: competitive interactions between green crab *Carcinus maenas*, and native introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* **225**:251–262.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**:199–204.
- Lipcius, R., and W. Stockhausen. 2002. Simultaneous decrease in abundance, female size and biomass of the blue crab spawning stock in Chesapeake Bay. *Marine Ecology Progress Series* **226**:45–61.
- Lohrer, A. N., and R. B. Whitlatch. 2001. Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Marine Ecology Progress Series* **227**:135–144.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Maron, J. L., M. Vilà, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. *Ecological Monographs* **74**:261–280.
- McDermott, J. 1991. A breeding population of the western pacific crab *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae) established on the Atlantic coast of North America. *Biological Bulletin* **181**:195–198.
- McDonald, P. S., G. C. Jensen, and D. A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology* **258**:39–54.
- Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* **51**:429–450.
- Mitchell, C. E., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* **421**:625–627.
- Peterson, C. H., and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Marine Ecology Progress Series* **111**:289–297.
- Pile, A. 1993. Effects of habitat and size-specific predation on the ontogenetic shift in habitat use by newly settled blue crabs. Thesis. College of William and Mary, Williamsburg, Virginia, USA.
- Pimm, S. L. 1989. Theories predicting success and impact of introduced species. Pages 351–365 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Posey, M. H., and A. H. Hines. 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology* **72**:2155–2169.
- Raffaelli, D., A. Conacher, H. McLachlan, and C. Emes. 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuarine, Coastal and Shelf Science* **28**:149–160.

- Reusch, T. B. H. 1998. Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. *Marine Ecology Progress Series* **170**:159–168.
- Robinson, J. V., and G. A. Wellborn. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: fish predation effects. *Oecologia* **77**:445–452.
- Rome, M. S., A. C. Young-Williams, G. R. Davis, and A. H. Hines. 2005. Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). *Journal of Experimental Marine Biology and Ecology* **319**:129–145.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* **241**:1460–1466.
- Ruiz, G. M., and J. T. Carlton. 2003. Invasive species: vectors and management strategies. Island Press, Washington, D.C., USA.
- Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99**:1–16.
- Sauriau, P. G. 1991. Spread of *Cyclope neritea* (Mollusca: Gastropoda) along the north-eastern Atlantic coasts in relation to oyster culture and to climatic fluctuations. *Marine Biology* **109**:299–309.
- Southward, A. J., G. T. Boalch, and L. Maddock. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to changes in climate since the 16th century. *Journal of the Marine Biological Association of the United Kingdom* **68**:423–445.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* **286**:1577–1579.
- Thresher, R., C. Proctor, G. Ruiz, R. Gurney, C. MacKinnon, W. Walton, L. Rodriguez, and N. Bax. 2003. Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. *Marine Biology* **142**:867–876.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**:1455–1474.
- Torchin, M. E., K. D. Lafferty, and A. M. Kuris. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* **3**:333–345.
- Torchin, M. E., K. D. Lafferty, and A. M. Kuris. 2002. Parasites and marine invasions. *Parasitology* **124**:S137–S151.
- Torchin, M. E., K. D. Lafferty, V. J. McKenzie, and A. M. Kuris. 2003. Introduced species and their missing parasites. *Nature* **421**:628–630.
- Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. R. J. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- von Suter, W. 1982. Der einfluss von wasservögeln auf populationen der wandermuschel (*Driessena polymorpha* Pall.) am untersee Hochrhein (Bodensee). *Schweizerische Zeitschrift für Hydrologie* **44**:149–161.
- Walton, W. 2003. Ecology of invasive populations of the European green crab *Carcinus maenas*. Dissertation. University of Maryland, College Park, Maryland, USA.
- Welch, W. R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. *Fishery Bulletin of the U.S. Fish and Wildlife Service* **67**:337–345.
- Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., USA.
- Wilson, K. A., K. L. Heck, Jr., and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fishery Bulletin* **85**:53–58.
- Wolfe, L. M. 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalist* **160**:705–711.
- Zimmer-Faust, R. K., D. R. Fielder, K. L. Heck, Jr., L. D. Coen, and S. G. Morgan. 1994. Effects of tethering on predatory escape by juvenile blue crabs. *Marine Ecology Progress Series* **111**:299–303.

APPENDIX A

Statistical tables for analyses described in the main text are available in ESA's Electronic Data Archive: *Ecological Archives* E086-185-A1.

APPENDIX B

Additional enclosure results (entering and exiting traps with heterospecifics) are available in ESA's Electronic Data Archive: *Ecological Archives* E086-185-A2.