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Importance of Season and Size of Release to Stocking Success for the Blue Crab in Chesapeake Bay

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A critical step toward optimizing the success of stock enhancement is to identify release strategies that maximize survival and enhance growth of released hatchery-reared individuals. A key, but often overlooked, consideration for optimizing release strategies is the interaction of factors (e.g., release season, release size, stocking density, release habitat, etc.). Here, we summarize seasonal and size-dependent patterns of survival and growth for juvenile blue crabs using long-term field tethering and experimental releases of hatchery-reared cohorts within the Rhode and South Rivers, Maryland, USA, and review the direct and interactive effects of these factors. Survival of both tethered and free-ranging hatchery-reared juvenile crabs was high in early spring and fall and lowest in summer. Survival was largely independent of size during spring and fall, but increased with size in summer, indicating that optimal size at release varies seasonally. Hatchery-reared juveniles from spring releases grew rapidly, matured during their first season, and migrated to the spawning sanctuary in the fall of their first year. While release season and size each had direct effects on enhancement success, the results also highlight the important interaction between release season and size on enhancement success using the blue crab in Chesapeake Bay as a model.

Keywords stock enhancement, release strategies, blue crab, *Callinectes sapidus*, survival

INTRODUCTION

The productivity of estuarine and marine ecosystems is declining worldwide principally as a result of coastal development and associated human impacts (Lotze et al., 2006). In response, fishery stocks that use coastal habitats are also declining (Food and Agriculture Organization (FAO), 2004). To halt these declines, researchers and managers are investigating the efficacy of recovering stocks using alternative strategies, such as habitat restoration and stock enhancement. Stock enhancement involves the release of hatchery-reared individuals to augment fishery stocks (Bell et al., 2006) and is a potential strategy that has received attention due to both its intuitive appeal and an aversion of managers to implement stricter fishery regulations (Travis et al., 1998). Stock enhancement may be particularly useful for severely depleted fisheries and has been used with varying success for a diverse range of taxa (e.g., Leber et al., 1995; Stoner and Glazer, 1998; Bannister and Addison, 1998; Davis et al., 2005b).

Despite a general increase in the use of stock enhancement, the experiments necessary to adequately assess its feasibility are often not conducted (Blankenship and Leber, 1995; Miller and Walters, 2004). Consequently, the effectiveness of many early stock enhancement programs remains uncertain. This information is now considered a critical aspect of stock enhancement, and scientific evaluation of stocking efforts is emphasized. In particular, experiments designed to identify release strategies that maximize survival of released individuals are necessary to fully evaluate the prospect for stock enhancement of a given species.

A suite of factors, including release size, release season, release habitat, and stocking density, have been identified as important to post-release survival and growth of stocked animals. Release size is widely recognized as an important factor impacting post-release survival and has been relatively well studied (Blankenship and Leber, 1995; Leber, 1995; Leber et al., 1995; Willis et al., 1995; Svasand and Kristiansen, 1990). Similarly,

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the effects of release season and stocking density have also been the subject of considerable effort (Glazer and Jones, 1997; Leber et al., 1997, 1998; Kellison and Eggleston, 2004). Fewer studies, however, have attempted to assess the interaction of multiple release strategies on enhancement success (Bilton et al., 1982; Leber et al., 1997, 1998), yet these interactions may be critically important in many species.

The blue crab is economically and ecologically important along the Atlantic and Gulf coasts of the United States, particularly in Chesapeake Bay. However, despite significant management efforts to reduce fishing pressure and improve habitat quality, the blue crab population remains near an all-time low in the bay's most lucrative fishery. Both the sustained period of decline and the persistence at low levels are unprecedented for the Chesapeake blue crab stock. Spawning stock biomass has declined by 84% since 1991, with concurrent declines in mean size of mature females at spawning grounds and larval recruitment (Lipcius and Stockhausen, 2002) providing additional reason for concern. Further, current evidence indicates that the stock is now recruitment limited. Persistent declines have spurred investigations into the feasibility of stock enhancement as a potential management tool to aid in restoration of blue crab stocks in Chesapeake Bay. Initial research to evaluate the prospect of blue crab enhancement in the Bay is encouraging and shows that hatchery-reared crabs can substantially augment natural populations at small scales (Davis et al., 2005b; Hines et al., 2008; Zohar et al., 2008). A key next step is to evaluate the effects of differing release strategies on stock enhancement success for this species. Herein, we present results from two distinct experimental methods: (1) long-term field tethering, and (2) small-scale releases of hatchery-reared cohorts, designed to assess the direct and interactive effects of release season and size on stock enhancement success for the blue crab in Chesapeake Bay.

STUDY AREAS AND METHODS

We conducted experiments using two methods: (1) field tethering and (2) small-scale field releases of hatchery-reared juveniles. Both techniques provide important results for assessing the impacts of release season and size on enhancement success. While field releases of free-ranging, hatchery-reared individuals provide the best test of release effects on survival, field tethering provided some advantages that warranted their inclusion: (1) they provided a long-term, standardized measure of relative survival, (2) they included a broader range of size classes, (3) they facilitated comparison with previous tethering studies, and (4) they provided an independent measure of survival for comparison with field releases. Both field tethering and release experiments were conducted at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland, USA, and in relatively small (0.2–8 ha) natural cove systems located within the nearby Rhode and South Rivers (Figure 1). Both river systems are temperate, mesohaline subestuaries with wide seasonal variation in temperature (2–30°C) and salinity (3–17 ppt). All field tethering was conducted at a single site (Canning House Bay) within the Rhode River (Figure 1c). In contrast, hatchery-reared cohorts of juvenile blue crabs were released into various relatively shallow cove systems (<1.5 m) throughout the Rhode and South Rivers, which serve as typical nursery habitats for wild juveniles in upper Chesapeake Bay (Figure 1c).

Field Tethering

Seasonal and size-dependent patterns of survival were assessed using field tethering data with wild juvenile blue crabs (20–70 mm carapace width (CW)) conducted annually during June–August. A total of 1,354 crabs were tethered during 1990–2005 (76–141 per year; 24–52 per month). Tethering experiments were also conducted in April, September, and October in some years. Although tethering experiments were conducted with wild juveniles, we observed few differences between survival rates of hatchery-reared and wild crabs both in tethering experiments and in simultaneous field releases of free-ranging, hatchery-reared and wild crabs (Hines et al., 2008; Young et al., 2008). Thus, survival rates of wild juveniles appear to be representative of hatchery-reared crabs. Tethering is an effective means to measure relative survival rates of mobile fauna, and the technique has been successfully employed to assess survival of blue crabs in previous experiments (Hines and Ruiz, 1995; Pile et al., 1996; Lipcius et al., 2005). Further, experimental bias often associated with tethering (Petersen and Black, 1994) was not problematic in earlier studies conducted in unvegetated habitats similar to those in this study (Hines and Ruiz, 1995; Lipcius et al., 2005).

To begin a monthly tethering trial, two groups of approximately 12–13 intermolt juvenile blue crabs were fitted with a monofilament harness around the lateral spines that secured the crab to the end of a steel leader and attached 0.75-m monofilament line. The steel leader minimized the ability of crabs to free themselves by cutting the monofilament line. A metal spike was attached to the monofilament on the end opposite the crab, and a small float was affixed to each spike so tethered crabs could be easily relocated in the field. Once tethered, crabs were deployed in the field by anchoring the spike into the substrate. Tethered crabs were placed at least 2 m apart in the field to eliminate interaction between individuals. Survival rates of tethered crabs were assessed after 24 h in the field by checking tethers and identifying the fate (e.g., alive or dead) of each of crab. Previous studies have identified characteristic remains of tethered blue crabs preyed upon by known predators in controlled laboratory experiments (Hines and Ruiz, 1995) and allowed for accurate identification of the source of mortality of field tethered crabs.

To assess the effects of season and size on survival rates, proportional survival (number alive after 24 hr/number tethered) was calculated for each month (April, June, July, August, September, October) and size class (small: CW

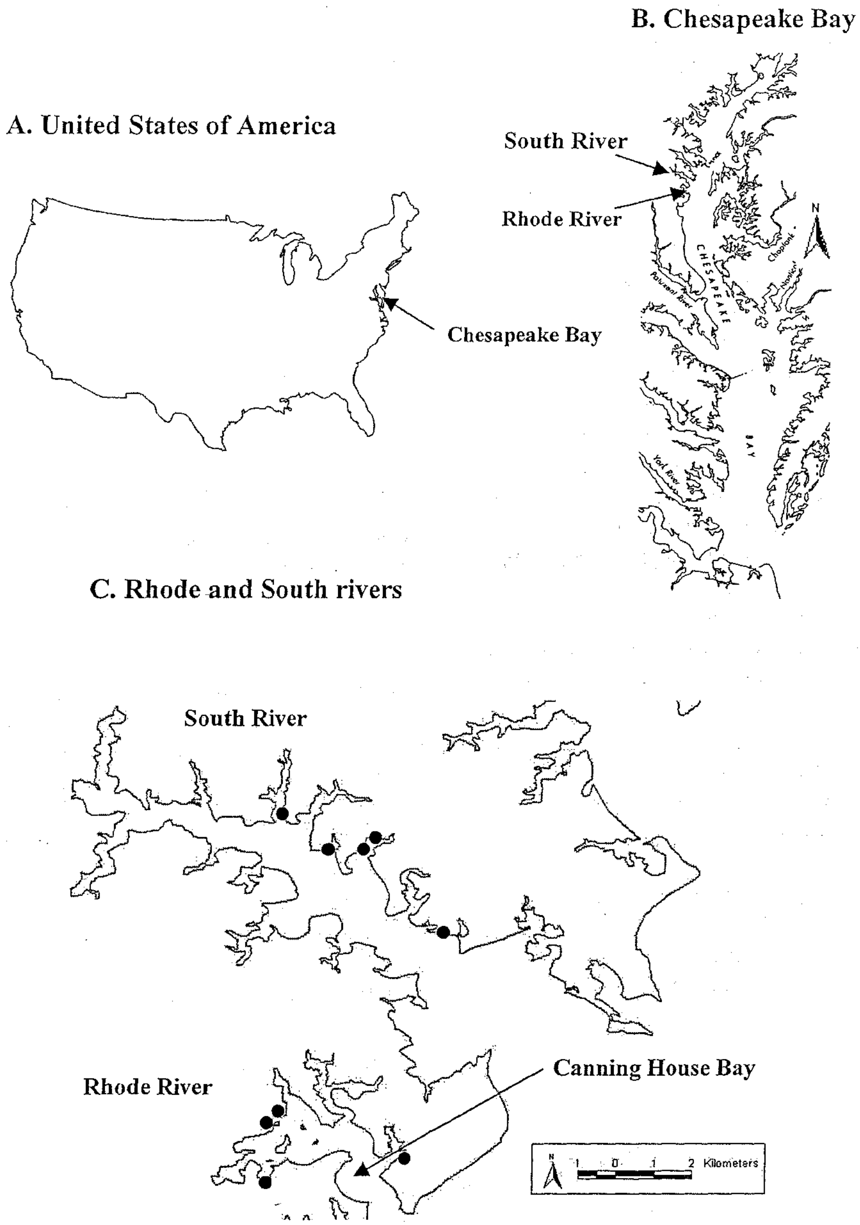

Figure 1 Locations of study sites in the Rhode and South River subestuaries in upper Chesapeake Bay: (A) United States of America, (B) Chesapeake Bay, (C) Rhode and South Rivers. The location of tethering experiments within the Rhode River (Canning House Bay) and release locations (solid circles) in the Rhode and South Rivers are shown.

<40 mm; large: CW >40 mm) within a given year. We compared proportional survival among months (June, July, August) and between size classes (small, large) using a two-way analysis of variance (ANOVA) model with a Ryan-Einot-Gabriel-Welsh-Q (Ryan's-Q) multiple comparison test. A non-significant Levene's test ensured that the assumption of homogeneous variances was met. All statistical analyses were conducted using SAS v.9.1.3 (SAS Institute, Inc., Cary, NC, USA). Because there was limited data for April ($n = 2$), September ($n = 2$), and October ($n = 1$), these months were not included in the ANOVA analysis. However, while insufficient replication in these months precluded formal statistical analyses, these data were useful to examine seasonal patterns of survival qualitatively.

Source of Hatchery-Reared Juveniles

Hatchery-reared juvenile blue crabs for field release experiments were obtained from the University of Maryland Biotechnology Institute's Center of Marine Biotechnology (COMB, Baltimore, MD 21202, USA). Hatchery crabs were spawned in the laboratory from mated mature females collected from the wild and reared through larval (zoea), postlarval (megalopae), and juvenile stages to 20 mm CW (Zmora et al., 2005). Hatchery-reared crabs were not exposed to natural conditions before use in field experiments.

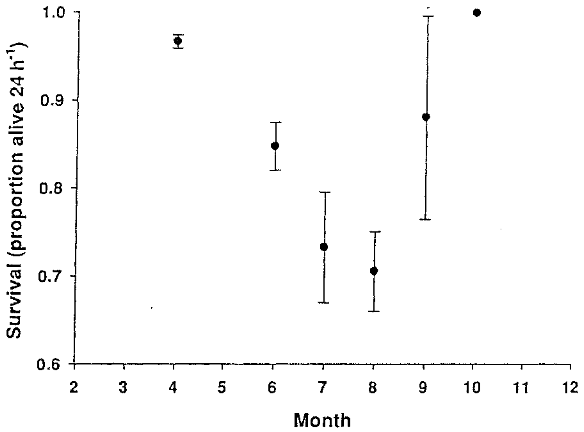

Figure 3 Seasonal variation in survival rates (mean ± SE) of tethered juvenile blue crabs (20–70 mm carapace width) over 24 hr. A total of 1,354 crabs were tethered over 16 years (1990–2005); the number of crabs contributing to each monthly mean varied and ranged from a minimum in April (24 crabs) to a maximum in August (449 crabs).

Field Releases

From 2002 through spring 2006, we tagged and released 124,000 hatchery-reared juveniles (17,000–31,000 juveniles per year) in 29 individual cohorts into nursery habitats of the upper Chesapeake Bay (Figure 1). Hatchery-reared cohorts were comprised of 1,000–14,000 individuals and were released from April–October. To distinguish hatchery-reared individuals from wild counterparts, hatchery crabs were double-tagged using coded microwire tags (CWTs) and elastomer tags before release. CWTs have been used successfully in previous studies with blue crabs (Davis et al., 2005b), have negligible effects on mortality and growth, and are retained through molting (Davis et al., 2004b). Release coves were then sampled over time at fixed stations with two gear types: a beach seine (16 m length, 2 m height, 6mm mesh size) and a benthic sled (1 m width, 6 mm mesh size), so that at least 10% of the release cove was sampled (range 10–37%). Beach seines allowed for effective recapture of hatchery-reared and wild individuals in shallow near-shore habitats, and trawls sampled deeper areas of the coves. Recapture data (CPUE) was adjusted for gear efficiency, tag loss, emigration, and area sampled (see Davis et al., 2004a, 2005b) to estimate the total number of hatchery-reared crabs alive within the release cove at each sampling period. Survival was calculated as the number of hatchery-reared crabs alive at each sampling period divided by the total number released. The mathematical equations used to calculate survival for releases of hatchery-reared crabs are detailed in Davis et al. (2005b).

We compared survival to maturity among release seasons (spring, summer, fall) using a one-way ANOVA model with a Ryan's-Q multiple comparison test. Because there was a limited number of releases in some months (e.g., only one release occurred in May), data from individual releases were pooled by release season: spring (April–May: $n = 7$ releases, 35,000 crabs total), summer (June, July, August: $n = 16$ releases, 59,000 crabs total), and fall (September–October: $n = 6$ releases, 28,000 crabs total). A non-significant Levene's test ensured that the assumption of homogeneous variances was met.

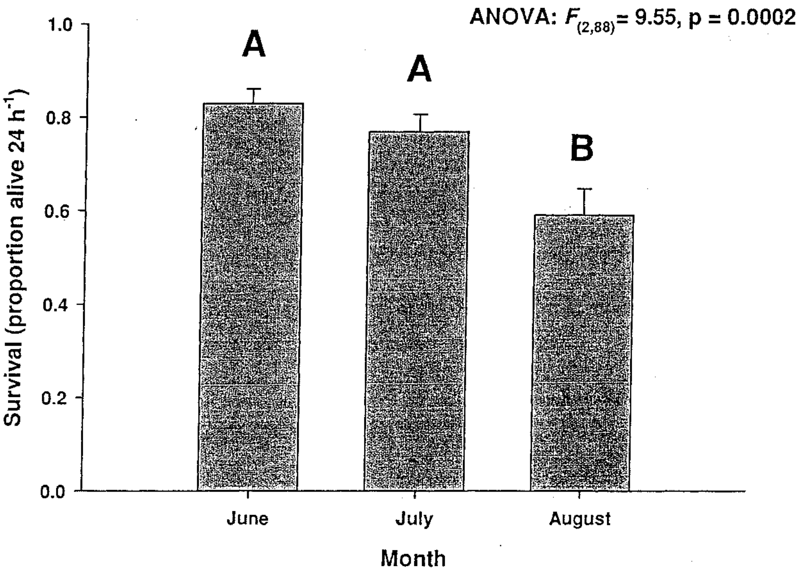

Figure 2 Mean survival (+SE) of tethered blue crabs (30–70 mm carapace width (cw)) over a period of 24 hr as a function of month ($n = 16$ for each month). Letters above the data denote significant differences ($p < 0.05$) between treatments (Ryan-Einot-Gabriel-Welsh-Q multiple comparison test; see text for details).

RESULTS AND DISCUSSION

Effects of Release Season

Survival of tethered juvenile blue crabs in the Rhode River declined from June–August and was significantly different among months (ANOVA, $F_{(2,88)} = 9.55$, $p = 0.0002$; Figure 2). When considering data from all months, survival of tethered crabs was high in April, declined to a minimum in August, and then increased through fall (Figure 3). Survival of tethered crabs in the Rhode River in summer–fall (0.70–0.88 24 h^{-1}; Figures 2–3) was comparable to survival rates of similarly sized blue crabs (25–55 mm CW) for upriver subtidal sand (0.87 24 h^{-1}) and mud flats (0.80 24 h^{-1}) in the lower Chesapeake Bay, but much higher than downriver sites (0.13–0.47 24 h^{-1}; Lipcius et al., 2005). Decreased survival in lower bay downriver sites was attributed to density-dependent growth and mortality, increased abundance and diversity of key fish and invertebrate predators (Lipcius et al., 2005), and reduced food availability (Seitz et al., 2005). In the upper Chesapeake Bay, releases of hatchery-reared juveniles in the spring and fall also resulted in the highest survival to maturity and maximized production of mature females from releases (Figure 4); however, differences were not statistically significant (ANOVA; $F_{(2,27)} = 1.86$; $p > 0.05$) among release seasons. Although survival to maturity from summer releases was 36% lower in summer relative to spring and fall (Figure 4), it is possible that our inability to detect significant differences was a result of high variability in survival related to differences in initial release conditions (e.g., stocking density, year, cove) other than release season, which are known to affect survival of juvenile blue crabs (see Hines et al., 2008). To remove confounding factors and isolate seasonal effects, we also compared two sets of releases that occurred within the same sites and years and at similar stocking densities, but in different seasons. Survival to maturity was higher for crabs released in spring than in summer (Figure 5a) and lower for crabs released in summer than in fall (Figure 5b). While these comparisons are qualitative due to a lack of replication, future analyses will focus on multivariate statistical analysis of survival data to separate the effects of multiple stocking variables.

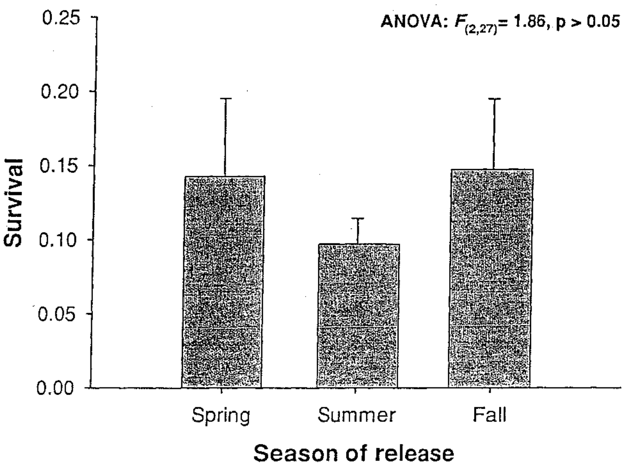

Figure 4 Survival to maturity (mean + SE) of hatchery-reared cohorts released in the Rhode and South Rivers during spring (April–May, $n = 7$), summer (June–August, $n = 16$), and fall (September–October, $n = 6$) pooled over all years (2002–2006).

Overall, observed seasonal patterns of survival were similar between tethering (Figures 2 and 3) and field releases (Figures 4 and 5), and appear to be primarily driven by seasonal changes in the abundance of key predators. The majority of mortality in our tethering experiments was directly attributable to cannibalism based on the characteristics of tethered crab remains that were indicative of predation by adult blue crabs (Hines and Ruiz, 1995). Further, peak mortality rates of juvenile crabs observed during August coincides with the period of highest abundance of large (CW >127 mm) blue crabs captured in an annual trawl survey conducted in the Rhode River (Hines, unpublished data). Previous studies have also identified inter-cohort cannibalism as the major source of mortality for juvenile blue crabs in the upper Chesapeake Bay (Ruiz et al., 1993; Dittel et al., 1995), and may account for as high as 97% of predation on juveniles in the Rhode River (Hines and Ruiz, 1995). Predation may also be exacerbated in summer as adult blue crabs switch from infaunal bivalves to alternative prey, such as juvenile blue crabs, as bivalve density declines. In late spring and early summer in the Rhode River, the abundance of large predatory blue crabs (CW >100 mm) is strongly correlated to bivalve density, indicative of an aggregative response of large crabs to bivalve prey (Clark et al., 1999). A similar aggregative response of crabs to infaunal clam (*Macoma balthica*) densities was also reported in upriver sites of the York River in lower Chesapeake Bay (Seitz and Lipcius, 2001; Seitz et al., 2003). Conversely, as clam densities declined within the Rhode River over the course of summer into fall, large crabs aggregated in areas with high densities of juvenile crabs as recruitment of wild juveniles increased. Thus, prey switching from clams to juvenile blue crabs, as relative prey abundances change seasonally, may be the mechanism underlying the observed patterns of mortality. Additionally, high predation rates during summer may be a result of high water temperatures which increase predator activity. Releasing during periods of low water temperature when predators are less active has been recommended for both queen conch (Stoner and Glazer, 1998) and scallops (Barbeau et al., 1996).

Our results add to a growing body of evidence showing that release season can have a direct and substantial impact on stocking success (Leber et al., 1997, 1998). For example, survival rates of cultured queen conch released in the Bahamas were higher in fall as water temperature declined (Stoner and Glazer, 1998). Similarly, reared juvenile lobsters released in coastal Norway suffered higher predation rates in summer than in winter due to high densities of labrid fishes during summer (van der Meeren, 2000). Recapture rates for red drum were higher for fish released in fall than in summer (Willis et al., 1995).

Although survival did not differ between spring and fall (Figures 3 and 4), releasing hatchery-reared blue crabs in the

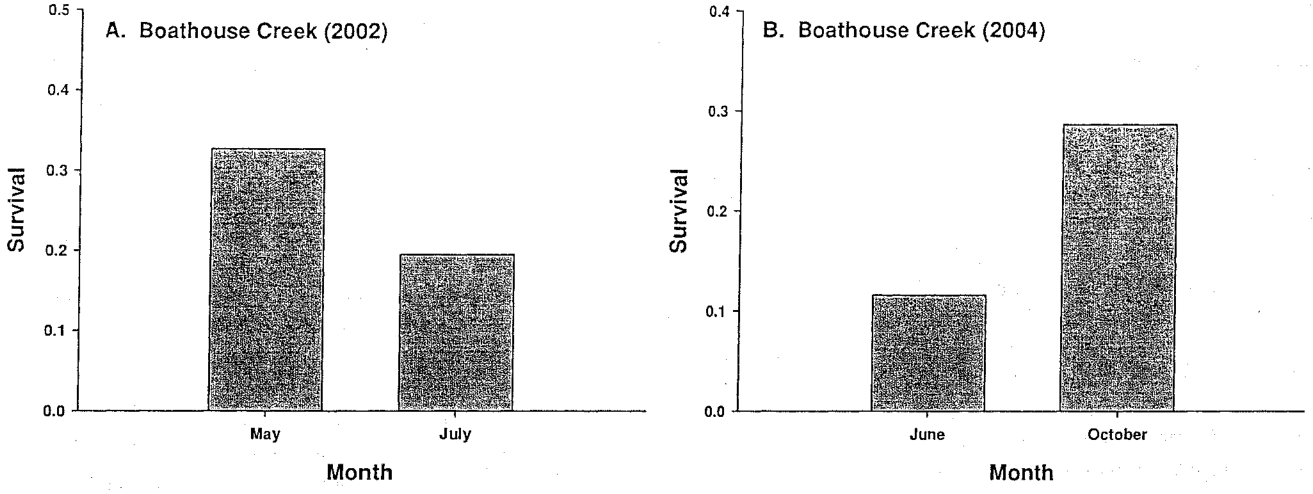

Figure 5 Survival to maturity of two hatchery-reared cohorts released into (A) Boathouse Creek during May and July of 2002, and (B) Boathouse Creek during June and October of 2004. No statistical analyses were conducted because the experiment was not replicated; therefore, only qualitative inferences can be made from patterns in the data (see text for details).

upper Chesapeake Bay in spring may be preferable for several reasons. Cohorts of juveniles released early in the season encountered abundant benthic prey resources and increasing water temperatures—conditions that allowed for rapid growth. Peak growth rates of 1.2 mm d^{-1} observed in our field releases are among the highest reported for blue crabs (Ju et al., 2001). Crabs released in spring grew to maturity within the first season (in as few as 3 mo.) of release, whereas cohorts released in fall overwintered in release coves and grew to maturity the next year (Figure 6). Thus, females from spring releases mate and migrate to spawning areas in the lower bay within their first year (Hines et al., 2008; Zohar et al., 2008). This is of particular importance because mature females are vulnerable to low water temperatures during winter in the upper Chesapeake Bay and can suffer substantial mortality during harsh winters (Rome et al., 2005). Crabs released in spring, however, will have migrated to lower Bay spawning areas during fall of the first season of release (Aguilar et al., 2005; Aguilar et al., 2008), where higher temperatures and salinity increase overwintering survival.

Interactions between hatchery-reared individuals and wild conspecifics is central to evaluating whether hatchery-reared individuals increase stocks or simply replace wild stocks (Hilborn, 2004). These interactions may be particularly important for the blue crab, given the cannibalistic nature of the species (Hines and Ruiz, 1995; Ryer et al., 1997). We observed no displacement of wild juvenile blue crabs from release coves in all release

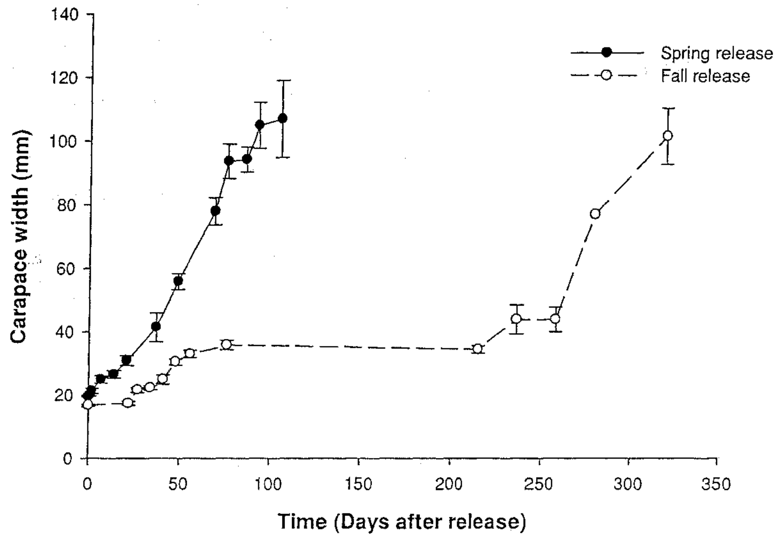

Figure 6 Mean size (carapace width; CW ± SE) of two typical hatchery-reared cohorts following release in spring in the South River (solid line) and fall in the Rhode River (dashed line). The cohort released in spring (14,295 hatchery-reared crabs) grew rapidly to maturity in the year of release, while the cohort released in fall (4,800 hatchery-reared crabs) overwintered in release coves and reached maturity in the following year. Modified from Davis et al., 2005b.

seasons and captured relatively few hatchery-reared crabs emigrating from release coves (Davis et al., 2005a). Further, current densities of wild juvenile blue crabs in the Rhode River are well below historical levels. Thus, collective evidence suggests that upper bay nurseries are currently below carrying capacity in all seasons. Spring releases may still be advantageous because cohorts released in spring will grow rapidly (Figure 5) and emigrate from shallow release coves before the peak recruitment of wild juveniles into these shallow nursery habitats in the fall, reducing the potential for cannibalism. However, we also recognize that particular caution is warranted when releasing animals outside of natural periods of recruitment, since these releases may result in unexpected inter- and intraspecific (Willis et al., 1995) interactions since hatchery-reared individuals will encounter a community structure different than wild stocks.

Effects of Release Size

Survival of tethered juveniles was significantly higher (ANOVA; $F_{(1,88)} = 12.35$; $p = 0.0007$) for large crabs (CW >40 mm) than for small crabs (CW <40 mm; Figure 7). Survival of juvenile blue cabs increased with size until a size of 40–50 mm CW, but crabs 40–70 mm CW had similar survival rates, indicating that individuals attain a partial refuge from predation at this size (Figure 8). Several mechanisms may explain the size-specific patterns of survival of juvenile blue crabs in our study. Larger individuals may attain a size refuge from gape-limited predators (Hart and Hamrin, 1988), or they may be more able to fight off (Hines and Ruiz, 1995) or escape (Christensen, 1996) predatory attacks. Additionally, molting frequency of blue crabs is inversely related to size, increasing the risk of mortality for small crabs since they are particularly susceptible to predation following molting when their shell is soft and they are effectively immobile (Ryer et al., 1997). Our observed patterns of size-specific survival rates from tethering experiments were consistent with previous studies in Chesapeake Bay which report increasing survival with size for blue crabs (Hines and Ruiz, 1995; Pile et al., 1996). In stocking experiments, release size is clearly an important factor mediating post-release survival in many species (Bilton et al., 1982; Svasand and Kristiansen, 1990; Leber, 1995, Leber et al., 1997). Size at release is an important consideration for blue crab stocking since releasing small hatchery blue crabs is advantageous to minimize behavioral deficits (Olla et al., 1998), avoid cannibalism in rearing tanks (Zmora et al., 2005), and reduce the costs of production associated with a prolonged grow-out phase necessary to rear larger crabs.

Interactive Effects of Release Season and Size

One important finding to emerge from our study was that the optimal release size may vary depending on the season of release. Because our ANOVA model detected a marginally significant interaction between release season and size (ANOVA; $F_{(2,88)} = 2.82$; $p = 0.065$), we also analyzed differences between size classes within each month separately. Release size was important for hatchery-reared cohorts released in summer (Figure 9b, c, d), but less important for those released during spring and fall (Figure 9a, e). The weak effect of release size on survival of hatchery-reared crabs released during spring and fall was likely because low predation pressure during these periods mitigated

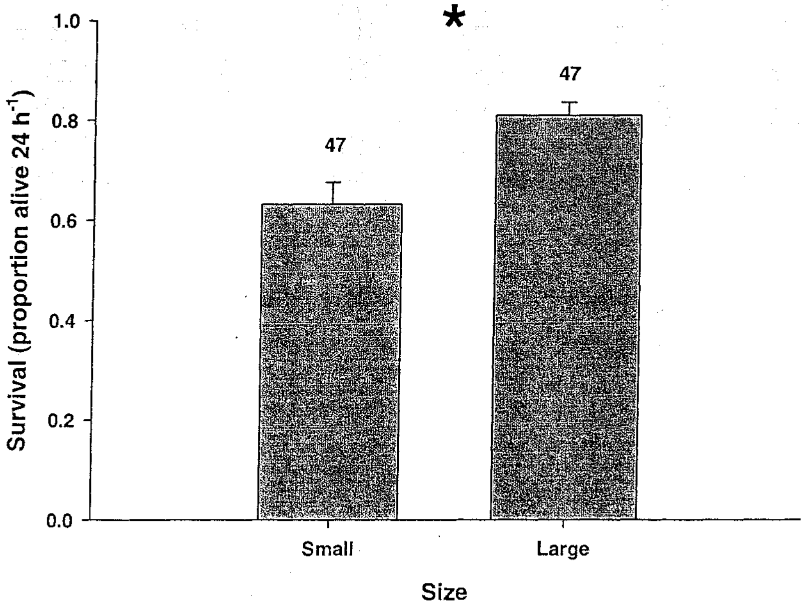

Figure 7 Survival (mean + SE) of small (carapace width; CW <40 mm) and large (CW >40 mm) tethered blue crabs over a period of 24 hr. Sample sizes are represented as numbers above data columns. Significant differences ($p < 0.05$) between treatments from a two-way ANOVA model are denoted by an asterisk (see text for details).

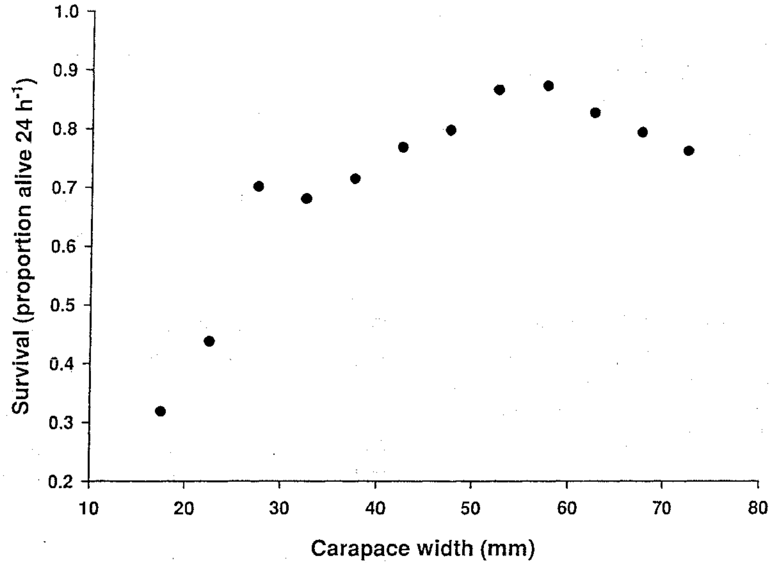

Figure 8 Survival (mean ± SE) of tethered blue crabs (20–70 mm carapace width; CW) over a period of 24 hr as a function of size (CW). Crabs were binned by 5-mm increments and pooled across all years and months to achieve adequate sample size for all size classes. The total number of crabs tethered was 1,354 crabs; however, the number of tethered crabs for each size class varied and ranged from 22–141 individuals.

the disadvantage of small size and allowed crabs of all sizes to persist. Thus, regardless of size, blue crabs released in spring grow rapidly to a size refuge of 40–50 mm CW before the period of heavy predation in summer. Small crabs released in summer (Figure 9b, c, d), however, probably suffered higher mortality as a result of the synergistic effects of size-dependent predation rates and overall high predation pressure in summer.

Our findings are similar to patterns reported for striped mullet in Hawaii in which recapture rates increased with increasing release size during summer, but not during spring when hatchery

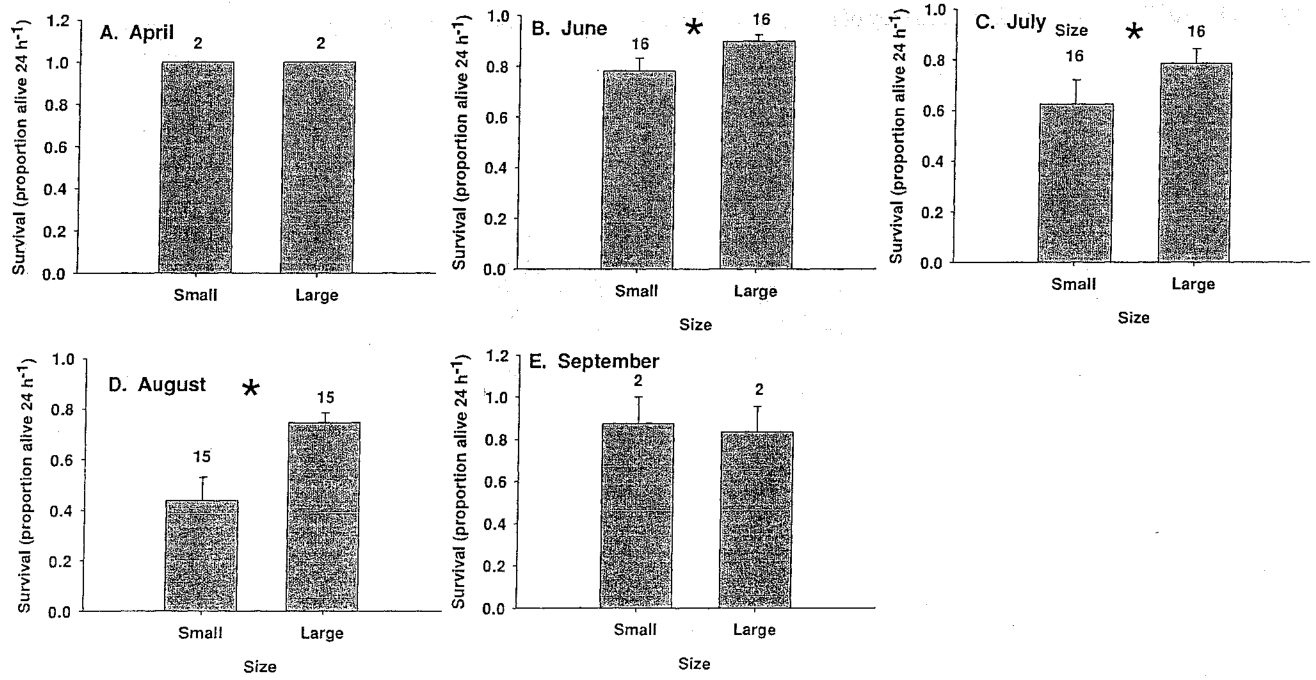

Figure 9 Survival of small (carapace width; CW <40 mm) and large (CW >40 mm) tethered juvenile blue crabs over a period of 24 hr by tethering month. Sample sizes are represented as numbers above data columns. Significant differences ($p < 0.05$) between treatments from a one-way ANOVA model are denoted by an asterisk (see text for details).

fish may have found refuge from predation by schooling with similar sized wild individuals (Leber et al., 1997). Similar interactions between release strategies were also reported for Pacific threadfin (Leber et al., 1998) and salmon (Bilton et al., 1982). Our results have clear implications for practical release strategies for blue crabs in upper Chesapeake Bay. From an ecological perspective, a strategy of releasing small individuals (~15–20 mm CW) in spring and fall when survival is largely independent of size (Figure 9a, e), and large individuals (CW >40–50 mm) in summer should maximize the contribution of hatchery crab released in upper bay nurseries to the spawning stock. A key next step is to evaluate these results within economic and logistical contexts (Kellison and Eggleston, 2004; Leber et al., 2005). For example, releasing large individuals during any season may not be cost-effective, or even logistically possible, when considering factors such as rearing costs or poor survival during the grow-out phase (Zmora et al., 2005).

CONCLUSIONS

The feasibility of stocking as a management tool to rebuild recruitment-limited fish stocks is often debated (Hilborn, 1998, 2004; Blaxter, 2000). However, there is a consensus among scientists that stocking programs should be based on "strong inference" (*sensu* Platt, 1964) obtained from ecological experimentation to evaluate their effectiveness (Miller and Walters, 2004). In this study, we summarize the impacts of release season and size on the effectiveness of enhancement for the blue crab in upper Chesapeake Bay. The key implications for blue crab enhancement include (1) survival rates of juvenile crabs varied seasonally and were high in early spring and fall and lowest in summer; (2) survival was largely independent of size during spring and fall, but increased with size in summer when predation rates peaked, indicating that optimal size at release varies seasonally; and (3) hatchery-reared juveniles from spring releases can mate and migrate to spawning grounds in lower bay during their first year, reducing the impact of mortality during harsh winters. Overall, the results illustrate the important direct and interactive effects of release season and size on enhancement success for hatchery-reared blue crabs released into upper bay nursery habitats. Whenever logistically possible, we suggest that experiments to determine optimal release strategies should include multiple factors and be conducted concurrently, since these designs allow for potentially important interactions between main factors to be examined.

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