Stock Enhancement and Carrying Capacity of Blue Crab Nursery Habitats in Chesapeake Bay

ROCHELLE D. SEITZ, ROMUALD N. LIPCIUS, KATHLEEN E. KNICK, MICHAEL S. SEEBO, W. CHRISTOPHER LONG, BRYCE J. BRYLAWSKI, and ALISON SMITH
Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, Virginia, USA

Declining populations of the blue crab, Callinectes sapidus, may be suitable for enhancement with hatchery-reared juveniles. For three years, field experiments were conducted to determine if shallow, unvegetated, marsh-fringed nursery habitats in lower Chesapeake Bay are below carrying capacity and thus capable of supporting additional juvenile crabs. The field experiments included sampling of wild and hatchery-reared juvenile blue crabs and their major benthic prey, and manipulative experiments to assess the survival of juvenile crabs and the abundance of benthic prey in enhanced and control coves. Densities of the clam Macoma balthica, a major prey of the blue crab, were initially high in enhanced coves and decreased to a level equivalent to that in control coves by the end of the experiment, but always remained well above a low-density threshold. Survival of juvenile crabs was lowest where clam densities were highest, suggesting that alternative prey did not deter predation on juvenile crabs, but instead led to higher densities of cannibalistic crabs through bottom-up control. Crab densities correlated with densities of major benthic prey and prey density never dropped below a low-density threshold. Marsh-fringed nurseries are apparently below carrying capacity for the blue crab and could be enhanced through the release of hatchery-reared juveniles.

Keywords: clams, benthos, bottom-up control, alternative prey, carrying capacity, Callinectes sapidus

INTRODUCTION

The blue crab, Callinectes sapidus Rathbun (Arthropoda: Crustacea: Portunidae), is abundant throughout Chesapeake Bay and is dispersed widely along the Atlantic and Gulf coasts of North America (Norse, 1977; Williams, 1984; Hines et al., 1987; Lipcius and Van Engel, 1990). The blue crab plays an important role both ecologically and economically in Chesapeake Bay. Blue crabs are benthic omnivores and are preyed upon by higher-order carnivores, thus facilitating energy transfer and benthic-pelagic coupling in estuaries (Baird and Ulanowicz, 1989). The blue crab is exploited extensively and supports one of the largest crustacean fisheries in the world, with the bulk of the landings coming from the Chesapeake Bay region (Miller et al., 2005). Exploitation rates have increased substantially in this decade, resulting in a decrease in total catch-per-unit effort in both the pot and winter dredge fisheries (Miller et al., 2005). Furthermore, the spawning stock has concurrently decreased by 84%, suggesting that the population is overexploited (Lipcius and Stockhausen, 2002). Now that the population is at such a low level, stock enhancement is being considered as one tool to increase spawning-stock abundance (Secor et al., 2002; Zohar, 2005; Stottrup and Sparrevohn, 2007).

One approach to stock enhancement of the blue crab in Chesapeake Bay involves supplementing nursery habitats with hatchery-reared juveniles, and it is therefore important to determine the carrying capacity of nursery habitats to ensure that they can sustain the increased numbers of juveniles. Carrying capacity is defined as “the maximal population size of a given species that an area can support without reducing its ability to support that species in the future” (Daily and Ehrlich, 1992). Specifically, it is a measure of the amount of renewable resources in terms of the number of organisms these resources can support (Roughgarden, 1979). The carrying capacity tends to be higher for larger or more productive areas, but it will vary depending...
on the species in question; animals that have lower resource requirements can be more easily supported in areas of lower productivity or resource availability. Though carrying capacity is well defined, it can be difficult to measure since many forcing factors control the carrying capacity. Here, we attempt to estimate carrying capacity of potential nursery habitats for blue crabs to predict if such habitats can support additional hatchery-reared crabs.

Blue crabs in Chesapeake Bay recruit and disperse into primary (seagrass beds) and secondary nursery habitats; typical secondary nurseries include shallow marsh-fringed unvegetated habitats (Lipcius et al., 2005, 2007; Seitz et al., 2005). Predators, food, habitat type or complexity, and physical transport can affect abundance of the blue crab in nursery habitats, and the relative importance of each is size dependent (Lipcius and Hines, 1986; Hines et al., 1990; Seitz et al., 2005; Lipcius et al., 2007). Recruitment is defined as the influx of young juveniles into the population’s nursery habitats after metamorphosis to the first juvenile instar, whereas secondary dispersal to alternative primary nurseries or to secondary nurseries is accomplished by slightly older juveniles (sensu Lipcius et al., 2007). Seagrass beds, where recruitment of small juveniles (<20 mm carapace width (CW)) is high, may provide a refuge from predation (Orth and van Montfrans, 1987; Pile et al., 1996; Lipcius et al., 2005, 2006), or elevated levels of food (Perkins-Visser et al., 1996; Clark et al., 1999a, b) and are thus excellent primary nurseries for small juveniles. Unvegetated habitats provide a secondary nursery habitat for larger juveniles (>30 mm) that have outgrown the protection afforded by seagrass beds (Lipcius et al., 2007). Moreover, seagrass beds are declining in Chesapeake Bay, thereby magnifying the relative importance of unvegetated habitats as nursery grounds. Predation, a top-down factor, is unlikely to control the distribution of large juvenile (>75 mm CW) and adult blue crabs, which obtain a size refuge from predation (Hines et al., 1990; Moody, 2001). However, food availability, a bottom-up factor, may be important in influencing the distribution and suitability of potential nursery habitats for young juveniles (Seitz et al., 2005).

Clams comprise up to 50% of the blue crab diet, while con-specifics, polychaetes, amphipods, and other benthic prey comprise the balance (Laughlin, 1982; Hines et al., 1990; Mansour and Lipcius, 1991; Mansour, 1992). The distance between prey patches, as well as patch density, may drive blue crab distribution at small scales (Clark et al., 1999a, b; Hines, 2007). Bivalves in Chesapeake Bay are a key component of the benthos and encompass up to 90% of the benthic prey biomass (Hagy, 2002); they are typically long lived and many species are considered “estuarine endemics” or residents (Boesch, 1977; Holland, 1985). Chesapeake Bay infaunal bivalve assemblages include major species such as the Baltic macon (Macoma balthica), the hard clam (Mercenaria mercenaria), and the stout razor clam (Tagelus plebeius) (Boesch, 1977; Holland, 1985).

High clam densities may increase juvenile blue crab survival by acting as alternative prey for the blue crab, which would decrease cannibalism, since large juvenile and adult blue crabs feed predominantly on clams where they are abundant (Seitz et al., 2005; Lipcius et al., 2007). The presence of alternative prey can reduce or eliminate predation on a target species if predators prefer or switch to the alternative prey (Svenning et al., 2005; Rickers et al., 2006). However, the benefits of alternative prey can be short-lived if predators prey first on the alternative prey, then proceed to prey on the target species once the alternative prey are depleted. Therefore, the target species may reap no net benefit over relevant time scales (Wong et al., 2005). In the case of “apparent competition” (sensu Bonsall and Hassell, 1997), whereby predators are attracted to a habitat due to the preferred alternative prey, the target species may actually suffer higher mortality than if the alternative prey were absent. Because of the importance of clams in the diet and as an alternative prey source for higher-order predators, we set out to examine infaunal abundance, concentrating on bivalves.

We focused on the productive shallow cove systems of Chesapeake Bay, where the high biomass of benthic prey attracts consumers (i.e., bottom-up control; Seitz et al., 2003, 2005), suggesting that the carrying capacity of these habitats is high. Our main objective in this 3-year study was to estimate carrying capacity of the shallow, unvegetated, subtidal zone of marsh-fringed coves to determine whether these secondary nurseries could support further enhancement. We examined this by comparing bivalve mortality in “enhanced” vs “control” coves, by examining the effects of predation upon the benthos in caged vs uncaged plots (in 2003), by projecting the population trajectory of major infaunal prey items over the course of the summer to determine whether they fell below a low-density threshold of 50 M. balthica per m² (Seitz et al., 2001), by examining the potential for benthic prey to serve as an alternative to cannibalism for juvenile crabs (in 2004), and by correlating juvenile crab abundance with prey availability to assess the possibility of bottom-up control (in 2005).

**STUDY AREAS AND METHODS**

In collaboration with The Smithsonian Environmental Research Center (SERC) and the Center of Marine Biotechnology (COMB), the Virginia Institute of Marine Science (VIMS) is examining the ecological effects of distributing hatchery-reared crabs into field locations in the upper Chesapeake Bay (SERC) and the lower Chesapeake Bay (VIMS) (Zohar et al., 2008). In 2003–2005, VIMS completed releases of 2–4 main batches per year of hatchery-reared crabs totaling approximately 50,000 juvenile crabs of ∼20 mm mean CW (range 10–50 mm). The hatchery crabs were tagged with microwire tags in the base of the swimming-leg muscle to allow differentiation between hatchery and wild crabs upon recapture. Subsequently, hatchery cohorts were released into small (10–100 ha) coves in the York River. Numbers of released crabs and release coves varied each year. During each study period, a set of shallow coves where no hatchery crabs were added served as control coves. Experimentally enhanced coves from one year may have served as controls.
in another year, and though this may have affected the overall number of crabs in the system initially, we always established baseline crab densities before enhancement.

Our study areas were in various coves of the York River, a 50 km-long subestuary of Chesapeake Bay (Figure 1). In 2003, we sampled 5 downriver sites—Aberdeen Mainstem, Aberdeen Cove, Eastern and Western Catlett Islands, and Timberneck Creek. Catlett West and Aberdeen Cove were enhanced with juvenile crabs. In 2003 we sampled during 5 periods, beginning May 16. The carrying capacity of each cove was assessed by examining the clam mortality rate over time using density at the 5 periods and fitting a 3-parameter exponential decay curve to the data. By projecting this curve into October, we were able to accommodate the full predation period of crabs and compare the estimated final clam densities with the low-density threshold of 12–50 clams/m² (Seitz et al., 2001).

In 2004, we sampled 4 upriver sites (Poropotank Bay, Purtan Bay, Ware Creek, and Taskinas Creek), as well as 5 downriver sites (Aberdeen Mainstem, Aberdeen Cove, Eastern and Western Catlett Islands, and Timberneck Creek). Catlett West was enhanced with juvenile crabs. In 2005, we sampled in Eastern and Western Catlett Islands, Timberneck, as well as Indian Field Creek, Felgates Creek, and King Creek. Timberneck Creek was enhanced with juvenile crabs. Within each cove, we had 6 replicate sampling locations for benthic suction cores and 6–20 replicate locations for crab scrapes.

Benthic infauna were sampled using a suction core, which samples a large surface area and penetrates ~40 cm into the sediment. This deep penetration is essential for accurate estimation of densities of large bivalves that dwell 30–40 cm in the sediment and are sparsely distributed (Hines and Comtois, 1985). The suction apparatus had an attached 1-mm mesh bag (Eggleston et al., 1992) and sampled within a cylinder of 0.17 m² (in 2003 and 2004) or 0.11 m² (in 2005) surface area to ~40 cm depth. The size of the cylinder did not affect the estimated densities of bivalves (R. Seitz, unpublished data). Bag contents were sieved on a 1-mm mesh screen and frozen. In the laboratory, the samples were sorted twice, and organisms were identified to the lowest possible taxonomic level (usually species) and enumerated. The biomass of bivalves was determined using length-weight regression curves (Seitz et al., 2006), while bulk ash-free dry weights (AFDWs) were obtained for polychaetes and crustaceans. For 2003–2004, only bivalve data are presented, as some of our benthic community samples were lost when Hurricane Isabel destroyed our lab building in 2003.

Abundance of crabs in all experimental coves was examined over several time frames using a modified crab scrape (1 m width) towed for 20 m at 6–20 replicate locations in each cove. The back of the scrape was comprised of a fine-mesh net (6 mm) that caught and reliably retained crabs >5 mm CW. Typically, we took scrape samples immediately before and after each release of hatchery-reared juvenile crabs to determine densities of ambient and tagged crabs in all coves.

Tethering was used in 2004 to estimate the relative survival of crabs due to predation. Sixteen crabs ranging from 10–60 mm CW (mean ~20 mm) were tethered in each of the enhanced and control coves. Crabs >20 mm were attached to 20 cm of monofilament line by tightening a sliding knot around the carapace spines and securing the knot with superglue. For crabs <20 mm CW, we tied a knot at the end of the line and affixed it to the back of the carapace with superglue. The line was fixed to a PVC pole in shallow water. These lines were flexible enough to let the crabs move without restraint and were firm enough to prevent tangling. We monitored the crabs every 24 hr to observe if experimental crabs were alive, dead, or absent (preyed upon). If a crab was absent, we recorded the condition of the tether and presence of any remaining pieces of carapace on remaining tethers. Tethering has been used successfully in numerous studies (e.g., Pile et al., 1996; Lipcius et al., 2005; see Lipcius et al., 2007, for review) with little or no indication of treatment-specific bias (Peterson and Black, 1994).

Densities of clams and crabs were compared among coves using an Analysis of Variance (ANOVA) model using cove as a fixed factor, with 6–20 replicates per cove. Relationships...
between crabs and clams for all coves in 2005 were compared using regression analysis of means from each cove.

RESULTS AND DISCUSSION

In 2003, crab densities before enhancement (May 15–30) were highest in Aberdeen Cove (enhanced) and Catlett West (enhanced) (Figure 2; ANOVA, df = 29, F = 5.78, p = 0.002), which were chosen as coves to enhance based on prey availability. Likewise, clam densities in May were significantly higher in Aberdeen Cove and Catlett West (ANOVA; df = 24, F-value = 6.33, p = 0.002) than in the other 3 control coves before enhancement (Figure 3). Eight thousand juvenile crabs were released into these coves in mid-summer. At the end of the summer, clam densities were significantly higher in caged plots than uncaged plots (p = 0.003), and clam mortality was significantly higher in experimental (e.g., enhanced) coves than control coves (Figure 4; 2-way ANOVA, total df = 9, F = 24.19, p = 0.003), indicating higher predation rates in experimental coves. This predation mortality brought the initially high clam densities of the experimental coves down to the densities of control coves during our last 2 sampling periods. In control coves, though predation on clams was significant, juvenile crabs were also likely feeding on polychaetes, amphipods, and detritus, as was determined for juveniles <40 mm in a companion study (see Figure 9 in Lipcius et al., 2007).

Using the densities of clams during the 5 time periods with an exponential decay model, densities of clams in enhanced or control coves in 2003 were not projected to dip below the low-density threshold of 12–50 clams/m² during the main predation period (May 15–September 1; Figure 5). Hence, the carrying capacity of the experimental coves apparently was high enough to support the increased crab abundance.

In 2004, we addressed whether alternative prey improved juvenile crab survival by reducing cannibalism. There was no significant difference in crab survival among coves differing in clam density (Figure 6; ANOVA, df = 48, F = 0.87, p = 0.541), including Catlett West (enhanced) where ∼11,000 hatch-
ery crabs were added, resulting in crab densities of over 1.5 crabs/m². In addition, little of the variation in crab survival was explained by clam density (regression: $r^2 = 0.05$, $p = 0.624$). Although high alternative prey densities may either increase juvenile crab survival by reducing cannibalism (Svenning et al., 2005; Wong et al., 2005), or increasing crab growth (Figure 7; Seitz et al., 2005), these benefits may be offset by concomitant increases in overall predator (i.e., cannibal) densities due to bottom-up control of crab density by benthic infaunal prey (Figure 8; Seitz et al., 2003). That is, where prey densities are elevated, densities of crabs (i.e., potential cannibals) also increase (Figure 8; Seitz et al., 2003). Though we recognize that correlation is not causality and that densities of predators and prey could be high at particular sites due to another independent factor, the high percentage of clams in the crab diet and increased growth rates where clam densities are elevated (Figure 7) indicate that crabs are aggregating where their main food source is abundant.

Previous work on cannibalism suggests that it accounts for a large percentage of juvenile blue crab mortality (see Heck and Coen, 1995; Heck et al., 2001; Heck and Spitzer, 2001). When crab densities in unvegetated habitats are low (0.1–1.0 m²), the potential for cannibalism is reduced in these unstructured habitats (Posey et al., 1995; Lipcius et al., 2005, 2007).

Figure 5 Estimated change in density of *Macoma balthica* over time, beginning with the day that the 2003 experiment was initiated (May 16, 2003) for (a) an experimentally enhanced site, Aberdeen Cove, and (b) a control site, Catlett East. Dashed line indicates nominal low-density refuge at 50 clams/m².

Figure 6 *Macoma balthica* densities (+1 SE) (left y-axis in clams per 0.17 m² sample) vs crab survival during tethering (right y-axis in days to mortality $\times$ 100) at the 9 different coves in 2004. Crab survival data were not available for Ware Creek and Taskinas Creek. Catlett West was enhanced with juvenile crabs in 2004.

Figure 7 (a) Juvenile blue crab (*Callinectes sapidus*) growth (log-transformed) inside of cages over 3+ months among 5 habitats in the York River, Chesapeake Bay, from 2000 and 2001 pooled data; (b) *Macoma balthica* densities from 5 habitats in the York River, Chesapeake Bay, in Summer 2000 from suction samples taken inside and outside of crab growth cages (Modified from Seitz et al., 2005).
In 2005, we focused on the entire benthic community. Average benthic densities varied substantially among coves during the May sampling before enhancement (Figure 9). Indian Field and Catlett West had significantly higher clam densities than Felgates and King Creeks (ANOVA; \( p < 0.0005 \)). There were high densities of small crustaceans in all coves except King and Felgates Creeks, and particularly high densities of polychaete worms in Catlett West (Figure 9). The small crustaceans in the benthos included amphipods, isopods, and mysids, which were abundant in May, but whose numbers decreased during all subsequent sampling periods. Though amphipods and isopods were extremely abundant in May (1,500/m² in some coves), the bulk of the biomass of infauna (84–94%) was molluscs (Seitz et al., unpublished data) due to the relatively large size of clams compared to other benthic organisms. Clam densities also decreased through time, but the pattern of relative density among the coves remained similar.

In May 2005, before the first crab release, the pattern in crab density was similar to that of benthic infauna, with significantly higher values in Catlett West and Indian Field Creek than the other coves, and Timberneck Creek with moderate densities (Figure 10). Crab densities were highly correlated with clam and polychaete densities (Figure 11; \( r^2 = 0.78, \ p = 0.0197 \)); significant but weaker correlations were detected for small crustaceans. These correlations suggest that bottom-up control drives crab abundance in these secondary nurseries and therefore that benthic invertebrate density could contribute to a robust habitat suitability index for determining sites for crab enhancement.

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**Figure 8** Scatter plot of crab and clam densities from sand and mud habitats (14 points) at the local scale from “upriver” and “head” zones of the York River (non-linear regression: \( y = 5.99 + 1.98 \times e^{0.006x} \)). *Callinectes sapidus* and *Macoma balthica* are depicted (modified from Seitz et al., 2003).

**Figure 9** Mean densities of 3 taxonomic groups of benthic prey at each of the 6 study coves (from 6 replicates per cove) during sampling prior to enhancement in May 2005 (listed as number of individuals per m²) (Seitz et al., unpublished data). In June 2005, Timberneck Creek was enhanced with juvenile crabs.

**Figure 10** Mean (+1 SE) crab density per scrape in 6 experimental coves during pre-enhancement in May 2005 (Lipcius et al., 2006). In June 2005, Timberneck was enhanced with juvenile crabs.

**Figure 11** Correlation between mean density of juvenile crabs (+1 SE) and potential benthic prey (i.e., clams and polychaetes) (+1 SE) in May 2005 (Seitz et al., unpublished data).
enhancement (Seitz and Lipcius, 2001; Seitz et al., unpublished data).

Timberneck Creek was enhanced with ~15,000 crabs from July–September in 2005, and in September, molluscs and polychaetes were still abundant. Clam densities remained above the low-density threshold at 88–267 m⁻² in all coves (Figure 12). This suggests that the released crabs did not exceed the carrying capacity of the coves. The biomass mainly consisted of molluscs (87–94%), representing a substantial food reserve for crabs. These results suggest that benthic food resources in unvegetated nursery habitats in the York River are high enough to support substantial juvenile crab enhancement, indicating that enhancement is an ecologically viable means of restoring the blue crab population in select shallow unvegetated nursery habitats of Chesapeake Bay.

**SUMMARY AND CONCLUSIONS**

In our 2003 caging experiments, both enhanced and control coves experienced a decreased abundance of clams outside of the cages due to predation. Blue crabs will stop foraging for *Macoma balthica* when clam densities drop to 12–50 clams/m² (Clark et al., 1999a, b; Seitz et al., 2001). Because the projected clam densities after the summer predation period (May–September) for all coves far exceeded 50 clams/m², we determined that the carrying capacity of these coves was adequate for an increased crab population.

During 2003, the initial densities of both clams and crabs (before release of hatchery crabs) were elevated in the two coves that were enhanced. Though the elevated densities of both taxonomic groups could be due to bottom-up control (Seitz et al., 2003), the elevated densities could also be due to an independent factor affecting both groups (e.g., sediment type, larval transport). The increased densities of both clams and crabs in the sites selected for enhancement may have increased the interactions between clams and crabs in these coves compared to the control coves; however, the increased availability of food for crabs suggested that these coves would have a sufficient carrying capacity for an elevation in crab abundance through enhancement.

In our comparison of crab survival with alternative benthic infaunal prey in 2004, enhanced coves had the highest clam densities and the lowest crab survival rates. This suggests that larger blue crabs (i.e., potential cannibals) and other predators may be drawn to the system by increased clam densities (bottom-up control; Menge, 1992; Posey et al., 1995; Menge et al., 1996, 1997), leading to an increase in cannibalism (Moksnes et al., 1997) or predation, and negating any positive effects of alternative prey (Wong et al., 2005). However, blue crab growth is elevated where clam densities are highest (Seitz et al., 2005), which could facilitate attainment of a size refuge from predation (Hines et al., 1990; Moody, 2001). Clearly, there is a trade-off between food availability and survival; both factors need to be considered when determining optimal enhancement locations. In this and previous field studies, densities of *Callinectes sapidus* and *Macoma balthica* have been positively correlated (Seitz et al., 2003); where benthic infaunal densities are high, blue crab densities will increase concurrently.

In conclusion, the findings of the experiments conducted on benthic crab interactions in 2003–2005 in the lower Chesapeake Bay serve to direct future efforts regarding crab enhancement in nursery habitats. The downriver coves we have used for crab release sites serve as suitable habitats for juvenile crabs, based upon abundant food resources. In all 3 years, clam densities in shallow, unvegetated secondary nurseries in the York River remained above a low-density threshold (Seitz et al., 2001) suggesting that crabs would remain in these habitats to forage. However, these abundant resources attracted additional crabs, sometimes resulting in higher mortality of the smallest juvenile crabs. We propose that there may be an optimal density of infauna that is sufficiently high to support additional hatchery-reared crabs, but not so high as to attract additional predatory conspecifics. A detailed examination of density-dependent survival of clams suggests that this abundance of clams may be around 500/m² (Seitz et al., unpublished data). Alternatively, there may be a ratio of crab:prey abundance that optimizes survival and growth of juvenile crabs through a range of crab and prey densities. In addition, these productive habitats provide quick growth to a size refuge from predation and, furthermore, are located in close proximity to the lower bay spawning grounds for easy access once the juvenile hatchery-reared crabs grow, mature, and migrate. The lower bay secondary nurseries have a sufficiently high carrying capacity that can support additional crabs and should be considered in future stock enhancement efforts. Combining the existing knowledge on food availability with that of larger wild crab and other predator abundance will help elucidate an optimal choice of habitats for future crab releases. Finally, an ecological approach considering predator-prey dynamics is
crucial in dictating selection of optimal habitats for release of hatchery-reared crabs in stock enhancement.

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