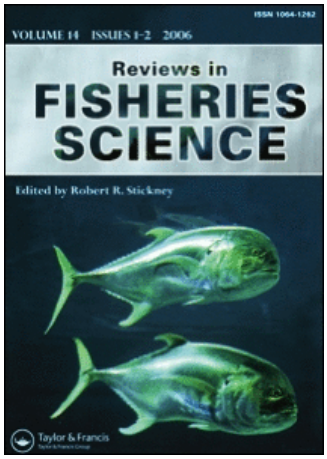

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Release Strategies for Estuarine Species with Complex Migratory Life Cycles: Stock Enhancement of Chesapeake Blue Crabs (**Callinectes sapidus**)

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Release Strategies for Estuarine Species with Complex Migratory Life Cycles: Stock Enhancement of Chesapeake Blue Crabs (*Callinectes sapidus*)

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Responsible stock enhancement requires rigorous experiments to develop release strategies that account for movement of all life-history stages among habitats across inshore-offshore and estuarine gradients. However, crab stock enhancement research to date has focused primarily on hatchery production, with only limited field assessments of the efficacy of releases to increase the target population. This paper summarizes ongoing research to develop effective release strategies for hatchery-reared juveniles to augment the spawning biomass of Chesapeake Bay blue crabs, which has declined >80% in 15 years and appears to be recruitment limited. Our release experiments focused on three factors: (1) components of preparation and release, which included life stage and size at release, pre-release conditioning to minimize differences between hatchery and wild crabs, and micro-habitat and micro-timing of release; (2) stocking variables, particularly seasonal timing of release and stocking density; and (3) site selection and coordination, including release macro-habitat and location of release sites along environmental gradients, emphasizing coordination of release site and fishing pressure with migration corridors linking nurseries to spawning areas. In the first 5 years of research, we demonstrated that small (1,000–10,000) cohorts of hatchery reared, 20 mm, 7th-instar juvenile blue crabs can be tagged and released into small (1–10 ha) coves, and that these cohorts can be followed successfully to quantify growth, survivorship, and productivity of the enhanced population. We also determined the timing and routes of migration using a tag-reward system with the cooperation of fishers. Our multifaceted research strategy provides a model for responsible approaches to stock enhancement of other species with complex migratory life cycles.

Keywords stock enhancement, release strategies, estuary, blue crab, *Callinectes sapidus*, Chesapeake Bay

INTRODUCTION

Responsible approaches to stock enhancement emphasize rigorous, quantitative, experimental tests of strategies for releasing hatchery-reared juveniles to restore reproductive stocks of fisheries (Cowx, 1994; Blankenship and Leber, 1995; Leber, 1999, 2002; Bell et al., 2005). Stock enhancement as a fisheries restoration strategy must focus on populations that are recruitment limited and on species with early life stages that either can be collected in large numbers from the wild and relocated, or reared in hatcheries in large numbers to life stages that bypass the environmental limitations on survival of the most vulnerable larvae and smallest juveniles. Many coastal fisheries rely on fish and invertebrate species with complex migratory life cycles that use multiple estuarine habitats during portions or all of their life cycles (McHugh, 1967) (Figure 1). Enhancement of recruitment-limited stocks for these species requires release strategies in optimal nursery habitats linked by migratory

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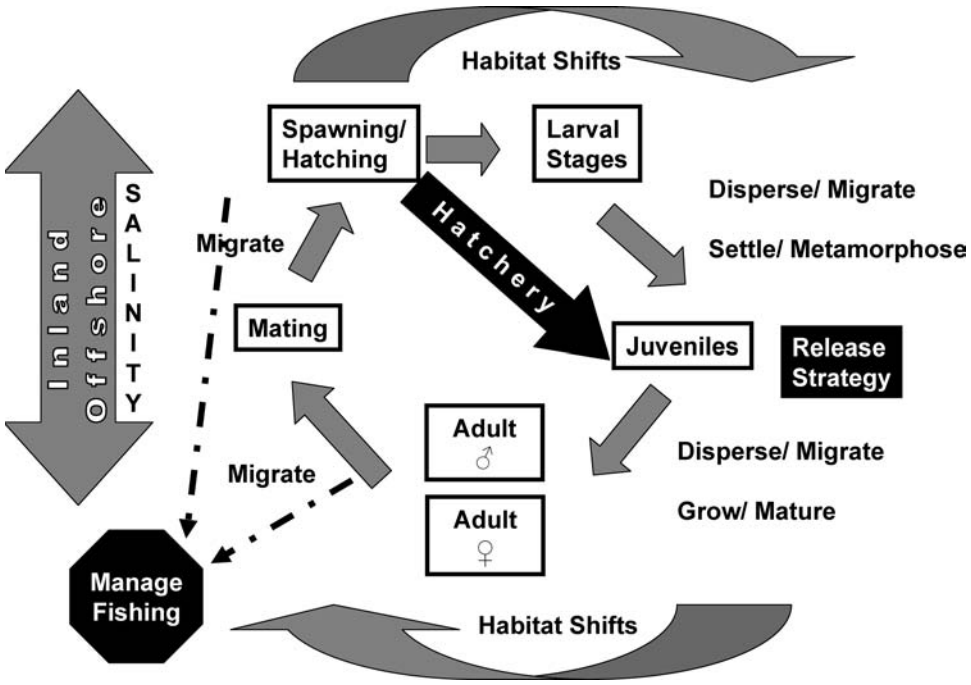

Figure 1 Representative complex life cycle for estuarine species that migrate among habitats along gradients of salinity and from on-shore to off-shore zones. When recruitment of juveniles limits the stock of adults, targeted releases of cultured juveniles can be used in stock enhancement programs to increase the supply of juveniles. Management of fishing pressure on adults must be coordinated along the migratory corridors to ensure that the spawning stock is increased. These interventions are shown in black.

corridors to spawning areas. Thus, release strategies must consider shifts in life stages among habitats across gradients from inshore to offshore and along estuarine salinity regimes. Release strategies need to consider both optimal life stage and the need to minimize differences between hatchery-produced and wild juveniles. This involves decisions about factors linked to the ecological requirements of the post-release life stages and the scale of their movement, such as stocking density, release habitat characteristics, and timing of releases. To be successful, the release strategy also must be linked to improved fishery management for spawning stock restoration.

A spectrum of approaches for restoring and supplementing stocks of many coastal fishes and invertebrates through stock enhancement has been reviewed recently (Cowx, 1998; Leber, 2004; Bell et al., 2005). These major reviews have highlighted penaeid shrimps and lobsters as the best studied examples for decapod crustaceans. However, initiatives to increase production of brachyuran crabs are also underway in some countries on large scales using an array of methods, including aquaculture, pond and pen culture, stock enhancement, and integrated habitat restoration. The mix of these approaches and the way statistics for culture production and wild catch data are reported, especially for China (Watson and Pauly, 2001), often make it difficult to distinguish how much of fisheries catch is supported by stock enhancement. However, stock enhancement approaches for crab fisheries have been tested at small scales in several countries in Asia and the Indo-West Pacific, and at large scales in Japan and China.

Outside the United States, restoration and stock enhancement of crabs has focused on the genera *Portunus* and *Scylla* in eastern and southeastern Asia and northern Australia (Keenan and Blackshaw, 1999; Secor et al., 2002; Le Vay et al., 2008), and *Eriocheir* in China (Cheng et al., 2008). Food and Agriculture Organization (FAO) production data indicate that the largest and most rapid increase in production appears to be for the Chinese mitten crab (*Eriocheir sinensis*), which is approaching 600 t annually, primarily from intensive culture of larvae and pond and pen culture of juveniles for release into freshwater ponds, pens, constructed habitats, and natural systems (Cheng et al., 2008). Restoration of declining portunid stocks has relied increasingly on hatchery production of juveniles, especially in Japan, China, several countries of Southeast Asia, and Australia (Keenan and Blackshaw, 1999; Secor et al., 2002). For example, Japanese hatcheries produced up to 60 million juvenile *Portunus trituberculatus* annually for release into a range of coastal systems over two decades (Hamasaki, 2000; Secor et al., 2002). Limited estimates indicate that release of hatchery-reared portunid juveniles is 25–150% of wild crab production across a wide range of spatial scales (Secor et al., 2002). Stock enhancement of *Scylla* spp. is successfully linked to mangrove restoration in southeast Asia on a scale of 5–100,000 ha (Keenan and Blackshaw, 1999; Lindner, 2005; Le Vay et al., 2008). New culturing approaches for mass production of soft crabs are also being applied at large scales, with pond systems in Thailand holding >100,000 wild-caught juvenile *S. serrata* to molting (Thomas Wilson, Thai Luxe Enterprises Public Co. Ltd.,

Amphur Muang, Samutsongkhram, Thailand, personal communication). However, as with many other species, crab stock enhancement research has focused primarily on hatchery production, with only limited field assessments of the efficacy of releases for augmenting populations (Secor et al., 2002).

DEVELOPING RELEASE STRATEGIES FOR BLUE CRABS

Fishery landings for the Chesapeake Bay blue crab (*Callinectes sapidus*) have declined substantially over the past 15 years, and the abundance of blue crabs has been at historic low levels for an unprecedented period (Bi-state Blue Crab Technical Advisory Committee (BBTAC, 2006)). The spawning stock has declined by >80% since 1991 (Lipcius and Stockhausen, 2002), and the number and biomass of females in spawning habitat has remained low for nearly a decade (BBTAC, 2006). This serious decline occurred despite sustained efforts of managers to reduce fishing pressure (BBTAC, 2006). The stock appears to be recruitment limited (Lipcius and Stockhausen, 2002).

This paper summarizes ongoing research on release strategies for hatchery-reared blue crabs in Chesapeake Bay by a consortium of researchers, the Blue Crab Advanced Research Consortium (BCARC) (Zohar et al., 2008). Asian hatchery approaches provided useful models for large-scale larval rearing (Hamasaki, 2000), and the BCARC project has committed to rigorous tests of release strategies for restoration of the *Callinectes sapidus* stock in this very large estuarine system.

The blue crab life cycle in Chesapeake Bay (Figure 2) involves larval dispersal out of the estuary, post-larval re-entry, and settlement in seagrass beds in the lower bay during summer and fall. After growing for about 2 months, small (20 mm, 7th instar) juveniles undergo secondary dispersal in late summer and fall, migrating up the main bay and tributaries into lower salinity nursery habitats. Juveniles over-winter in the nursery areas as water temperatures decline below 10°C, and the following summer they grow rapidly to sexual maturity and mate. Inseminated females migrate in fall back to high salinities to over-winter a second time before beginning to brood eggs in the spawning area of the lower bay.

The BCARC project presents an approach of integrating multiple facets of the release strategy and of incremental steps to test the success of stock enhancement at increasing spatial scales. The BCARC strategy is to rear larvae to small juvenile crabs in hatcheries and to release them into natural nursery areas at a size when they are less vulnerable to predation and are behaviorally adapted to remain within the key nursery habitats. We used replicated small-scale releases of hatchery-reared blue crab cohorts to test release strategies for this model species with a complex migratory life cycle.

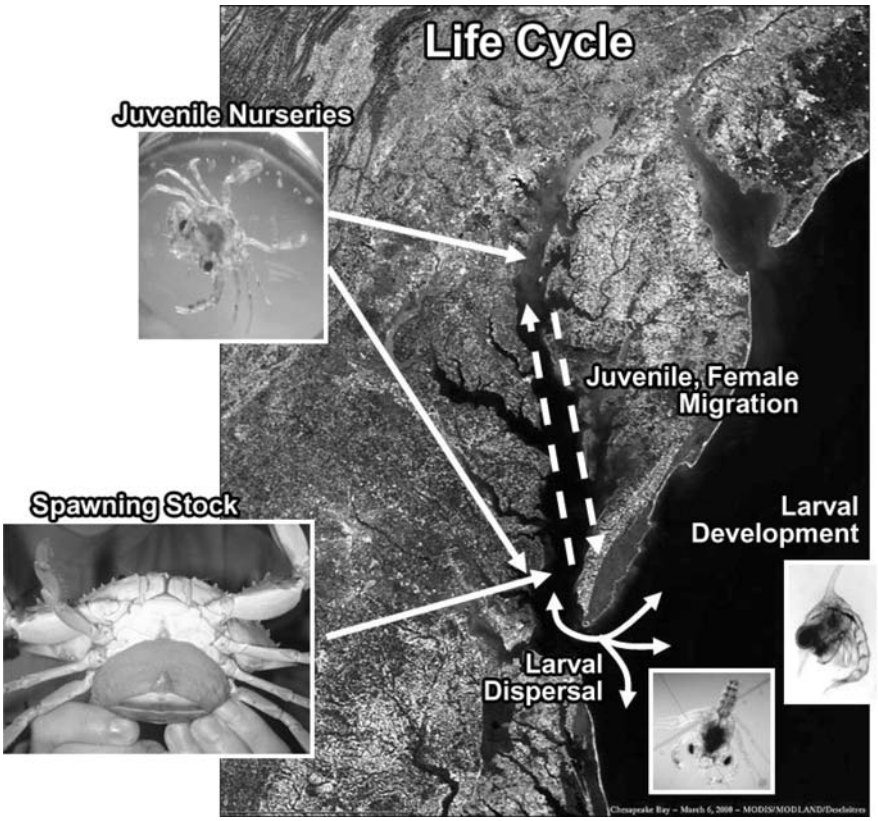

Figure 2 Complex migratory life cycle for the blue crab (*Callinectes sapidus*) in Chesapeake Bay, showing distribution of key life stages among ecosystems distributed along the salinity and on-shore to off-shore gradients of the 300 km long estuary.

We focused initially on small western shore sub-estuaries of the Chesapeake Bay (especially the Rhode River and South River in the upper bay and York River in the lower bay), where the Smithsonian Environmental Research Center and the Virginia Institute of Marine Science have extensive background information on the population and community ecology of juvenile and adult crabs. In this article, we focus on the 500–2,000 ha sub-estuaries of the upper bay. Using replicated batches of 1,000 to 10,000 tagged hatchery-reared juveniles produced by BCARC (Zmora et al., 2005), we demonstrated experimentally that juveniles stocked into small (1–10 ha) coves in typical nursery habitats survive, grow rapidly to maturity, and significantly enhance the numbers of blue crabs produced in the release areas (Davis et al., 2005; Hines et al., unpublished). We tagged all hatchery reared crabs (15–25 mm) with micro-wire and colored elastomer injected into the rear legs, which persists through molting during the life of the crabs (Davis et al., 2004a). These tags allowed us to distinguish hatchery-reared juveniles from wild crabs and to distinguish among crabs from different experimental treatments. We tested spatial and temporal variation in growth, survival, enhancement effect, and production with 39 juvenile cohorts released in multiple sites and at multiple times during spring to fall over 5 years (2001–2006). Depending on fluctuations in predators, wild crab abundance, and water quality conditions, outcomes of releasing hatchery-reared juveniles vary annually from 5 to 25% in survival to mature adult, 50 to 300% in enhancement of the wild adult crab population within the release coves, and from 150 to 550 adult crabs per hectare within the release coves (Davis et al., 2005). We tested effects of three groups of factors on survival of release cohorts and their growth to sexual maturity in the coves: preparation and release, stocking aspects, and site selection and coordination. These factors form the main components of release strategies. We summarize below the progress we have made in testing the variables involved with these factors for blue crabs.

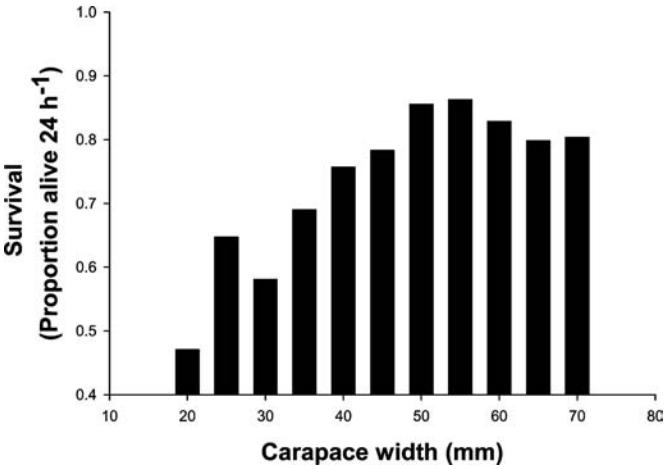

Figure 3 Survival of juvenile blue crabs as a function of body size (carapace width). Juvenile crabs were tethered in shallow water (50 cm deep) in the Rhode River using methods in Hines and Ruiz (1995) and checked for mortality after 24 hr. Nearly all (>95%) mortality was attributed to predation by cannibalistic adult crabs (>120 mm).

COMPONENT VARIABLES FOR RELEASE STRATEGIES

Preparation and Release Variables

Successful release strategies evaluate the characteristics and status of the life stage at the time they are removed from the hatchery and transferred to the field. Decisions about when to transfer the organisms from the hatchery to the wild must evaluate the trade-off between minimizing hatchery expenses and potential laboratory artifacts, and maximizing early survival and habitat use at release. The factors that need to be considered are presented below.

Life Stage at Release

Typically, hatchery rearing for stock enhancement of most coastal species proceeds beyond the limiting larval, metamorphosis, post-larval, and early juvenile stages. Thus, the life stages that exhibit the highest mortality in the field are passed, and a more sedentary life stage that will remain within an identified release habitat is produced. For blue crabs, considerations of release stage focused on variables of size and behavior that correlate with juvenile secondary dispersal and settlement into nursery habitats: 20 mm carapace width (7th instar), and transition to more sedentary benthic existence (Hines et al., 1987; Pile et al., 1996). In the field, juvenile crabs <20 mm tend to swim frequently, emigrate from release sites, and have high mortality rates; for sizes >20 mm, however, juvenile emigration (Johnson et al., in review) and survival increase markedly in release coves (Figure 3). The advantage of holding juveniles until they grow to larger sizes is not without cost, because juvenile mortality in the hatchery is largely attributed to cannibalism at rates that increase with crab size. At a size of 20 mm, mortality can be 25% per week in hatchery conditions (Zmora et al., 2005). To avoid rapidly diminishing returns, release should occur as soon as juveniles grow to this size.

Pre-Release Conditioning

Hatcheries may condition organisms in ways that are maladaptive upon release in the wild. Therefore, it is important to evaluate performance of hatchery-reared juveniles compared to wild organisms and to assess whether differences may be eliminated or reduced by conditioning before release. For blue crabs, we conducted a series of laboratory and field experiments that compared performance of hatchery-reared versus wild juveniles for growth, feeding, survivorship (as a function of morphology, predator avoidance/refuge use, burial), competition, and aggression (Davis et al., 2004b, 2005; Young et al., 2008). For example, hatchery-reared juveniles, which were not exposed to bottom sediments, spend significantly less time buried than wild juveniles (Davis et al., 2004b; Young et al., 2008).

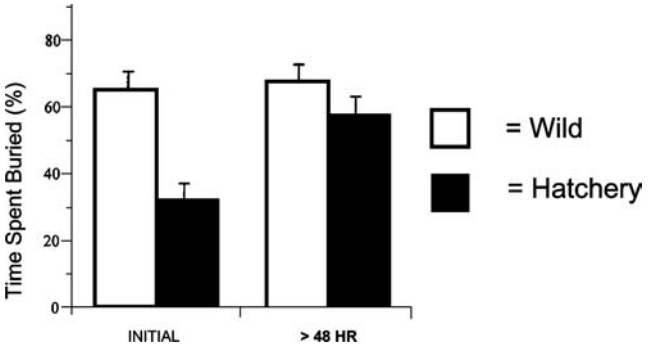

Figure 4 Burial rates of wild versus hatchery-reared juvenile blue crabs, before and after exposure to sediments for 48 hr. From Davis et al. (2004b); see also Young et al. (2008).

Because burial may be an important predator-avoidance behavior, we tested effects of preconditioning hatchery-reared juveniles to sediment at intervals of 24 and 48 hr before release. Within 48 hr of preconditioning, burial rates of hatchery crabs do not differ from wild crabs (Figure 4). Our combinations of laboratory and field experiments showed that hatchery-reared blue crabs do not differ significantly from wild juveniles in most traits, such as growth rates, feeding and diet, habitat use, and movement (Davis et al., 2004b; Young et al., 2008; Johnson et al., in review). Although hatchery-reared juveniles initially have shorter lateral spines and do not bury into sediment as frequently as wild crabs, these anomalies soon disappear and do not result in differences in survival (Young et al., 2008). Thus, release strategies for juvenile crabs include only minimal preconditioning in the hatchery.

Micro-Habitat and Micro-Time of Release

The specific site and timing of release may effect success. Blue crabs exhibit significant habitat partitioning by size, sex, and molt stage (Hines et al., 1987; Hines, 2007), and juveniles obtain refuge from predation by moving into fringing shallow water (Figure 5) and structured habitats, such as sea grasses and coarse woody debris (Everett and Ruiz, 1993; Hines and Ruiz, 1995). Releasing crabs into these micro-habitats increases survival (Johnson et al., in review). Timing of releases in accord with diel or tidal cycles may also be important if, for example, visual predators are most active at certain times of day and tidal regimes. Upper Chesapeake Bay nursery areas for blue crabs have low tidal amplitude and murky water, so these factors appear to be less important sources of juvenile mortality than cannibalism by large, chemosensory blue crabs (Hines and Ruiz, 1995; Hines, 2007).

Stress of Transport and Handling or Tagging

In our experiments, we routinely conducted experimental controls to test the effects of stress associated with transporting juveniles from the hatchery to the release site and tagging them. For blue crabs smaller than C4–C5 (10 mm), collection and transport caused increased mortality, because molting frequencies are high in such small crabs, and a large proportion is soft or undergoing stressful ecdysis. Whereas mortality from mechanical tagging and handling increases markedly at sizes <16 mm, survival at sizes >16 mm is consistently greater than 92%. However, for larger batches of juveniles, mechanical tagging will be replaced by genetic identification with mitochondrial DNA (Zohar et al., 2008).

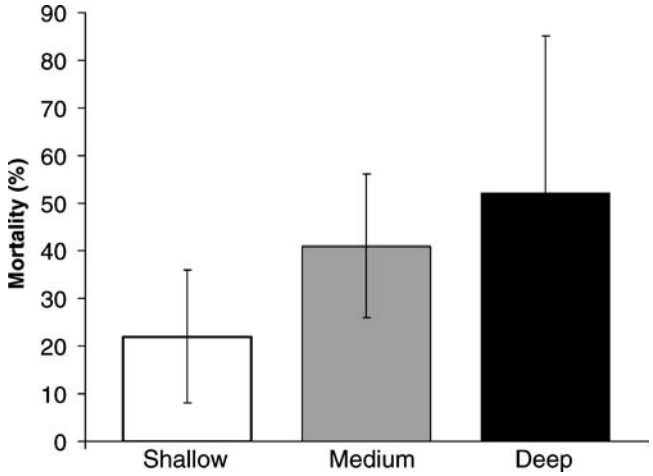

Figure 5 Mean (+/− range) mortality of juvenile (30–70 mm) blue crabs tethered for 24 hr in shallow (20 cm), medium (45 cm), and deep (100 cm) water of the nearshore habitat in the Rhode River sub-estuary of upper Chesapeake Bay ($N = 3$ trials of 10 crabs at each depth in each of 3 summer months for each of 5 years). Modified from Hines and Ruiz (1995).

Stocking Variables

Release strategies must also consider variation in the carrying capacity of the environment. The time of year when releases are made and stocking density can be expected to interact with the ecological processes that determine production within the ecosystem, yet releases of cultured juveniles often circumvent natural seasonal processes and seek to maximize stock density. Our experiments with blue crabs show that quantitative experimental assessment of these factors can optimize survival.

Season

Season of release has marked effects on growth and mortality of blue crabs because water temperature regulates primary and secondary production (food) and predation rates. Cohorts of hatchery-reared blue crabs released in upper Chesapeake Bay early in the season grow rapidly to maturity within as little as 2 months (Figure 6). They then mate and migrate from the nursery habitat in their first season, thus supplementing the spawning stock within 1 year (Davis et al., 2005). In contrast, crabs released later over-winter and grow to maturity in their second year. These crabs supplement the spawning stock in their third year, which is the same schedule as wild crabs. Juvenile mortality increases markedly with summer foraging of cannibalistic adult crabs: survival of both tethered and released juveniles is highest

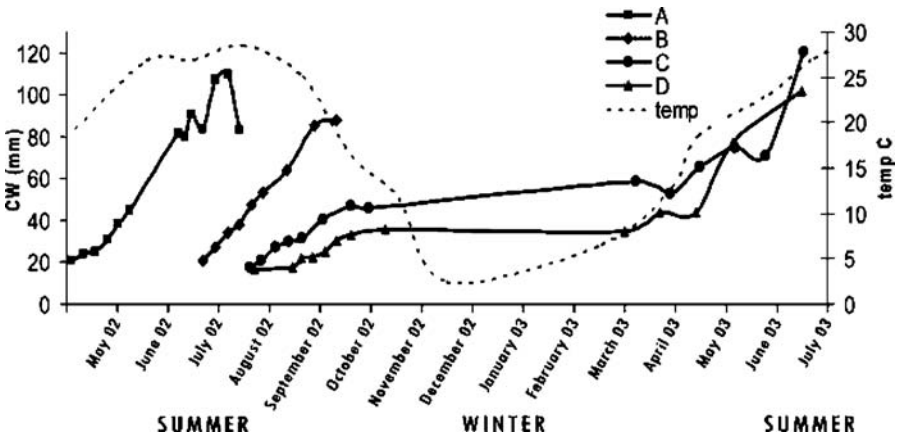

Figure 6 Seasonal variation in water temperature and growth of hatchery-reared juvenile blue crab cohorts released into coves of upper Chesapeake Bay. Cohorts A and B were released in early summer (May–June) and grew rapidly and matured in the first year. Cohorts C and D were released in late summer (August–September) and ceased growing as temperatures declined markedly in fall. The later crabs must over-winter before resuming growth to mature in the second year, which is a schedule that is similar to wild juvenile crabs. From Davis et al. (2005).

in early and late summer, when predation rates are low (Figure 7). Analysis of instantaneous growth in released cohorts, and mortality in tethering experiments, has provided analytical models for predicting the seasonal trade-off of increasing growth rate and decreasing survivorship over the summer season (Johnson et al., 2008).

Stocking Density

Density-dependent mortality and growth characterize most marine and estuarine populations and fluctuations in carrying capacity limit maximum densities for stocking. At the same time, the complexity of interacting factors regulating population density often makes it difficult to match stocking density with the dynamics of carrying capacity. Thus, survival of cohorts of hatchery-reared juvenile blue crabs is inversely related to stocking density, but the variance of the relationship is large (Figure 8). While functional relationships of carrying capacity for food and other factors can be important (Seitz et al., 2008), this variance results from interactions of these cohorts with seasonal and annual fluctuations in a myriad of conditions. It may be difficult to quantify carrying capacity in advance of releases in highly variable ecosystems like estuaries, but effects of key variables (e.g., food, predation, shelter) can be tested experimentally and factored readily into selection of sites for releases.

Site Selection and Coordination

Choosing the best sites to release cultured juveniles can be difficult because suitable macro-habitats are often distributed patchily and vary in size. In addition, coastal ecosystems usually have steep physical and biological gradients, including fishing pressure. In the case of blue crabs, the position of nursery areas along these gradients creates variation in the length and configuration of migratory corridors that link nursery areas to the spawning habitat. Successful release strategies for blue crabs must consider effects of variation in suitable macro-habitats and location of these habitats sites along these gradients, with respect to migration corridors and with regard to patterns of fishing pressure.

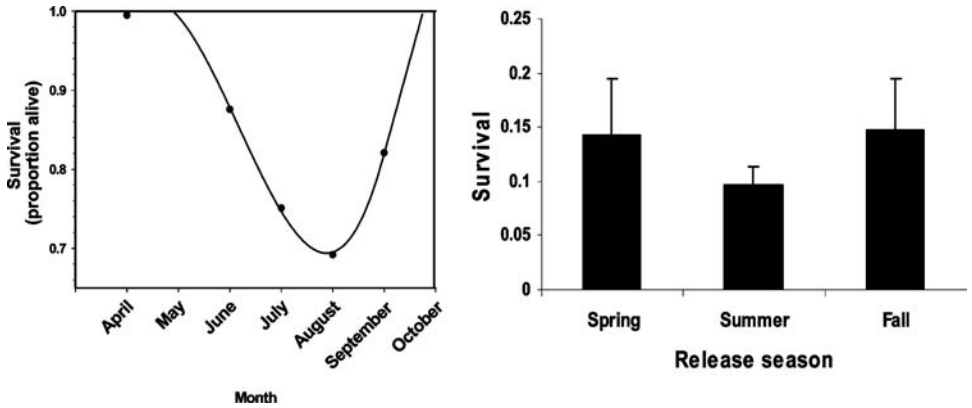

Figure 7 Seasonal variation in survival of juvenile blue crabs in tethering experiments (left) or released hatchery-reared cohorts (right) in coves of upper Chesapeake Bay. See also Johnson et al. (2008).

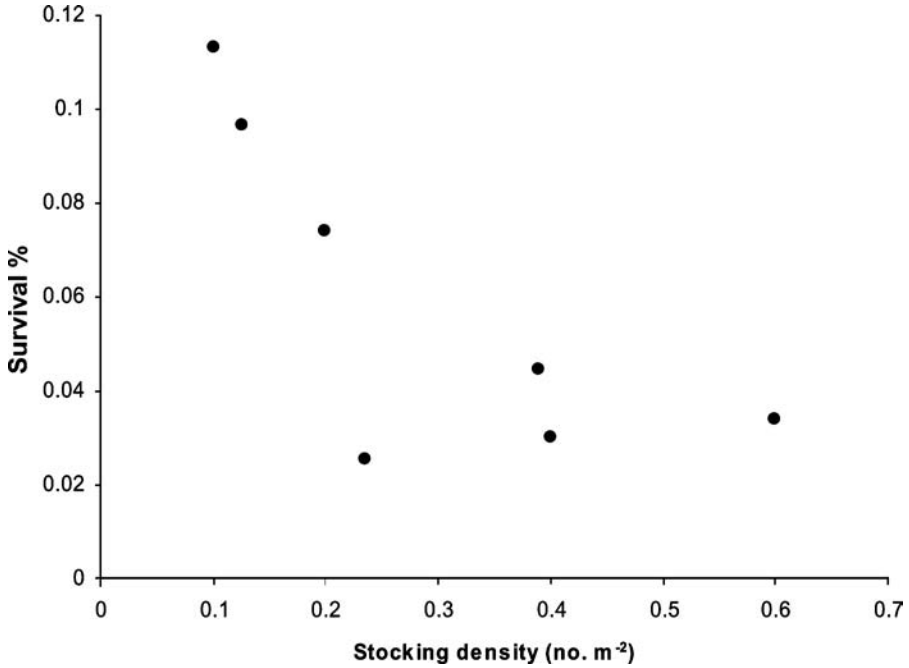

Figure 8 Survival to sexual maturity as a function of stocking density for cohorts of hatchery-reared juvenile blue crabs released into small coves of upper Chesapeake Bay during summer of 2003.

Macro-Habitat

Optimal release sites have few predators and competitors, low incidences of diseases or parasites, and ample shelter and food. The main nursery habitats for juvenile blue crabs are muddy coves with fringing marshes that provide detritus to support the benthic invertebrates, especially clams, as food resources for crabs (King et al., 2005; Seitz et al., 2008). Coarse woody debris along the shoreline of these sites also provides important refuge habitat for molting juvenile crabs (Everett and Ruiz, 1993; Johnson et al., in review). Survival of hatchery-reared juveniles varies significantly among such coves in upper Chesapeake Bay and among seasons and years (Figure 9).

Location Along Gradients

Research on effects of environmental gradients in coastal systems, especially estuaries, often focuses on variation in salinity

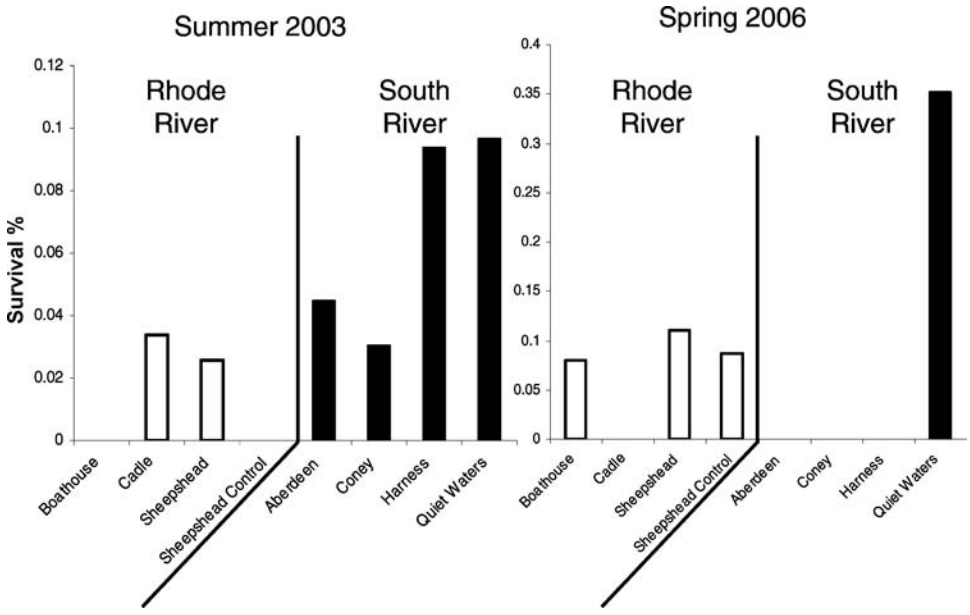

Figure 9 Variation in survival of hatchery-reared juvenile blue crabs released in four coves of the Rhode River sub-estuary and four small coves of the South River sub-estuary of upper Chesapeake Bay in spring 2003 and summer 2006.

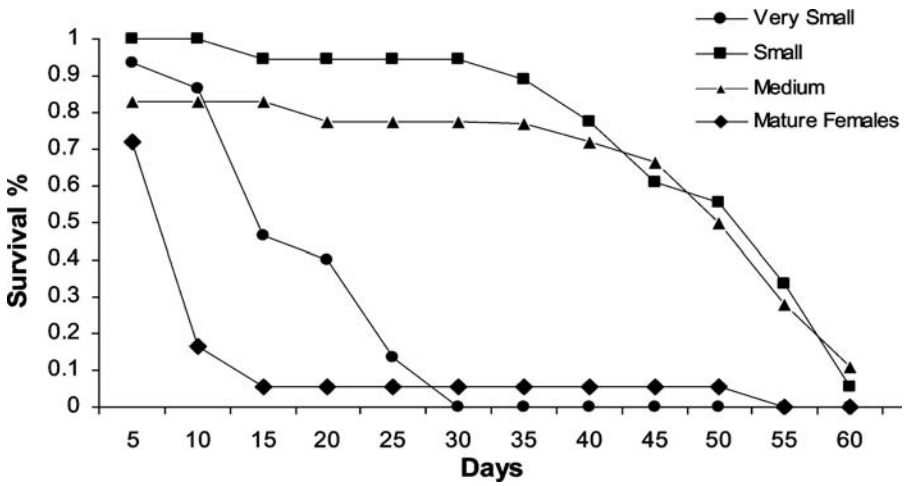

Figure 10 Variation in survival among four life stages of blue crabs exposed to harsh winter conditions of cold (3°C) and low salinity (6 ppt). From Rome et al. (2005).

as the dominant variable. However, other physical variables such as temperature and oxygen concentration may be important. For blue crabs in Chesapeake Bay, harsh winter conditions of cold water temperature combined with low salinities may be lethal, especially to very small (<15 mm) juveniles and adult females (Figure 10) (Rome et. al., 2005). Accordingly, crabs released late in the season benefit by being released at a size of at least 20 mm before onset of winter in upper bay sites or released into less harsh lower bay sites. Biological factors such as predation and competition may also vary significantly along estuarine gradients. For example, mortality rates of juvenile blue crabs in tethering experiments appear to be much less in upper than lower Chesapeake Bay sites (Figure 11). Lower and upper bay nursery areas differ in composition and density of predator guilds, with predation by fishes and cannibalistic adult crabs causing higher mortality in the lower bay than upper bay sites, where the declining adult crab population and lower fish predation resulted in much higher survival. Further, disease mortality (especially associated with *Hematodinium*) can be significant at high salinity and negligible at low salinity sites (Shields and Overstreet, 2007).

In Chesapeake Bay, inseminated mature female crabs migrate in September–November as much as 250 km along a corridor on the eastern side of the deep mainstem channel to reach the lower bay spawning sanctuary (Figure 12) (Hines et al., 1995; Aguilar et al., 2005). Fishing pressure on adult crabs varies by gear and season within the nursery areas and along the migration corridor (Aguilar et al., 2008). Analysis of migratory behavior is being used to identify sites that maximize connectivity of nursery habitats with spawning sanctuaries (Figure 13). Tag reward systems involving the participation of watermen are used to assess fishing pressure on migrating females and to identify migratory corridors that optimize probability of inseminated females reaching the spawning sanctuary. Ultimately, detailed knowledge of the timing, route, and mode of migration of crabs to the spawning grounds will allow management to focus fishing restrictions more narrowly to maximize the number of migrating females reaching the spawning sanctuary. It will also minimize impacts of unfocused regulations on other unintended segments of the fishery.

DISCUSSION

We are developing elements of a release strategy that ultimately will maximize the contribution of hatchery-reared juveniles to the spawning stock, specifically increasing the number of inseminated females incubating eggs and releasing larvae within the spawning area of the estuary. The general goal is to restore the fishery to pre-1991 levels (i.e., pre-recruitment limitation), which is estimated to require a spawning stock that is at least double its present level of 4 to 8 million females (Lipcius and Stockhausen, 2002; Zohar et al., 2008). Annual increments of

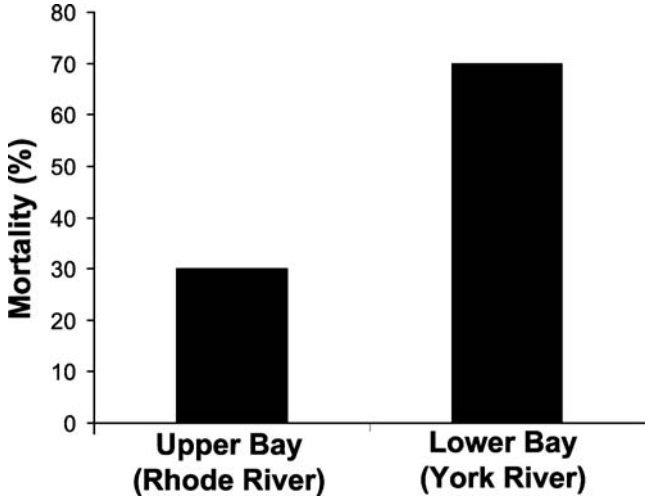

Figure 11 Mortality rates of juvenile (30–70 mm) blue crabs in summer (August) during tethering experiments in upper versus lower Chesapeake Bay subestuaries (represented, respectively, by the Rhode River and York River). After Hines and Ruiz (1995) and Johnson et al. (2008).

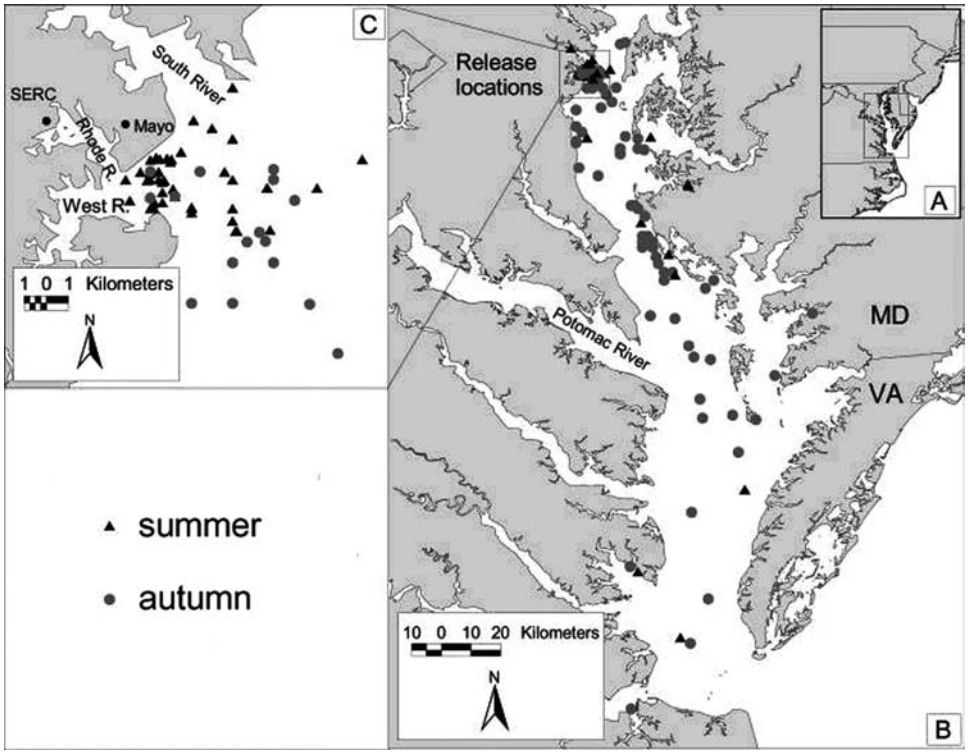

Figure 12 Recapture sites of tagged mature female blue crabs released in summer and fall off the Rhode River sub-estuary of upper Chesapeake Bay. Recapture sites indicate the migratory corridor along the eastern shoulder of the deep channel en route to the spawning area in the lower bay. From Aguilar et al. (2005).

10% increase to the current spawning stock appear to be a reasonable target (Zohar et al., 2008). Our approach is to develop a release strategy in stages that allow incremental increases in numbers of released crabs at increasing spatial scales. Importantly, our experimental releases allow us to develop mechanistic understanding of the factors regulating production of each subsequent life stage, so that we can maximize production under varying spatial and temporal conditions.

In the first 5 years of our research, we have shown that small (1,000–10,000) cohorts of hatchery-reared, 20-mm, 7th-instar juvenile blue crabs can be tagged and released into small (1–10 ha) coves, and that these cohorts can be followed successfully to quantify growth, survivorship, and productivity of the enhanced population (Davis et al., 2004b; Zohar et al., 2008). These initial releases provide estimates of variation in these parameters over a wide range of natural conditions. This information helps to determine reasonable expectations for production rates of mature crabs in release sites, and to identify release strategies to attain such production. Because "optimization" is a relative term, it would be easy to set unrealistic goals for release strategies without conducting releases across the array of experimental combinations we have tested. Our experiments gave us confidence in our understanding of factors affecting growth and survival of juveniles in the release sites.

We are now assessing "optimal release sites" throughout this large estuary based on an array of characteristics grouped in two main considerations. First, based on our experimental releases, we seek to identify the characteristics of potential release areas that will maximize juvenile growth and survival for production of mature crabs, especially inseminated females. Analysis of juvenile dispersal behavior is being used to select sites that receive low abundances of wild juveniles and where habitats may usually be below carrying capacity. Fringing marshes that provide detrital enrichment of infaunal food resources for crabs form major nursery habitats and release sites in both upper and lower Chesapeake Bay sub-estuaries. Throughout the estuary, shallow fringing water and structural components of the habitat, particularly submerged vegetation and coarse woody debris, provided crucial refuges for molting crabs to avoid predation by adults and predatory fishes. Second, analysis of migratory behavior is being used to identify sites which maximize connectivity of nursery habitats with spawning sanctuaries, so surviving released crabs have a high probability of contributing to the spawning stock. We seek to identify potential "source sites" (Lipcius et al., 2008) for inseminated females. Tag reward systems are being used to assess both population abundance using mark-recapture methods in larger-scale sub-estuaries, and as effective ways to employ spatial management of fishing pressure on migrating females.

To optimize release strategies for maximizing enhancement of the spawning stock, the next phase of research will extend and expand this analysis throughout the large Chesapeake estuary to encompass the full gradient of salinity and other physical factors, as well as crucial biological factors. We have begun to measure spatial variation in recruitment of wild juveniles, the suite of predators and diseases, food resources, and refuges.

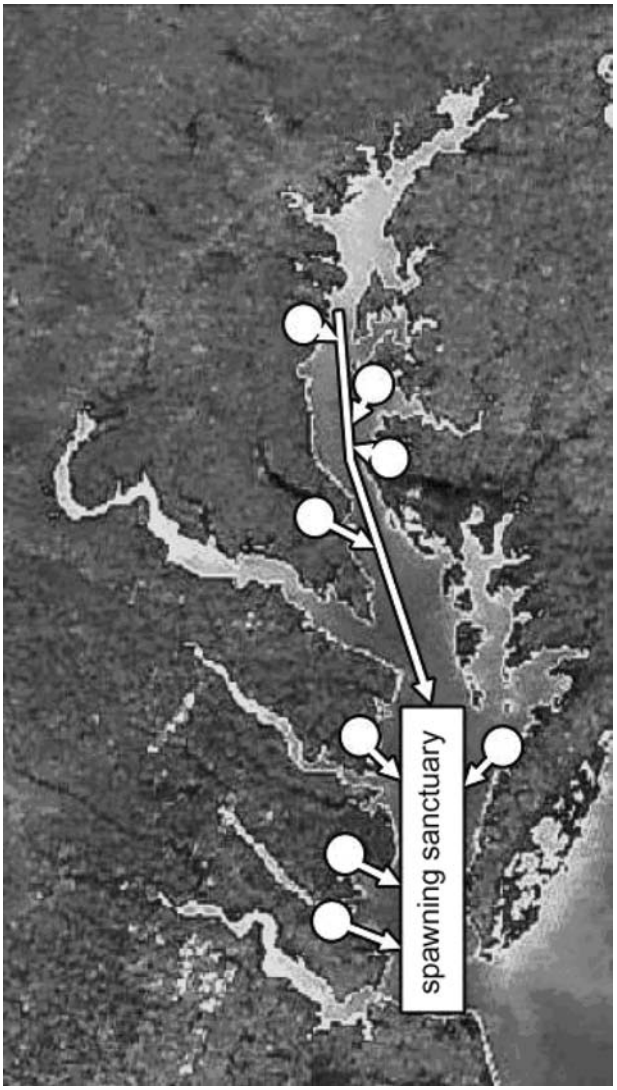

Figure 13 Concept for release sites along the estuarine gradient of Chesapeake Bay that would take into consideration the physical and biological gradients, as well as migratory corridors with protections from fishing en route to reach the lower bay spawning sanctuary.

These measures are being used to develop a multivariate indicator of release site quality that will be tested and refined with additional experimental releases into a range of predicted "good" and "poor" sites. Our next research steps also include increasing the scale of experimental releases (30,000–50,000 juveniles per cohort in multiple 100–500 ha sites), combined with molecular tagging to compare production of females in stocked and non-stocked sub-estuaries. Additionally, we are measuring variation in survival (fishing returns) of migrating mature females tagged and placed in a range of potential release areas along the estuarine gradient at different distances from the spawning area.

In combination, these approaches will allow us to predict optimal migratory corridors for inseminated females to reach the spawning sanctuary from our release sites in nursery areas. These releases will allow us to test whether the small scale results of the first phase allow us to predict optimal sites for larger releases. Further, these tests will supply parameters for robust models assessing the potential to provide significant and responsible enhancement of the Chesapeake blue crab spawning stock.

This large multifaceted program provides the most detailed experimental analysis available for release strategies for stock enhancement of a crab species. In combination with improved management strategies, our research strategy provides a model for responsible approaches to stock enhancement for other estuarine species with complex migratory life cycles.

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