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Effect of predation by the invasive crab *Hemigrapsus sanguineus* on recruiting barnacles *Semibalanus balanoides* in western Long Island Sound, USA

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ABSTRACT: Since its introduction fewer than 20 yr ago, the spread of the Asian shore crab *Hemigrapsus sanguineus* along the east coast of the US has been remarkable. By many accounts it is now the numerically dominant brachyuran in rocky intertidal sites in Long Island Sound. Evidence from several laboratory studies has suggested that *H. sanguineus* could have significant consequences for barnacle abundance and distribution. In this study we used field caging experiments to determine the effect of this invader on recruitment (sampled at weekly intervals) of the indigenous barnacle *Semibalanus balanoides*. We found that although *H. sanguineus* readily consumed settling cypris larvae and early post-settlement juveniles, crab predation did not have a negative impact on barnacle recruitment when predator density was low (15 crabs 0.25 m^{-2}). We also found a measurable decrease in barnacle density at medium (45 crabs 0.25 m^{-2}) and high (90 crabs 0.25 m^{-2}) predator densities after the larval settlement period had ended, but this effect was short-lived. Based on available estimates of Asian shore crab abundance in Long Island Sound, we conclude that crab predation will not have a significant impact on the recruitment success of *S. balanoides* populations.

KEY WORDS: *Hemigrapsus sanguineus* · Asian shore crab · Predation impact · Caging study · *Semibalanus balanoides* · Barnacles · Recruitment · Long Island Sound

INTRODUCTION

As the numbers of documented occurrences of marine and estuarine invasions by nonindigenous species increase, there is growing concern among ecologists that these invasions pose a serious biological threat with potentially harmful consequences for the ecology of invaded environments (Cohen & Carlton 1998). In some instances, dramatic changes in prey species abundance and alterations in community structure and function have resulted when exotic species have become numerically dominant in invaded communities (Nichols et al. 1990, Lambert et al. 1992, Travis 1993, Grosholz et al. 2000). For the majority of recent marine invasions, however, it is less clear what effect, if any, will be felt on the distribution and abundance of native species, because experimental field tests designed to demonstrate and quantify their effects are rare.

The Asian shore crab *Hemigrapsus sanguineus* is a recent and particularly successful introduction to the east coast of the United States. It was first observed in New Jersey in 1988 (Williams & McDermott 1990) and now ranges from Maine to North Carolina. In less than 20 yr, it has become the most abundant crab species of many rocky intertidal habitats in Long Island Sound (Lohrer & Whitlatch 2002, Ahl & Moss 1999). The remarkable success of this invader is probably due to

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its large reproductive capacity and extended spawning season (Fukui 1988, McDermott 1998a), the wide dispersal of its planktonic larvae (Parks et al. 2004), high adult mobility (Brousseau et al. 2002), and adaptability to a broad range of environmental conditions (Gerard et al. 1999).

As an opportunistic omnivore, *Hemigrapsus sanguineus* consumes widely diverse prey including small invertebrates such as amphipods, bivalves, barnacles, gastropods, and polychaetes, as well as macroalgae and detritus (Lohrer & Whitlatch 1997, Brousseau et al. 2000). It is particularly adept at scraping food from hard surfaces (McDermott 1998b), but it can crush or chip open small shelled prey. In the laboratory *H. sanguineus* has a demonstrable impact on juvenile shellfish prey (Brousseau & Baglivo 2001, Lohrer & Whitlatch 2002, Bourdeau & O'Connor 2003) and the green crab *Carcinus maenas* (Jensen et al. 2002). Microcosm experiments run under laboratory and natural conditions also show that predation by *H. sanguineus* causes significant declines in juvenile mussels, barnacles, and ephemeral algae (Tyrrell et al. 2006). While some investigators have suggested that Asian shore crab impact will be minimal, others have predicted negative effects from crab predation and grazing. It remains unclear, however, if the observed competitive and predatory behavior of *H. sanguineus* has an impact on the abundance and distribution of these species in nature.

Caging experiments have been widely used in marine ecology to measure the importance of predation on rocky shores (Paine 1966, Connell 1970, Lubchenko & Menge 1978), in benthic soft-sediment environments (Thrush 1986, Fishman & Orth 1996, Armitage & Fong 2006, Moksnes & Heck 2006), on fouling assemblages (Brown & Swearingen 1998), and by nonindigenous species (Grosholz et al. 2000, Walton et al. 2002 Lohrer & Whitlatch, 2002). Since barnacles are important space competitors and dominant organisms in structuring the intertidal zone, it is important to understand the role of nonindigenous species such as *Hemigrapsus sanguineus* in controlling barnacle population dynamics.

Recruitment is defined here as the combined result of larval settlement and early post-settlement mortality (for discussion see Minchinton & Scheibling 1993), both of which are influenced by physical and biological factors. Our study was conducted during the spring recruitment period of *Semibalanus balanoides* using settling plates to capture naturally-occurring cypris larvae. Since annual barnacle recruitment in this region is both consistent and predictable (Lang & Ackenhusen-Johns 1981, and authors' pers. obs.) there was no need to artificially manipulate prey density (as is often required in studies of this sort). Consequently, our experimental design allowed us to assess effects of crab predation in a dynamic system controlled solely by natural recruitment processes. In this study, we designed and conducted field caging experiments to assess the impact of *Hemigrapsus sanguineus* predation on recruitment of the barnacle *S. balanoides* in western Long Island Sound.

MATERIALS AND METHODS

Caging experiments. From 2003 to 2005 we conducted a series of caging experiments to determine the effects of the invasive crab *Hemigrapsus sanguineus* on recruitment (settlement and early post-settlement survival) of the native barnacle *Semibalanus balanoides*. All experiments were conducted in the mid-intertidal zone at the mouth of Black Rock Harbor, Bridgeport, Connecticut (41° 08.8' N latitude, 73° 13.5' W longitude). This site is characterized by a gently sloping tidalflat densely covered with rocks of various sizes. A seawall constructed of large boulders forms the shoreward boundary of the study area. Natural crab densities at the site were determined along 2 vertical transects within the intertidal zone by counting all Asian shore crabs present within a metal frame (0.25 m^2) placed on the substrate at each haphazardly-determined sampling point ($N = 15$).

Caging experiments were conducted in each of the 3 yr from April to mid-June. We used different cage treatments to test the null hypothesis that Asian shore crab predation has no effect on annual barnacle recruitment. In 2003 and 2004 enclosure treatments (crabs added; 15 $cage^{-1}$) were used to measure predation effects of the shore crabs on barnacles. Exclosure cages (with crabs removed) measured background mortality in the absence of shore crab predators too large to enter the cages (~12 mm). Open plots (no cages) were used to measure natural mortality and partial cages tested for possible cage artifacts. These treatments also allowed us to account for any potential cage effects on barnacle larval settlement from the plankton. In 2005 we tested for the effects of predator density on barnacle recruitment. Treatments included exclosure cages (crabs removed) and enclosure cages at low crab density (15 $cage^{-1}$), medium crab density (45 $cage^{-1}$), and high crab density (90 $cage^{-1}$).

Four replicates of each treatment were used in all experiments. Vinyl-coated wire mesh (10 mm) open-bottomed cages with a single, hinged access door on top were used. The cages were buried in the sediment to an approximate depth of 10 cm resulting in an enclosed area of 0.6 × 0.4 × 0.2 m high. All cage and open plot treatments were placed approximately 1 m apart using a Latin square pattern.

Prior to the start of each experiment, Plexiglas™[1] settling plates (35.5 × 22.5 cm), each with 8 rectangles (7.5 × 5.0 cm) of 3-M™ non-skid tape were placed in each cage and open plot. Previous studies in the laboratory had shown non-skid tape to be an effective 'settling surface' for *Semibalanus balanoides* larvae and it provided a uniform surface area for comparisons. Once barnacle settlement had occurred (usually within 1 wk of field placement), tagged crabs were added to the enclosure cages. Experimental crabs were collected by hand haphazardly from the field site and were representative of the general size distribution and sex ratio of the natural population. Crabs smaller than 12 mm were excluded since these crabs could pass through the mesh openings of the cages. Crabs were returned to the Milford Laboratory for tagging and each crab was marked by gluing with cyanoacrylate a small color/shape-coded plastic tag to the carapace. Recovery rates were estimated by counting the number of tagged crabs present in the enclosure cages at the end of each experiment. For all tagged crabs, maximum carapace width (CW) was measured to the nearest 0.1 mm with Vernier calipers and sex was determined. Mean CW of crabs collected from the natural population and used in the experiments was 17.8 ± 0.3 SE in 2003, 22.9 ± 1.7 SE in 2004, and 17.9 ± 0.2 SE in 2005. Overall the CW of crabs collected in all years ranged from 13.7 to 38.5 mm. The sex ratio of crabs in 2003 was approximately 2:1; in 2004, 4.5:1; and in 2005, 2.2:1. Only crabs whose chelae and other appendages were intact were used. Crabs were held overnight in running seawater and placed in cages the following day. Prior to release, caged plots were cleared of all visible *Hemigrapsus sanguineus*.

Once a week, all settling plates were photographed in the field using a digital camera. Numbers of live barnacles attached to the 8 'settling surfaces' on each plate were determined by counting from printed digital images. These weekly counts were cumulative in that they included both newly settled cyprids and those which had successfully settled and recruited to the plates during the experimental period. The mean maximum basal diameter of *Semibalanus balanoides* at the end of each experiment was 2.48 ± 0.11 mm. Because of noticeable fouling of the settling plates by green macroalgae (primarily *Ulva* sp.) at the termination of the experiment in 2005, we returned the plates to the laboratory to determine relative amounts of algae in each experimental treatment. We used a transparent dot grid (N = 192) superimposed on the settling surface to estimate percentage algal cover. Upon conclusion of each experiment, all tagged and untagged *Hemigrapsus sanguineus* were removed from the cages and counted.

Diet analysis. During the experimental period, wild crabs (8.8 to 38.3 mm CW) were collected weekly during low tide from the area immediately adjacent to the experimental site. On collection day, stomachs were removed from live crabs and their contents flushed with seawater into a Petri dish and examined under a dissecting microscope to determine food type. Cypris larvae were counted and the presence of barnacle shell fragments was noted. Sample sizes ranged from 20 to 50 crabs. In 2005, stomachs of experimental crabs (N = 34) retrieved from cages at the end of caging experiments were also analyzed for content.

Statistical analysis. Counts of barnacles from the 8 settling surfaces on each plate were averaged to produce 1 value for each of the 4 replicate experimental units of each treatment. Data were tested for normality and homogeneity of variance. When these assumptions were met, 1-way ANOVA ($\alpha = 0.05$) was used to compare barnacle density and percentage cover of macroalgae on the settling plates in the different treatments. Post-hoc comparisons were made using Student-Newman-Keuls tests. In the few cases when data did not meet the assumptions of ANOVA, a non-parametric Kruskal-Wallis analysis of variance on ranks was used for comparison. All analyses were performed using SigmaStat 3.1 software (Systat Software).

RESULTS

Caging experiments

In 2003, the beginning of the experiment coincided with the active larval settlement period of *Semibalanus balanoides*. Initial *Hemigrapsus sanguineus* densities of 15 crabs 0.25 m^{-2} within enclosure cages approximated natural Asian shore crab density on the tidalflat within the immediate study area (10 ± 1.3 crabs 0.25 m^{-2}). Mean recovery rate of tagged crabs within enclosures at the end of the experiment was 85%. Statistical comparison of all treatments combined (enclosure, exclosure, partial, open) showed a statistically significant difference in barnacle density on the initial sampling date only (Fig. 1a). This was due to significantly higher barnacle density in open plots than in the cage treatments ($F = 4.78$, df = 3,12, $p = 0.02$), suggesting cage interference with larval settlement onto the plates. This apparent cage effect disappeared after the first week and there was no measurable difference in barnacle density among treatments ($p > 0.05$) throughout the remainder of the active settlement and early post-settlement period.

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[1] Use of trade names does not imply the endorsement of the National Oceanic and Atmospheric Administration

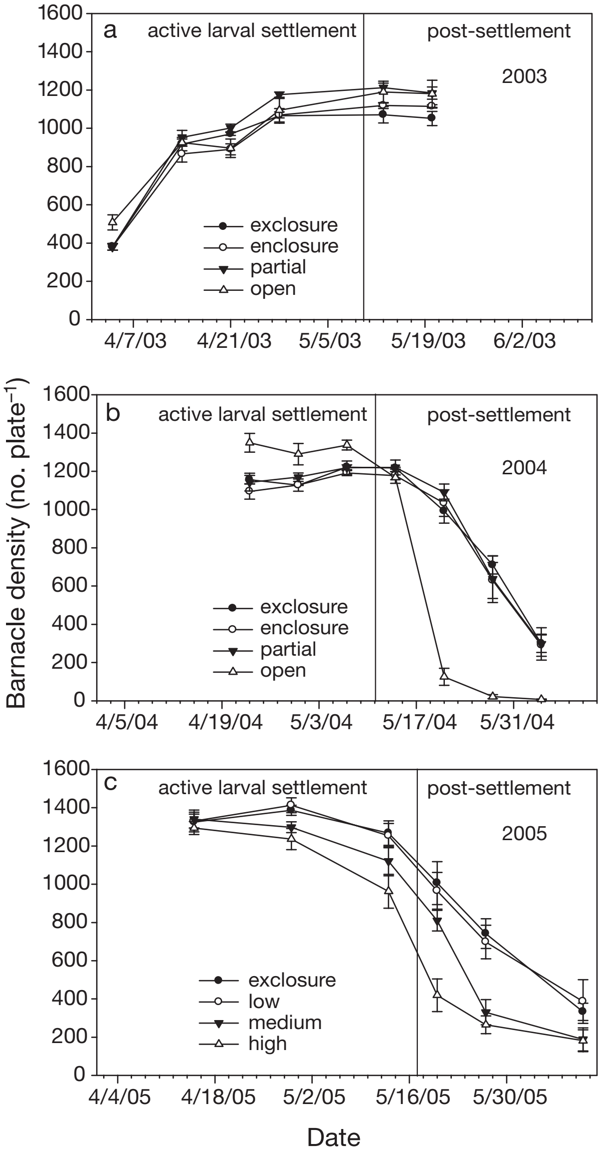

Fig. 1. *Hemigrapsus sanguineus* and *Semibalanus balanoides.* Mean (±SE) barnacle density in 4 experimental treatments (predator exclosure, predator enclosure [15 crabs 0.25 m^{-2}], partial cages, and open cages) on each sampling date in (a) 2003, (b) 2004, and (c) predator exclosure and enclosure (low, medium, and high = 15, 45, and 90 crabs 25 m^{-2}, respectively) in 2005. Vertical line marks observed transition from active larval settlement to post-settlement phase during the barnacle recruitment period. Dates = mo/d/yr

In 2004, the experiment began later in April than the previous year, but extended an additional 2 wk into the barnacle post-settlement period. Initial crab densities were the same as in 2003, but the mean recovery rate of tagged crabs was slightly lower (75%). As in 2003, open plots had significantly more larval recruits than caged treatments during the settlement period ($p < 0.05$). On all post-settlement sampling dates, except the first (May 15), there were statistically significantly lower barnacle densities in the open treatments compared to the cage treatments (Fig. 1b). The lower barnacle post-settlement survival in open treatments may have been due to added predation pressure from other species, to lack of cage shading resulting in higher desiccation mortality, or both. When open treatments were removed from the analysis, no statistically significant differences in barnacle density were found among the cage treatments ($p > 0.05$).

In the 2005 experiment to test the effect of predator density, there was no statistically significant difference in barnacle density among treatments (exclosure, low, medium, high) during the larval settlement period on the first 2 sampling dates ($p > 0.05$), despite the 6-fold difference in initial crab densities (Fig. 1c). By the third sample date, May 13, differences in survival among the treatments began to emerge ($F = 2.67$, df = 3,12, $p = 0.043$). Post-hoc tests indicated statistically significantly lower barnacle densities in the May 20 and May 30 samples ($p < 0.05$) in the enclosures with high and medium crab densities after settlement ceased. At the end of the experiment, barnacle density was reduced by 70% in all treatments with no statistically significant differences ($p > 0.05$). Exclosure and low density predator treatments were not statistically significantly different throughout the entire experiment ($p > 0.05$). Mean crab recovery rate in all enclosures combined was 70%, but recovery rates among enclosure treatments varied. Percentage recovery increased in each treatment in relation to stocking density (low density = 86.5 ± 0.06 SE, medium density = 69.4 ± 0.06 SE, high density = 55.8 ± 0.09 SE).

Although not statistically significant ($F = 2.18$, df = 3, 12, $p = 0.143$), there was a strong trend of decreasing percentage cover of algae (*Ulva* sp.) on settling plates in relation to higher crab densities in the experimental treatments, probably caused by increased grazing activity. At the end of the experiment, percentage algal cover was 71.8 ± 22.6 SE in the exclosure treatment, 67.7 ± 18.7 SE in the low crab density treatment, 35.1 ± 12.3 SE in the medium crab density treatment, and 22.9 ± 7.3 SE in the high crab density treatment.

Diet analysis

Of the *Hemigrapsus sanguineus* examined, 86% (681 of 796) had consumed food before capture; the rest had empty stomachs when dissected. Food items found in crab diets varied in type and amount. In addition to barnacles *Semibalanus balanoides*, detritus, macroalgae, and juvenile polychaete worms were present in some crab stomachs. Cypris larvae appeared in 43.5% of crab stomachs sampled during April when data from all years were combined. They were absent from those sampled after the first week in May 2003 and the second week in May 2004 and 2005, signaling the end of settlement. Crushed barnacles (shells) were present in crab stomachs on every date sampled and were found in at least 45% of crabs from mid-April to mid-June. By the end of May, the numbers of crabs feeding on green algae increased dramatically, especially in 2003 and 2004. Experimental crab stomachs analyzed in 2005 contained similar proportions of the same food items as those of wild crabs collected on the same date (Fig. 2). Numbers of cypris larvae present in crab stomachs varied with sampling date, but averaged fewer than 10 crab^{-1} for all dates, with 1 exception (W3-Apr 03), when 2 crabs were found with more than 100 larvae in their stomachs (Fig. 3).

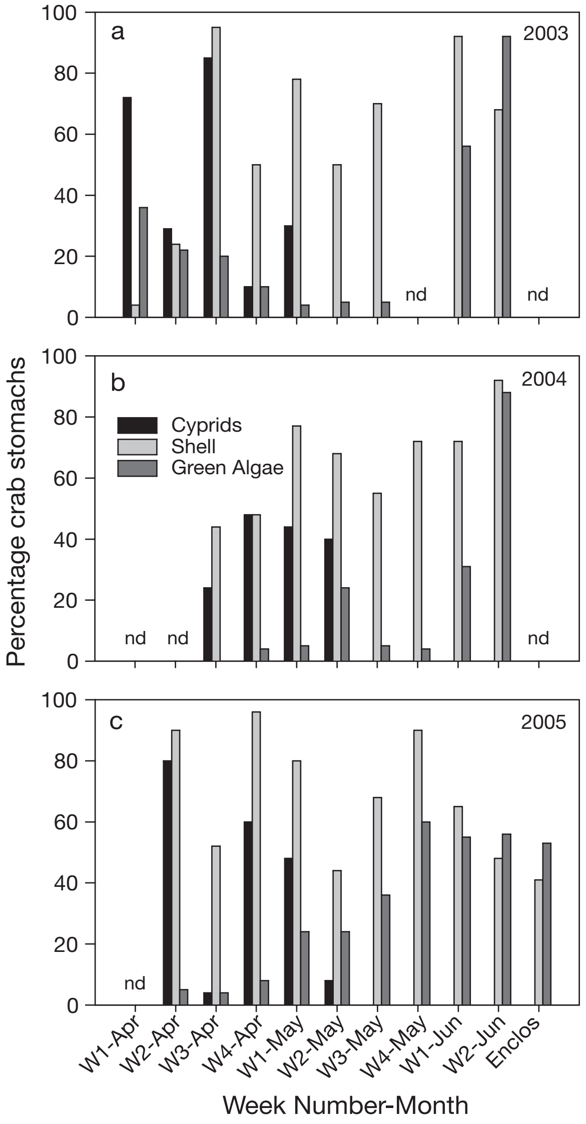

Fig. 2. *Hemigrapsus sanguineus* and *Semibalanus balanoides.* Percentage of crab stomachs analyzed weekly in (a) 2003, (b) 2004 and (c) 2005 containing 1 or more of the food items barnacle cyprids, barnacle shells, and green algae. Enclos = crabs from predator enclosure cages sampled on June 10, 2005; nd = no data

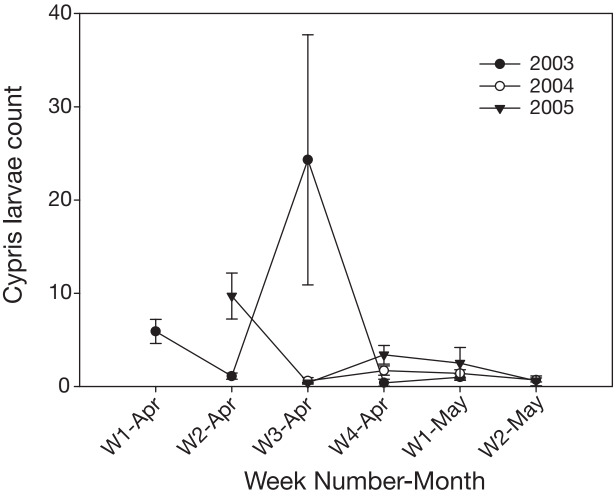

Fig. 3. *Hemigrapsus sanguineus* and *Semibalanus balanoides.* Mean (±SE) number of barnacle cypris larvae found in stomachs of crabs analyzed weekly during the larval settlement phase in 2003 to 2005. (No data available for W1-Apr 04, W2-Apr 04, W2-Apr 05)

DISCUSSION

The importance of biotic processes in determining the abundance and distribution of barnacles in rocky environments has been well documented (for reviews see Connell 1985, Rodriguez et al. 1993, Caley et al. 1996, Jeffrey 2003). Studies focusing on the role of predation in controlling barnacle recruitment success have shown that the impact of predation is dependent on predator type, barnacle species, and position on the shore relative to tidal height. Intertidal limpets and periwinkles affect barnacle recruits directly by 'bulldozing' them off the settling surface (Buschbaum 2000, Holmes et al. 2005) or inadvertently consuming them while grazing algae (Miller & Carefoot 1989). Exclusion experiments have shown that recruitment of the barnacle *Balanus crenatus* to subtidal mussel beds is strongly affected by green crabs *Carcinus maenas* and seastars *Asterias rubens*, but impacts of these non-molluscan predators on the intertidal barnacle, *Semibalanus balanoides* are minimal (Buschbaum 2002).

The Asian shore crab *Hemigrapsus sanguineus* resides primarily in the intertidal zone, where it seeks the shelter of rocks at low tide and emerges to feed when the tide is high. Laboratory observations confirm that the Asian shore crab readily removes recruited barnacles from substrate surfaces (rocks, settling plates) and consumes them (McDermott 1998b, D. J. Brousseau unpubl.). Because of its small size (generally <50 mm CW), however, it is capable of eating only juvenile shelled prey (Brousseau & Baglivo 2001), suggesting that the greatest predation impact in natural populations would occur early in the barnacle life cycle. In western Long Island Sound the recruitment period of *Semibalanus balanoides* overlaps with the onset of the seasonal activity cycle of *H. sanguineus* in mid- to late March. Our diet analyses indicate that the majority of dissected crabs had cyprids and/or barnacle shells in their stomachs, pointing to the importance of both larval and early postlarval barnacles as a food source for crabs at a time of the year when the diversity of other available food items (i.e. barnacles, algae, clamworms, detritus) is low.

Despite such evidence supporting the hypothesis that *Hemigrapsus sanguineus* predation is a potentially important process in determining barnacle recruitment success, our caging studies revealed little or no effect on barnacle recruitment at the crab densities tested. Barnacle density on the settling plates increased over time in almost all treatments during the settlement periods in each of the 3 yr. In addition, no statistically significant difference was found among predator enclosures and exclosure treatments, indicating that feeding activity by *H. sanguineus* has no measurable effect on cyprid recruitment. Although grazed areas were visible on the settling plates on each sampling date, there was photographic evidence that the empty space was subsequently utilized by new recruits. The effect of cyprid removal by crabs was offset by recolonization, suggesting that an abundant planktonic larval supply is an effective barnacle adaptation to minimize the effects of predation pressure on settling barnacle larvae.

A negative impact on barnacle survival was measured after larval settlement had ended, but the effect was temporary and highly dependent on predator density. During the last 2 wk in May 2005, post-settlement survival in moderate and high density enclosures was statistically significantly lower than that in exclosure cages. By early June, however, this predation effect had disappeared, resulting in no lasting impact on barnacle density. No effect on barnacle survival in low density cages was observed in either 2004 or 2005. After active larval settlement had ended, the gradual decline in barnacle survival in the low and predator exclusion cages approximated a rate of background mortality in nature resulting from biotic and abiotic factors.

The low to moderate density of Asian shore crabs at our experimental site (40 crabs m^{-2}) is similar to that reported for other sites in Long Island Sound (New Haven: 2.6 to 5.6 crab m^{-2}, Hammonasset: 17.9 crabs m^{-2}, Lohrer & Whitlatch 1997; Greenwich Point: 22.8 crabs m^{-2}, Ahl & Moss 1999; Crane Neck Point: 7.1 to 10.3 crabs m^{-2}, Gerard et al. 1999). Based on our experiments, we predict that little impact on barnacle population size and/or distribution would be expected at any of these sites. At 1 site in eastern Long Island Sound where reported maximum crab densities often exceed 150 crabs m^{-2} (Millstone Point; Lohrer & Whitlatch 2002), Asian shore crab predation could potentially cause modest decreases in barnacle abundance in intertidal communities.

Non-quantitative estimates of relative food abundance derived from stomach content analyses show that Asian shore crabs take advantage of the availability of barnacle food items (cyprids and post-metamorphic juveniles) during the spring months. Since crab predation pressure in spring may not be as intense as it is later in the year because of decreased metabolic activity resulting from lower water temperatures, the timing of barnacle recruitment may help reduce predation impacts. In June (Fig. 2) and throughout the summer, an increased number of crabs eat algal species, suggesting that the diet of Asian crabs broadens as additional food items become available and feeding pressure intensifies. By the end of July, the number of crabs with barnacles in their diet has decreased considerably (<20% in 2003 to 2005; D. J. Brousseau unpubl.). Studies in the laboratory have shown that increased crab density also leads to increased diet breadth in *Hemigrapsus sanguineus* (Brousseau & Baglivo 2005). The trend of decreased algal cover on settling plates in cage enclosures at the end of our study supports the occurrence of a diet shift in the field. Crab dependence on barnacles would be expected to diminish as juvenile barnacles approach a size-refuge from predation.

It is well documented that populations of the invasive Asian shore crab *Hemigrapsus sanguineus* have exploded in rocky intertidal habitats in eastern Long Island Sound. Lohrer & Whitlatch (2002) report average densities exceeding 70 crabs m^{-2} and a numerical dominance of >90% over other crabs in several areas in this region. Because of these alarming statistics, many have hypothesized that this invader is likely to cause substantial ecological changes in the resident marine benthic community. In a manipulative field study comparing the relative impacts of 2 exotic species on native blue mussels *Mytilus edulis*, Lohrer & Whitlatch (2002) found *Carcinus maenas* to have the higher prey consumption rates, but speculated that impact by *H. sanguineus* would be more important from a blue mussel population standpoint, because of this crab's extraordinary abundance in some intertidal locations. The results of our study do not support this conclusion for the impact of the invasive crab on barnacle recruitment, and emphasize the need for specific process-oriented studies.

The Asian shore crab invasion is arguably the most significant by a brachyuran predator of the NE coast of North America since the introduction of the green crab *Carcinus maenas* almost 200 yr ago. This invasion has been viewed by some as a potentially influential structuring force in rocky intertidal communities of this region. Our study has shown, however, that despite its numerical dominance and opportunistic feeding behavior, *Hemigrapsus sanguineus* has only transitory effects on barnacle recruitment. While future studies may show *H. sanguineus* to be a risk to other organisms of rocky intertidal environments, we conclude that at present population levels crab predation will not have a significant negative impact on recruitment success in *Semibalanus balanoides* populations in western Long Island Sound.

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