Assessing the potential for stock enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*)

Jana L.D. Davis, Alicia C. Young-Williams, Anson H. Hines, and Yonathan Zohar

Abstract: In certain cases of severely depleted fishery stocks, combining stock enhancement with traditional management techniques may be a useful way of returning stocks to an exploitable size. The Chesapeake Bay stock of blue crabs (*Callinectes sapidus*) has declined over the past decade and appears to be recruitment-limited, making it an appropriate candidate for enhancement efforts. This study serves as a first step in determining whether large-scale enhancement of blue crab stocks is feasible. Four hatchery-raised cohorts of 4000 – 10 000 (25 000 in total) juvenile (6–30 mm carapace width, 58–70 days old) crabs were released in upper Chesapeake Bay coves. Sixty days after release, these crabs constituted 22%–79% of all crabs in the hatchery-crab size range (corresponding to an enhancement level of 28%–366%). Crabs released earlier in the summer reached maturity at the age of 6 months, younger than their wild counterparts. Estimated survivorship to maturity was 16%–20% for early-released crabs and 5–15% for late-released crabs. Late-released crabs, like wild crabs, had to overwinter before becoming mature. Our study suggests ways to improve success of hatchery-raised individuals that can be broadly applied across taxa. The results also contribute specifically to determining whether large-scale stock enhancement is possible in the case of the Chesapeake Bay blue crab.

Résumé : Chez certains stocks fortement réduits, la combinaison de mesures d'amélioration des stocks et de méthodes de gestion courantes peut être utile pour rétablir les stock à une taille exploitable. Le stock de crabes bleus (*Callinectes sapidus*) de la baie de Chesapeake a décliné au cours de la dernière décennie et semble limité par des problèmes de recrutement; c'est donc un bon candidat pour les efforts d'amélioration des stocks. Notre étude constitue une première étape pour déterminer si une amélioration du stock de *C. sapidus* à grande échelle est possible. Quatre cohortes de 4 000 à 10 000 (total de 25 000) jeunes (largeur de carapace, 6–30 mm; âge, 58–70 jours) crabes de culture ont été relâchés dans les anses supérieures de la baie de Chesapeake. Soixante jours après l'ensemencement, ces crabes représentaient 22–79 % des tous les crabes des classes de taille des crabes de culture, ce qui correspond à un niveau d'amélioration de 28–366 %. Les crabes relâchés plus tôt au printemps atteignent la maturité à l'âge de 6 mois, donc plus rapidement que les crabes sauvages. La survie à la maturité est estimée à 16–20 % chez les crabes relâchés tôt et à 5–15 % chez les crabes relâchés tard. Les crabes relâchés tard, tout comme les crabes sauvages, doivent passer l'hiver avant d'atteindre la maturité. Notre étude suggère des méthodes pour augmenter le succès d'individus élevés en culture qui sont largement applicables à d'autres taxons. Nos résultats contribuent aussi de façon spécifique à évaluer si des améliorations de stock à grande échelle sont possibles chez le crabe bleu de la baie de Chesapeake.

[Traduit par la Rédaction]

Introduction

Stock enhancement has been used in the management of severely exploited fisheries for over a century in several areas around the world with various degrees of success. Enhancement efforts encompass many approaches, such as increasing the amount of habitat to bolster habitat-limited populations and releasing juveniles to augment recruitment-limited populations (e.g., Masuda and Tsukamoto 1998; Castro et al. 2001). Within the approach of releasing juveniles, the range of techniques includes seeding areas in cases of sessile species (e.g., Barbeau et al. 1996), releasing mobile juveniles into isolated areas where they can be followed (e.g., Davenport et al. 1999), and releasing juveniles into the open ocean (Masuda and Tsukamoto 1998).

In an ideal stock-enhancement program directed toward recruitment-limited populations, individuals are reared in an aquaculture facility until they are beyond the initial phase of high early-life-history mortality and are then released into the natural population. Ideally, after release, these hatchery-

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Table 1. Aspects of the four batches (A–D) of hatchery-raised blue crabs (*Callinectes sapidus*).

Batch	Hatch date	Release date	Batch size (no. of crabs)	Release site (cove)[a]	Cove size (ha)	Mouth length (m)[b]	Initial density (no.·m^{-2})[c]
A	14 Feb.	2 May	3800	Boathouse Creek, RR	5.5	120	0.07
B	13 May	19 July	4800	Boathouse Creek, RR	5.5	120	0.09
C	17 June	15 Aug.	9600	Logan Pond, SR	3.0	5	0.33
D	30 June	9 Sept.	7000	Sheepshead Cove, RR	3.5	15	0.20

[a]RR, Rhode River; SR, South River.
[b]Size of the cove opening.
[c]Based on the number of hatchery-raised crabs initially released.

reared individuals contribute to the spawning stock, with a potential exponential impact on overall population size in subsequent generations depending on the degree of recruitment limitation.

Because stock enhancement may be accompanied by potential problems, enhancement is a controversial management method for many reasons (Washington and Koziol 1993; Bell and Gervis 1999; Li 1999). Hatchery-raised animals may not survive in the wild. Release of genetically homogeneous hatchery-raised individuals may reduce genetic variability in wild populations through inbreeding (Tringali and Bert 1998; Utter 1998). Hatchery animals may compete with and displace wild animals (Bannister et al. 1994; Castro et al. 2001). The potential for enhancement success may reduce or excuse management activities needed to reduce fishing effort or habitat degradation (Lichatowich 1999). Finally, increases in stock size due to hatchery successes may provoke a rise in fishing effort, and therefore greater pressure on the remaining wild individuals (Hilborn 1998; Bannister 2000). The controversy is fueled by the fact that most enhancement efforts, which date from at least a century ago, have not been studied in a quantitative manner (Bannister et al. 1994; Heppell and Crowder 1998; Crowe et al. 2002). Such study did not begin until the late 1980s (Leber 1999).

The recent recognition of these problems has led in some cases to refinement of the enhancement process. Methods to better select candidate species have been developed (Blackenship and Leber 1995). Advances in tools such as tagging have allowed better assessment of survivorship of both hatchery-raised and wild animals (Blackenship and Leber 1995). Most importantly, calls have been made for quantitative study of small-scale enhancement efforts before investment in large-scale programs begins (Leber 1999; Crowe et al. 2002). To date, such studies have concentrated on finfishes, as this group is the focus of most enhancement efforts (Secor and Houde 1998; Thorpe 1998; Wilson et al. 1998). For example, Japan has enhancement programs for 34 finfishes but only 12 crustaceans (Masuda and Tsukamoto 1998). Mollusks (but see Kojima 1995; Arnold 2001; Beal et al. 2002) and crustaceans (but see Bannister and Addison 1998; Su 1988; Castro et al. 2001), groups with different life cycles and habitats and for which different fishing methods are used, have received less attention.

The goal of the present study is to provide a quantitative assessment of small-scale experimental enhancement of the blue crab, *Callinectes sapidus*. This crab, ecologically important, also supports the most economically important fishery in Chesapeake Bay, Maryland, USA (Rugulo et al. 1998). Over the past decade, spawning-stock abundance has declined by 81%, mean size at maturity by 9%, and postlarval recruitment by an order of magnitude (Lipcius and Stockhausen 2002). The optimal means of achieving sustainable stocks of highly exploited species such as the blue crab is to manage the natural population effectively (Hilborn and Walters 1992). However, the level of decline exhibited by the Chesapeake Bay population suggests that effective management may ultimately require, in addition to more traditional management techniques, responsible stock enhancement aimed at restoring breeding stocks.

Though the success of some enhancement efforts has begun to be quantified for several decapods, mostly lobsters (e.g., Bannister and Addison 1998; Castro et al. 2001), these species have very different life histories than blue crabs in the Chesapeake Bay. The most similar decapod for which stock enhancement has been attempted is the swimming crab, *Portunus trituberculatus*, of which 28–42 million hatchery-reared juveniles are released annually in Japan (Masuda and Tsukamoto 1998; Ariyama 2000; Secor et al. 2002). However, analysis of enhancement success of the *P. trituberculatus* program has been minimal (Secor et al. 2002). In this study, we aimed to determine whether enhancement of blue crab populations is possible at small spatial scales. Specific goals were to (*i*) determine survivorship of hatchery-raised crabs released into the field, (*ii*) measure how long hatchery crabs remain in local release areas, (*iii*) compare growth rates of crabs released at various times of the spring and summer, and (*iv*) determine whether hatchery crabs displace wild crabs or populations are far enough below carrying capacity that overall population size is enhanced by the release of hatchery crabs. Our goal was to provide a rigorous, quantitative test of the potential for stock enhancement on an initially small scale for blue crabs in Chesapeake Bay.

Methods

Hatchery-raised crabs

Hatchery-raised blue crabs were produced at the University of Maryland Biotechnology Institute's Center of Marine Biotechnology (UMBI-COMB) according to methods described by Zmora et al. (2005). Four batches of crabs were hatched in February (batch A), May (batch B), mid-June (batch C), and late June 2002 (batch D) from four mature females collected from Chesapeake Bay and therefore already storing the sperm of wild males. Approximately 2 months after hatching and 1 month after metamorphosis to first instar, at a mean size of 18 mm carapace width (CW) (range 6–30 mm CW), crabs in each batch were tagged with visual-implant elastomer, microwire, or both (Davis et al. 2004*a*).

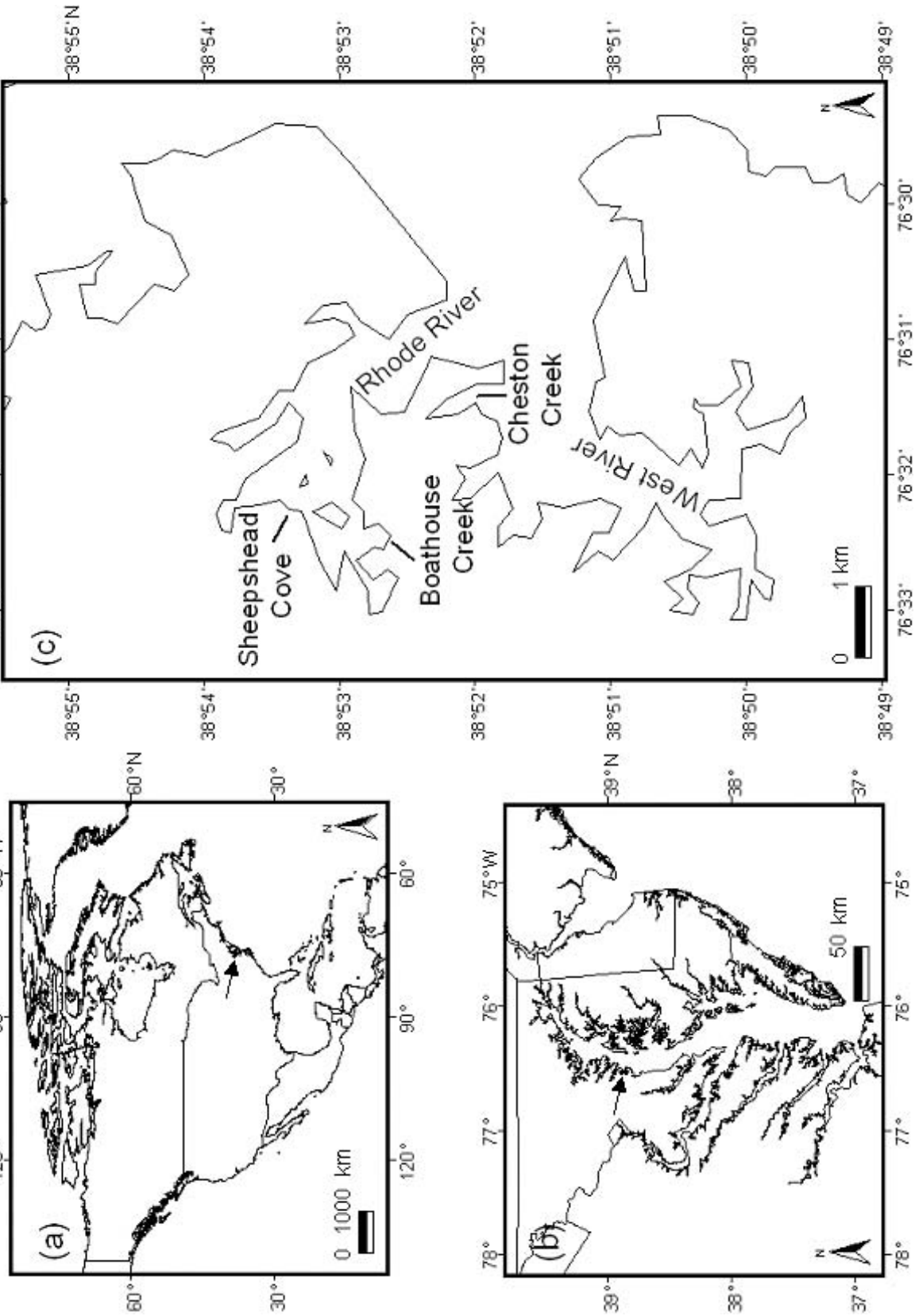
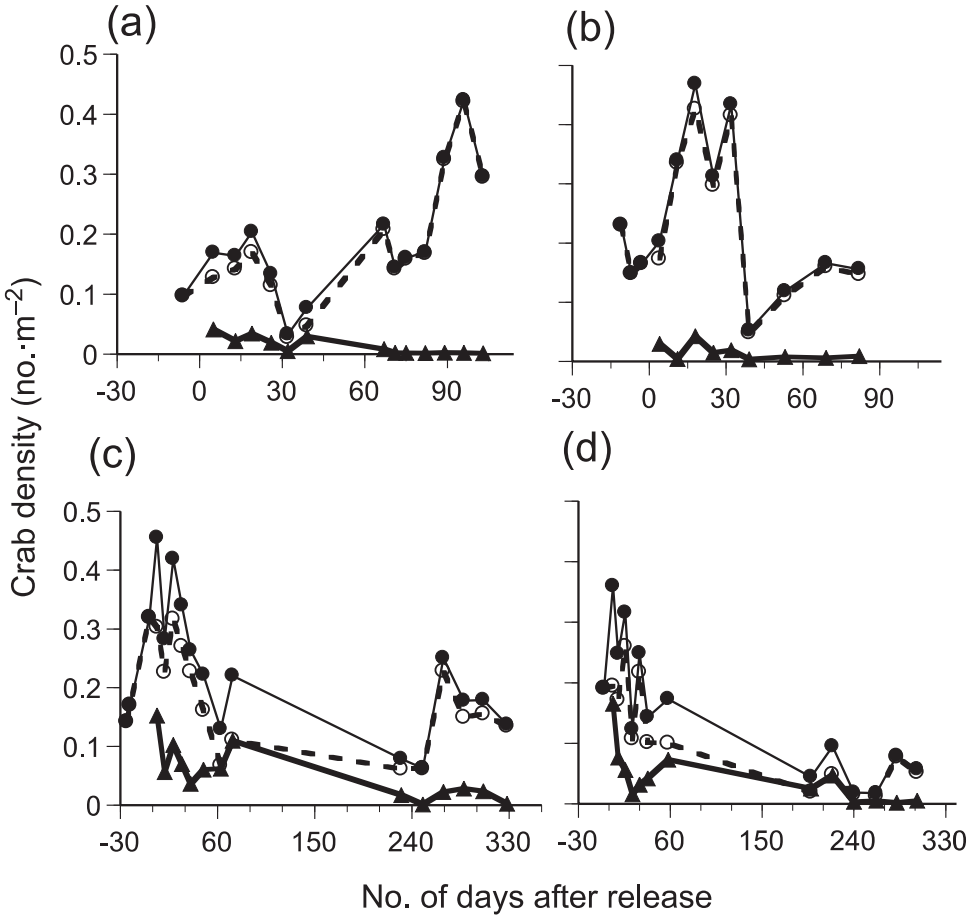


Fig. 1. Locations of several of the sites used in Chesapeake Bay, USA. Sheepshead Cove and Boathouse Creek were enhancement sites and Cheston Creek was used as a control site. The arrow in *a* shows the location of Chesapeake Bay within the USA and the arrow in *b* indicates the location of the study sites within Chesapeake Bay.

Fig. 2. Densities of blue crabs (*Callinectes sapidus*) in the enhancement sites (- -○- -, all wild crabs; —▲—, all hatchery-raised crabs; —●—, total crabs (hatchery + wild)). (*a*) Batch A, which had an average enhancement value of 7%. (*b*) Batch B, also with an enhancement value of 7%. (*c*) Batch C, which had an enhancement level of 39%. (*d*) Batch D, with an enhancement level of 40%.



The number of released crabs in each batch ranged from 3800 to 9600 (Table 1).

Enhancement and control sites

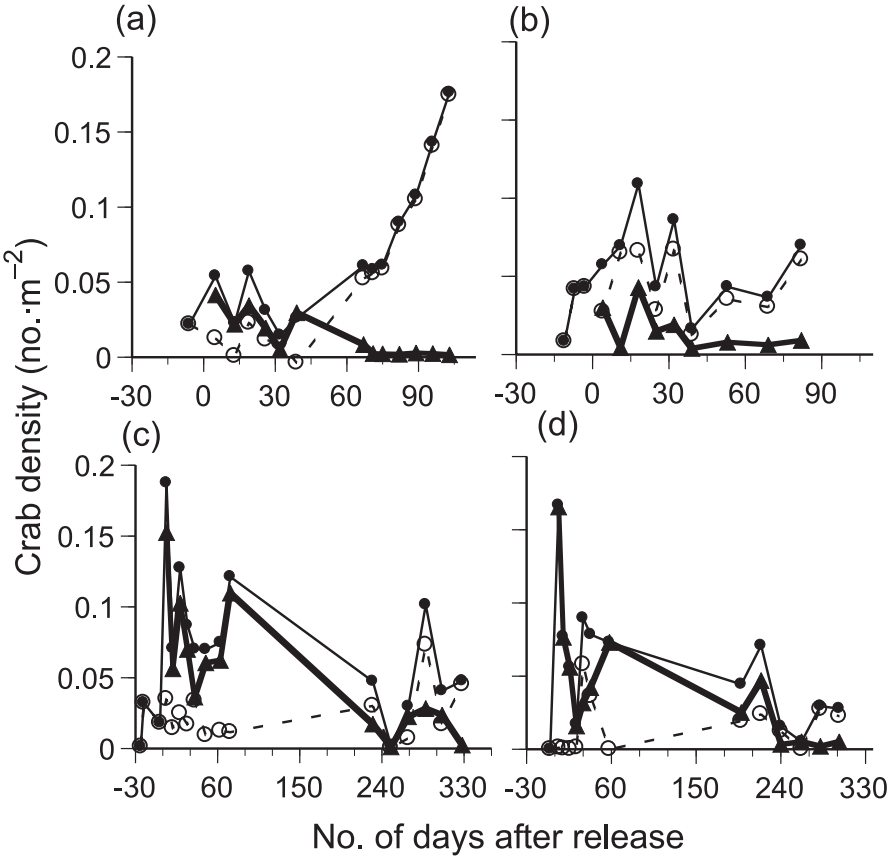
The batches of tagged hatchery crabs were released into the wild in three semi-enclosed coves (Boathouse Creek, Sheepshead Cove, and Logan Pond) in the Rhode and South rivers, two subestuaries of the upper western Chesapeake Bay (Table 1; Fig. 1). Semi-enclosed coves were chosen to encourage retention of crabs within the sampling region, thereby limiting the loss of hatchery crabs due to emigration that would be erroneously attributed to mortality. Crabs were distributed along several 50- to 100-m lengths of shoreline near the heads of the coves, away from the cove mouths. These regions are referred to as release areas. The ambit scale of crabs in this small size range has not been studied in detail, but previous studies of juvenile crabs in similar areas (van Montfrans et al. 1991) and in these coves (Davis et al. 2004*b*) indicated that few emigrated over a period of several weeks.

Wild crab densities were also measured in several control areas both before and after release of hatchery crabs of batches B, C, and D in the experimental sites. These dates of control-site sampling fell within 1 week, usually within 1 or 2 days, of experimental-site sampling. Several different control sites were used for comparisons. Cheston Creek in the West River (Fig. 1) was used as a control site for the releases of batches B and C. Sheepshead Cove, prior to the release of batch D, was used as a control site for batch C. Logan Pond, prior to the release of batch C, was used as a control site for batch B. Boathouse Creek, though hatchery crabs had been released here 1 month before batch C and 2 months before batch D, was used as an additional control site for these last two batches, ignoring those hatchery crabs present. The main stem of the Rhode River was used as a control site for batches B, C, and D.

Field sampling

Each cove was sampled 1–3 times before the addition of hatchery crabs to determine background levels of wild blue crabs, and at approximately weekly intervals after release of each cohort. Two sampling methods were used: beach seining and epibenthic sled tows. Beach seines were 16 m long, were 3 m tall, had 6 mm mesh, and were pulled 25 m parallel to shore by two people standing approximately 9 m apart, and therefore sampled approximately 225 m^2 in surface area. The 1 m wide, 50 cm tall epibenthic sled had a 2 m long, 6 mm mesh net with a 500-μm cod-end. The sled was pulled for 100 m by a shallow-draft boat powered by a small outboard motor. Gear efficiency was determined in separate studies: for the seine net by releasing known numbers of tagged crabs of 10–130 mm CW into enclosed regions and

Fig. 3. Densities of just wild crabs in the hatchery crab size range (- -○- -), all hatchery crabs (—▲—), and total crabs (hatchery + wild) in the hatchery crab size range (—●—) in the enhancement sites. (*a*) Batch A, which had an average enhancement value of 24%. (*b*) Batch B, with an enhancement value of 35%. (*c*) Batch C, which had an enhancement level of 225%. (*d*) Batch D, with an enhancement level of 352%.



seining immediately afterward (J.L.D. Davis and A.C. Young-Williams, unpublished data), and for the sled by towing over known densities of tagged crabs (A.C. Young-Williams and J.L.D. Davis, unpublished data).

Both pre- and post-release sampling was conducted at predetermined sites within each cove. Owing to the large area surrounding the coves and the low probability of recovering tagged crabs outside the focus regions, sampling was confined to the coves. In Boathouse Creek, 10 seining stations were distributed around the cove perimeter and 21 sled-tow sites were identified throughout the cove. Logan Pond contained 6 seine and 10 sled-tow sites. Sheepshead Cove had 5 seine and 10 sled-tow sites. All major habitat zones of each cove were represented; however, sampling sites were not distributed uniformly. Sampling effort was proportionally high in crab release areas. In total, 7% of the surface area of each cove was sampled; however, 25%–32% of the area within 300 m of the initial release points was sampled, as opposed to 4%–5% of non-release areas. Consequently, calculations of population abundance were adjusted to account for the spatial distribution of sampling efforts.

For all blue crabs collected in each seine and sled tow, both tagged and wild, we measured CW and identified gender. All crabs were then returned to the cove in the approximate catch location. Sampling was conducted in each cove usually once per week, though at times once per 2 weeks, until tagged crabs were no longer recaptured (4–12 months). However, sampling was discontinued during December–February, when crabs cease activity.

All control sites but the Rhode River main stem were sampled with the same gear (beach seines and epibenthic sled) as the release sites. In the Rhode River main stem, crab densities were sampled in four 2250-m^2 areas with a 2.5-m otter trawl (as described in Hines et al. 1987) at times matching "before" and "after" sampling of the three batches B, C, and D. Though the sampling equipment was different, before and after comparisons of crab densities at this site provided an indication of whether background crab densities changed.

Data analysis

The number of hatchery crabs in the release and non-release areas of each cove during each sampling period was estimated as the number of tagged crabs collected plus the number of crabs estimated to have lost their tags (see Davis et al. 2004*a*) and corrections for catch efficiency, divided by the percentage of each area (release or non-release) sampled. To account for the difference in sampling proportions for release areas versus non-release areas, crab abundances were estimated separately for these two area types.

The number of hatchery crabs (H) present in an embayment at time t was therefore estimated as

$$(1) \qquad H = (N_R / A_R + N_{NR} / A_{NR})$$

Fig. 4. Contribution and enhancement of hatchery crabs. Contribution is defined as the proportion of all crabs that are of hatchery origin (hatchery/total crab densities). Enhancement is defined as the increase over wild crabs provided by hatchery crabs (hatchery/wild densities). (*a* and *c*) Contribution and enhancement of hatchery crabs, respectively, considering all wild crabs. (*b* and *d*) Contribution and enhancement of hatchery crabs, respectively, considering only wild crabs in the hatchery crab size range (—●—, batch A; —■—, batch B; - -○- -, batch C; - -□- -, batch D).

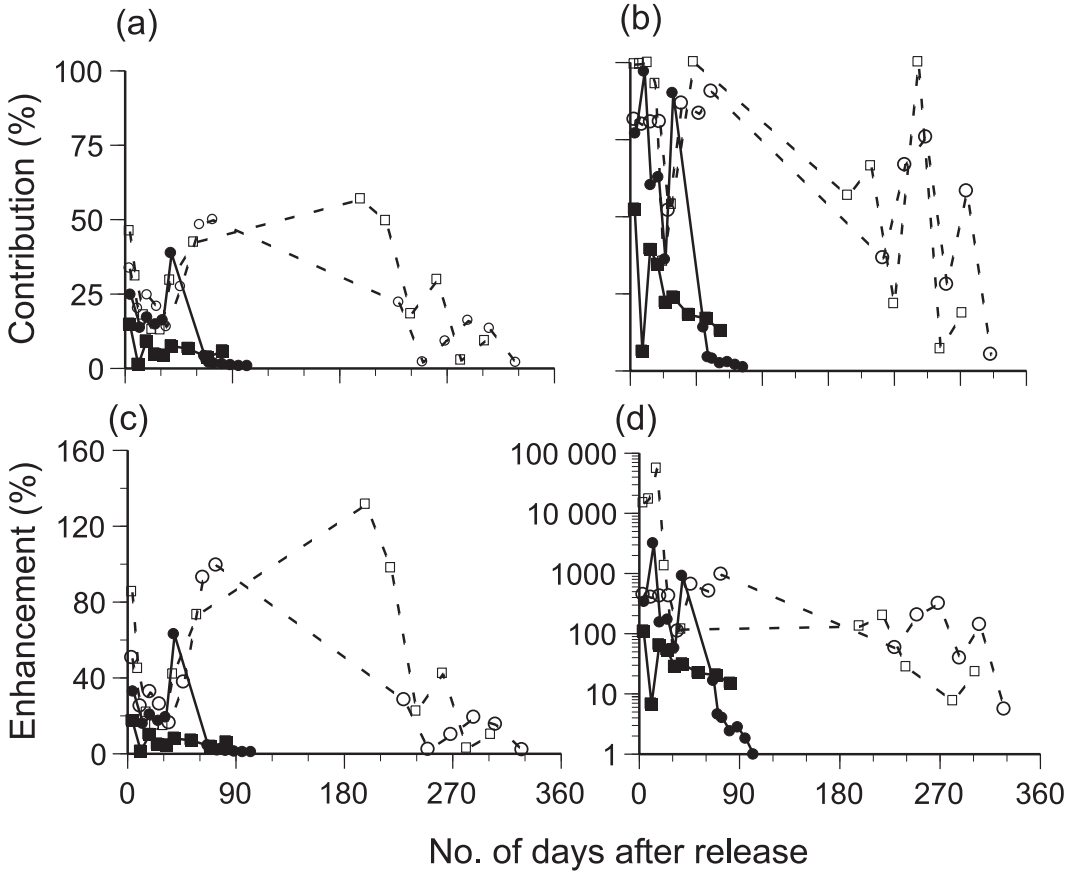
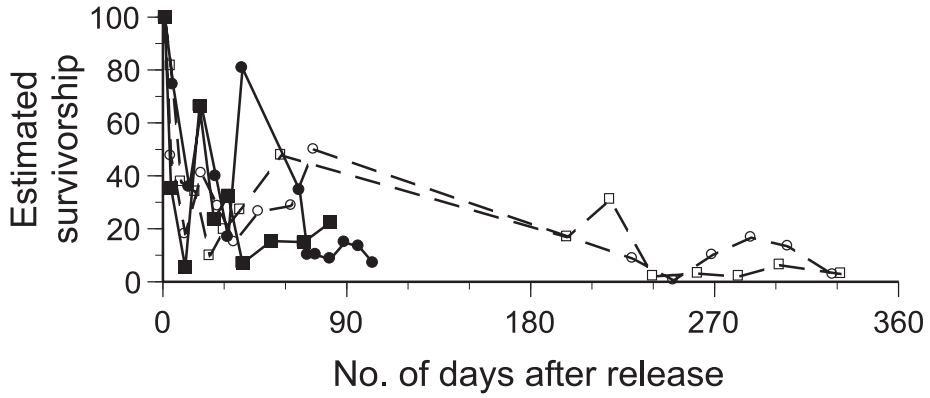


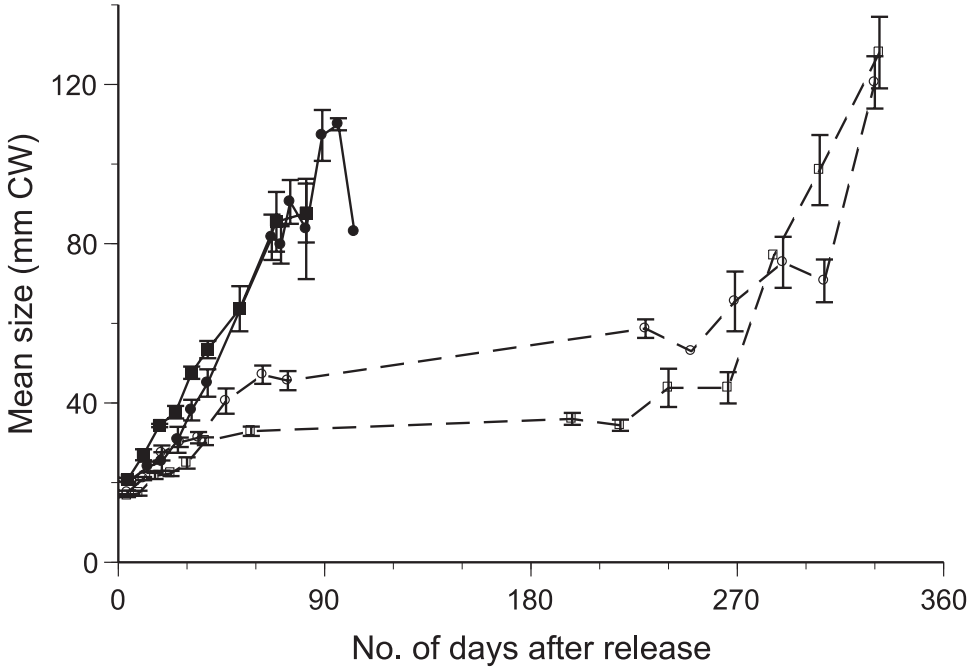
Fig. 5. Estimated survivorship of each hatchery batch over time after release into the field. Survivorship values are calculated as the percentage surviving from the initial release date to the time indicated on the *x* axis. The *p* value listed represents significance of the test for differences in slope (—●—, batch A; —■—, batch B; - -○- -, batch C; - -□- -, batch D).



where N_R is the number of hatchery crabs in the release area; A_R is the percentage of the release area that was sampled (between 19% and 26% for the four coves); N_{NR} is the number of tagged crabs in the non-release area; and A_{NR} is the percentage of the non-release area that was sampled (between 4% and 5%). The estimated number of tagged hatchery crabs (N_{tagged}) present in each area (release or non-release) at time *t* incorporates gear-specific estimates of gear efficiency (GE):

$$N_{tagged} = (N_{tow}/GE_{tow} + (N_{small\ seine}/GE_{small\ seine}) + N_{large\ seine}/GE_{large\ seine}) \quad (2)$$

Fig. 6. Mean size (carapace width, CW) of hatchery crabs over time after their release into the field. Blue crabs are legally harvestable as soft crabs at 100 mm CW (soft-shell fishery) and 125 mm CW (hard-shell fishery). They reach maturity at approximately 120 mm CW. Error bars represent standard errors. The number of crabs contributing to each mean ranged from 10 to 158 within the first 30 days after release and from 1 to 36 beyond 30 days after release (—●—, batch A; —■—, batch B; - -○- -, batch C; - -□- -, batch D).



where N_{tow} is the number of tagged crabs recaptured in the tows; $N_{small\ seine}$ and $N_{large\ seine}$ are the numbers of small (<20 mm CW) and large (≥20 mm CW) tagged crabs recaptured with seines, respectively; GE_{tow} is the tow-gear efficiency (5.5%); and $GE_{small\ seine}$ and $GE_{large\ seine}$ are the gear efficiency for small (10%) and large (50%) crabs, respectively. Estimates of the total number of hatchery crabs (N) present in an area (release or non-release) requires a correction for tag loss, which is related to the mean size of hatchery crabs at time t (Davis et al. 2004*a*):

$$(3) \qquad N = N_M/[1-(0.63\mathrm{CW}-11.1)] + N_E/(1-0.77e^{0.066\mathrm{CW}})$$

where N_M is the number of hatchery crabs tagged with microwire; CW is the mean size of crabs caught at time t; and N_E is the number of hatchery crabs tagged with elastomer.

Survivorship (S) of crabs in each batch at a given time t was then calculated as

$$(4) \qquad S_t = (H_t/E_t)/H_0$$

where H_t is the estimated number of hatchery crabs present in a cove at time t; E_t is an emigration coefficient; and H_0 is the initial number of hatchery crabs released into the embayment. E, estimated from a telemetry experiment described in Davis et al. (2004*b*), was time-dependent and estimated as a step function: for the first 2 weeks $E = 1$, after which $E = 0.833$. Most likely, more than 16.7% of the hatchery crabs emigrated from the embayment over time (e.g., see Hines et al. 1995); however, with no data to support this hypothesis (because juvenile crabs molt often, telemetry can only be used for the duration of one molting cycle), we used this conservative estimate.

Two corrections applied to densities of hatchery crabs were also applied to estimates of densities of wild crabs. In the event that wild crabs were also not distributed evenly within the release coves, sampling area (release or non-release) was also taken into account when calculating the density of wild crabs. Corrections were also made for gear efficiency, though not for emigration or tag loss.

A number of ways exist to consider enhancement, and we used several in order to maximize comparability with other studies. First, we calculated the percentage of all crabs at a site that were hatchery-raised, which we refer to as the contribution:

$$(5) \qquad \text{Contribution} = N_H/(N_H + N_W) \times 100$$

where N_H is the number of hatchery crabs in an embayment and N_W is the number of wild crabs. Second, we calculated "enhancement" as

$$(6) \qquad \text{Enhancement} = N_H/N_W \times 100$$

which can be reorganized into

$$(7) \qquad \text{Enhancement} = \text{contribution}/(100 - \text{contribution}) \times 100$$

Hatchery contribution and enhancement, in turn, were considered (*i*) relative to the entire wild population and (*ii*) in terms of only the segment of the population (those crabs within the size range of our hatchery crabs (±10% of the extreme sizes)) that was enhanced.

Levels of contribution were compared among the four batches with a repeated-measures analysis of variance

(ANOVA) using weekly values at seven time periods: weeks 1, 2, 3, 4, 5, 6–7, and 8–9. Contribution values were arcsine square root transformed to meet assumptions of normality. To obtain values of hatchery-crab density and contribution at specific time points (30 and 60 days after release) for qualitative comparisons of the four batches, logarithmic regression equations were fit to relationships of these factors with time. Estimated values of density and contribution were calculated based on these equations.

To determine whether survivorship differed among the four batches within the first 3 months of release, we used analysis of covariance (ANCOVA) in which batch was a categorical factor and time (number of days after release) was a contiguous covariate. To meet assumptions of normality, arcsine square root transformations were applied to survivorship values and number of days after release was log-transformed. Crab growth rate was similarly compared with mean size of hatchery crabs on a sampling day as a response variable, batch as a factor, and time (number of days after release) as a covariate.

Assessing wild crab displacement

Two methods were used to assess whether the release of hatchery crabs resulted in displacement of wild crabs in the release coves. First, all coves were sampled 1–2 weeks both before and after hatchery releases. To determine whether an immediate decline in the wild population occurred, two-way fixed effects ANOVAs were used to compare wild crab densities between the "before" time period and 1 week after release, and between "before" and 2 weeks after release. In these ANOVAs, crab batch (A, B, C, and D) and time period (before and after) were factors. Second, we used *t* tests to compare the change in wild crab density from "before" to "after" time periods between control and experimental coves for batches B, C, and D.

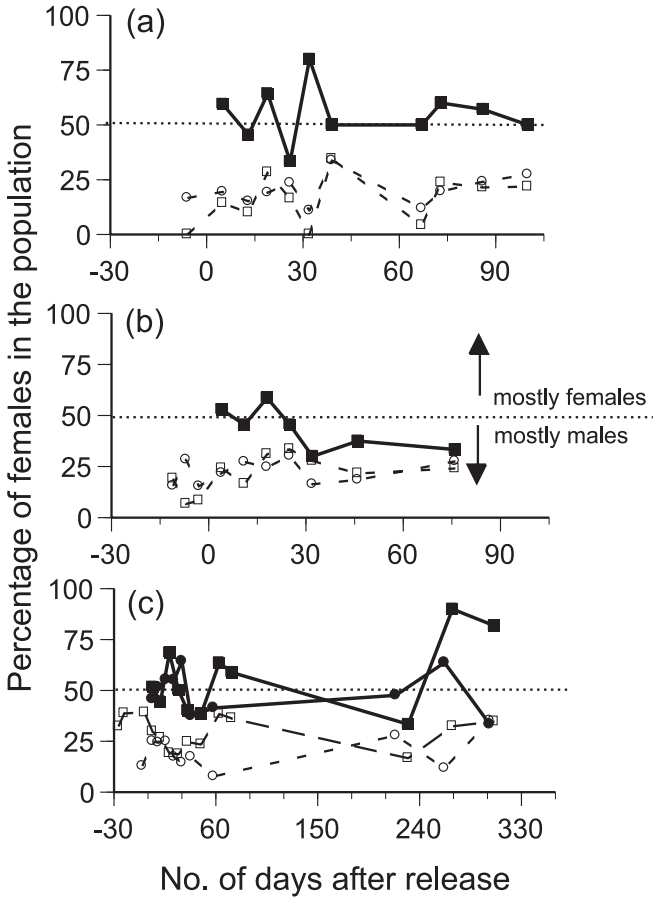
Results

Enhancement, contribution, and survivorship

Densities of hatchery crabs, which were released at levels of 0.07–0.33·m^{-2} (Table 1), were estimated after 60 days in the field to range from 0.008 to 0.06·m^{-2} (Fig. 2). Densities of hatchery crabs were always less than total densities of wild crabs (Fig. 2) but often, especially for batches C and D, greater than densities of wild crabs in the size range of hatchery crabs (Fig. 3). Crabs in batches A and B, released early in the summer, experienced losses (death and emigration) during the midsummer period, when wild juveniles were moving up Chesapeake Bay and settling into upper-Bay habitats, causing an increase in the wild population (Figs. 2*a*, 2*b*, 3*a*, 3*b*). In contrast, crabs in batches C and D were released after the temporal peak in wild population size, and therefore changes in densities of hatchery and wild crabs over time were more similar (Figs. 2*c*, 2*d*, 3*c*, 3*d*).

Considering only wild crabs within the size range of hatchery-raised individuals (target population segment), the contribution of hatchery crabs in the four batches ranged from 32% to 85% 30 days after release and from 22% to 79% 60 days after release (Fig. 4). Corresponding enhancement values ranged from 47% to 580% after 30 days and from 28% to 366% after 60 days (eq. 7; Fig. 4). Considering

Fig. 7. Percentages of females in the hatchery group and the wild population over time for batch A (*a*), batch B (*b*), and batches C and D (*c*). The dotted line represents the scenario in which the number of males equals the number of females (—■—, hatchery batch A; —●—, hatchery batch B; - -□- -, wild (total) in batch C; - -○- -, wild (total) in batch D). In *a* and *b* the gender ratios for both the total wild population as well as just those wild crabs in the size range of the hatchery crabs are presented (—■—, hatchery; - -□- -, wild (hatchery size range); - -○- -, wild (total)). In *c*, for batches C and D, few wild crabs in the appropriate size range were present.



the total wild population, the contribution of hatchery crabs ranged from 10% to 38% 30 days after release of hatchery crabs and from 8% to 36% 60 days after their release (Fig. 4). Averaged over the duration of sampling within each cove and over all four batches, the contribution of hatchery crabs to the total population was 17.4% (an enhancement level of 21.0%) and to the target population segment was 50.2% (an enhancement level of 100.7%). These values indicate that half of the crabs in this size range were of hatchery origin and that addition of hatchery crabs doubled this segment of the population.

Enhancement levels varied among the four batches of hatchery crabs (repeated-measures ANOVA, $F_{[3,18]} = 21.0$, $p < 0.001$ considering wild crabs in the hatchery size range, and $F_{[3,18]} = 15.9$, $p < 0.001$ considering all wild crabs). Enhancement of the two late-summer 2002 sites, Logan Pond and Sheepshead Cove, was higher than that of the sites of the two releases into Boathouse Creek in early summer 2002

Fig. 8. Movement of hatchery crabs away from initial release areas in each enhancement cove. Each diagonal regression line represents the linear relationship between time and percentage of hatchery crabs in the release area. The horizontal dotted line represents the percentage of hatchery crabs that would be present in the release area if all were evenly distributed in the enhancement cove. The intersection of the regression line with this dotted line indicates that crabs have become evenly distributed. The batch letter is indicated on each regression line (—■—, batch A; —●—, batch B; - -□- -, batch C; - -○- -, batch D).

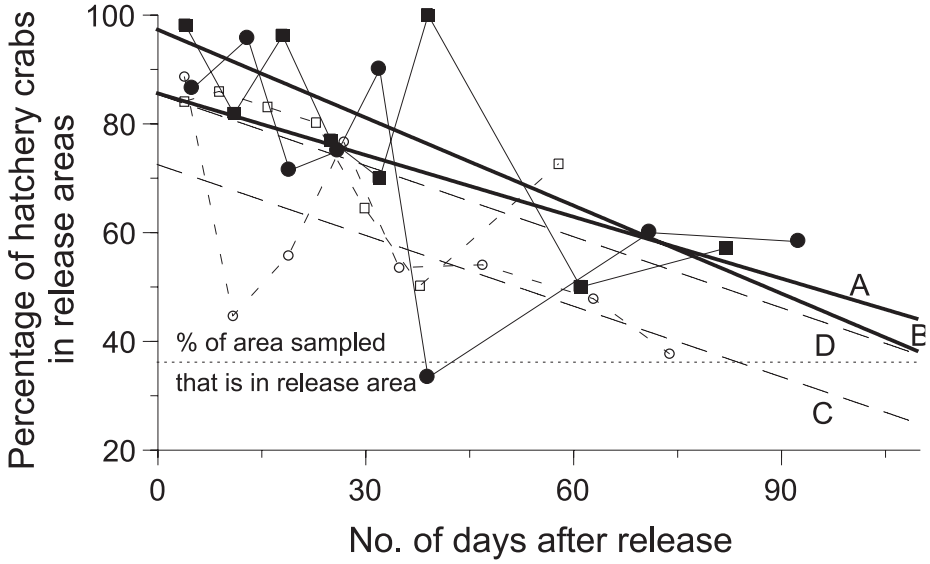


Table 2. Results of a two-way analysis of variance of a comparison of wild crab densities before and after (1 week and 2 weeks) the release of hatchery-raised juveniles.

			1 week after		2 weeks after	
	df group	df error	*F*	*p*	*F*	*p*
Total wild crabs						
Before vs. after release	1	155	12.5	**0.001**	4.5	**0.036**
Batch	3	155	5.2	0.002	7.4	<0.001
Interaction	3	155	1.6	0.193	3.8	0.011
Juvenile crabs only						
Before vs. after release	1	155	0.53	0.469	0.03	0.864
Batch	3	155	10.8	<0.001	10.4	<0.001
Interaction	3	155	0.06	0.980	0.1	0.940

Note: Boldface indicates statistical significance.

(Fig. 4). Considering just hatchery-sized crabs, contribution values were estimated to be 70% and 79% for the late-summer batches C and D, but only 33% and 22% for batches A and B, respectively. This difference was driven by lower wild crab abundances later in the summer when batches C and D were released, not by better survivorship of hatchery crabs in batches C and D than in batches A and B. Survivorship over time was not significantly different among the four batches (ANCOVA, effect of batch, $F_{[3,49]} = 0.8$, $p = 0.49$) (Fig. 5). After 60 days, mean survivorship of the four batches was 28 ± 7%. However, because late-released batches had to overwinter before reaching maturity, survivorship to size at maturity was higher for the first two batches (16%–20%, with maturity occurring 70–100 days after release) than for the last two batches (5%–15%, with maturity occurring 300–330 days after release) (Fig. 5).

Growth, gender ratio, and dispersal

Growth rates varied among batches (Fig. 6). The two batches released earlier in the summer had significantly higher growth rates than those released later in the summer (ANCOVA, effect of batch, $F_{[3,49]} = 6.6$, $p = 0.001$; Tukey's post-hoc tests, batches A,B ≠ C,D). Some crabs in the first two batches, A and B, grew to a size of 120 mm CW in 14 weeks (which is size at maturity; Hines et al. 1987) before recaptures ceased. Crabs in batch C reached a mean size of 46 mm CW in 11 weeks before the overwintering period. By April 2003, 9 months after release, these crabs were only 58 mm CW. Crabs in batch D only grew to a mean size of 33 mm CW in 8 weeks before winter, resuming growth in spring 2003 and requiring about a year to reach 120 mm CW (Fig. 6).

Hatchery crabs of each batch contributed a greater proportion of females to the blue crab subpopulations in their respective sites than did wild crabs (Fig. 7). Gender ratios of hatchery crabs were approximately 50:50 but differed from those expected from the wild crab population (χ^2 tests: $\chi^2 = 88$, $p < 0.001$, for batch A; $\chi^2 = 136$, $p < 0.001$ for batch B; $\chi^2 = 51$, $p < 0.001$, for batch C; $\chi^2 = 116$, $p < 0.001$, for batch D). For example, over the 15-week sampling period

for batch A, 55.3% of all hatchery crabs caught were female, while only 23.0% of all wild crabs and 20.9% of just those wild crabs within the size range of hatchery crabs were female. In the case of batch B, the percentage of females was 53.7% for hatchery crabs, 22.9% for all wild crabs, and 23.0% for only those wild crabs within the size range of hatchery crabs. This gender discrepancy cannot be explained solely by habitat differences between maturing wild males and females (Hines et al. 1987), as it was apparent even when very small wild crabs <35 mm CW were considered.

Recaptures of hatchery crabs for several months after release into the four embayments revealed low dispersal away from release sites (Fig. 8). An even distribution of crabs would exist when the proportion of hatchery crabs caught in the release area was equal to the proportion of total sampling effort (area (m^2) sampled) concentrated in the release area. Only by 10–15 weeks after release did hatchery crabs approach an even distribution within the embayments (Fig. 8).

Displacement

Comparisons of densities in the four coves prior to hatchery releases with densities 1 and 2 weeks after release reveals that the density of wild crabs did not decrease as a result of the addition of hatchery juveniles. This suggests that displacement of wild crabs by hatchery crabs did not occur. Instead, in all four cases, the total number of wild crabs increased significantly (Table 2; Fig. 9). The number of wild juveniles, however, did not change significantly (Table 2).

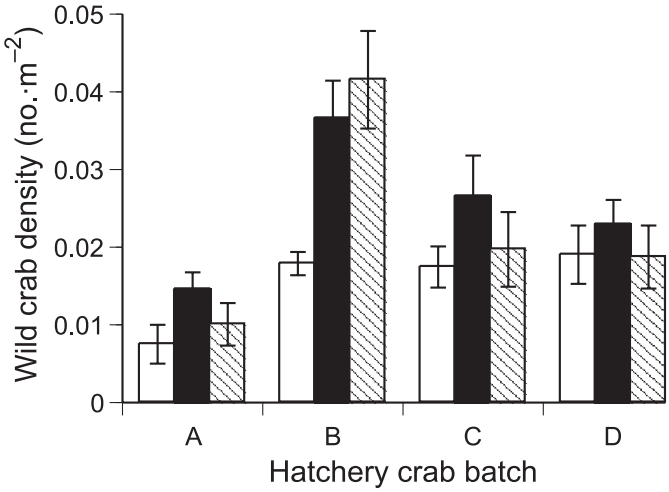
Comparing wild crab densities in control sites before and after the release date enables determination of whether wild crab densities were increasing in other areas as well. If this were the case, an increase in wild crab density in enhancement sites would have been independent of the addition of hatchery crabs. However, in almost every control-site case, the change in density of wild crabs was either negative or not as positive as the change in wild crab density in the enhancement sites (Table 3; Fig. 10).

Discussion

The results from these relatively small-scale enhancement experiments suggest that it is possible to enhance local (sub)populations of blue crabs. We estimate that about 16%–20% of crabs released early in the summer survived to maturity, at the age of 5–6 months, and about 5%–15% of crabs released later in the summer survived to maturity, at the age of 12–13 months, both groups likely contributing to the overall spawning stock of Chesapeake Bay. Because an even ratio of hatchery females to males resulted, rather than the much lower ratio of female to male wild crabs (even very small juveniles) we observed in the field, the hatchery crabs may have made an even greater contribution to the next generation than an equal-number, but male-dominated, group of wild crabs maturing in these coves.

The growth rate of hatchery crabs released in early summer represented more than a 50% reduction in the time to maturity generally required by wild blue crabs in the Chesapeake Bay region. In Chesapeake Bay, wild crabs generally mature in 1.5 years (Fischler 1965; Hines et al. 1987). Larvae are released by wild females during the summer at the mouth of the Bay, followed by megalopal recruitment

Fig. 9. Wild crab densities before hatchery crab release (open bars), 1 week after hatchery crab release (solid bars), and 2 weeks after hatchery crab release (hatched bars). Densities presented are not corrected for gear efficiency.



back into the Bay in the fall. Resulting juveniles must overwinter before resuming growth the next spring and reaching maturity by late summer. By bypassing the overwintering period and producing hatchery juveniles hatched in the spring, we were able to shorten the time to maturity, which in turn lessens the period during which crabs undergo mortality before producing offspring. However, hatchery juveniles produced and released later in the summer were forced, as wild juveniles are, to overwinter before reaching maturity; therefore, no advantage in time to maturity was achieved in those groups. We acknowledge that differences in growth between batches cannot be definitively attributed to season alone, as several other factors differed between the two early- and two late-summer releases. These factors included cove location and size, hatchery crab density, and fishing pressure (low in coves used for late-summer releases but appreciable in Boathouse Creek, as indicated by observations of trotline fishermen during summer).

Three processes could explain why we did not continue to recapture hatchery crabs after they reached maturity. That they had all died of natural causes is unlikely, as we estimated low mortality rates from week 4 to maturity. The second potential explanation is that mature crabs emigrated from our experimental sites. At this size, blue crabs in the study area exhibit a significant amount of emigration from sampling sites as females move down-bay to spawn (Hines et al. 1987, 1995). Third, mature crabs might have been lost to the fishery. For example, as many as 50–100 crabs, some potentially of hatchery origin, were removed from Boathouse Creek per day, which constitutes a significant proportion of the 1200–4000 crabs estimated to occupy the cove at any time.

Difficulty in judging success

One of the goals of these enhancement experiments was to begin to assess whether larger scale enhancement programs might prove fruitful. However, because quantitative studies of enhancement efforts are relatively new, though very much needed (e.g., Bannister et al. 1994; Heppell and Crowder 1998; Leber 1999; Crowe et al. 2002), objective

Table 3. Comparison of the change in wild crab densities after the release of hatchery-raised juveniles in control sites versus experimental sites.

Batch	No. of days between "before" and "after" sampling	No. of days after release[a]	Change in density (no.·m^{-2})[b] Enhancement sites	Control sites	t	p
B	14	11	+0.0246	+0.0002	3.3	0.002
C	25	6	+0.0119	+0.0039	1.3	0.192
D	34	16	+0.0062	–0.0241	5.0	<0.001

[a]Time elapsed between release of hatchery-raised crabs and "after" sampling.
[b]The change in wild crab density ("after" sampling minus "before" sampling) in both enhancement and control sites.

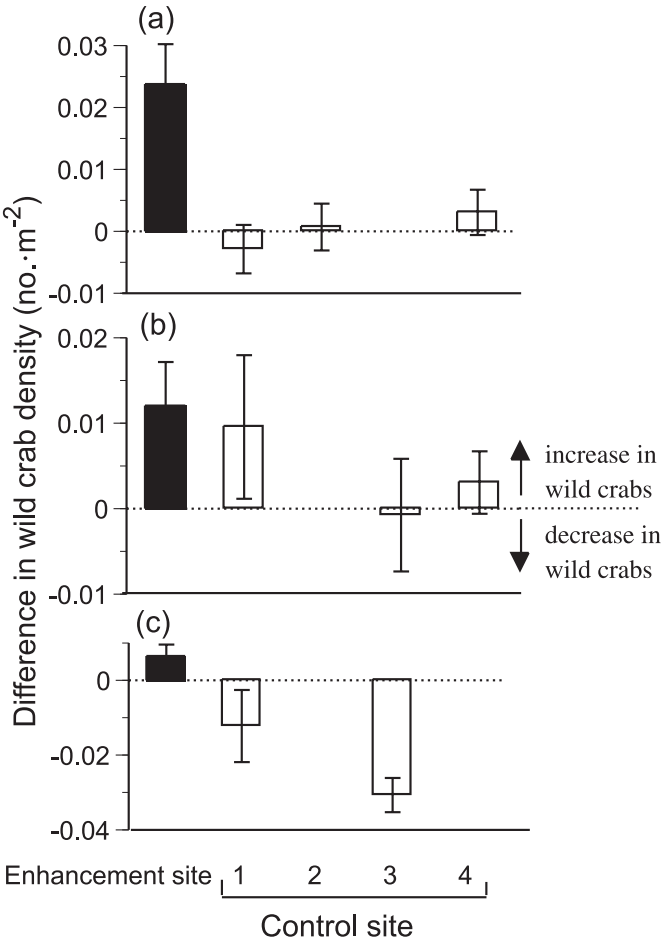


Fig. 10. Differences in wild crab density before and after release of hatchery crabs at enhancement and control sites for (*a*) batch B, (*b*) batch C, and (*c*) batch D. Control site 1 is the Rhode River from trawl samples; control site 2 is Logan Pond (before it was used as a release site); control site 3 is Boathouse Creek (1–2 months after it was used as a release site); and control site 4 is Cheston Creek. Densities used to calculate differences ("after" minus "before") were not corrected for gear efficiency.

standards have not yet been established against which to measure our results.

It has been suggested that the ultimate test of enhancement success lies in determining whether a hatchery is economically sustainable (Hilborn 1998), which, in turn, is measured by calculating the number and value of hatchery individuals appearing in the fishery. However, many benefits of enhancement, other than increased fishery catch, are difficult to judge in an economic context. In particular, enhancement programs may result in improvement of the reproductive output of a population by way of hatchery individuals surviving to maturity (Crowe et al. 2002). Therefore, while the economic value of a landed hatchery-produced mature female can be easily calculated, the unlanded hatchery-produced mature female, which is the goal of this program, may have a much amplified value through the spawning stock – recruitment relationship (Bannister et al. 1994; Bannister and Addison 1998; Crowe et al. 2002). These noncaught hatchery-produced individuals, which have economic value that is not easily estimated (because of the uncertainty of their reproductive contribution and the time lags associated with generation times) may be the most biologically valuable products of enhancement programs. Assessing the success of enhancing the reproductive output of a depressed or endangered stock is likely to be much more difficult, time-consuming, and complicated than estimating the direct transfer of hatchery-raised individuals into the fishery.

Relatively few other studies are available for comparison of enhancement levels. Many that do exist report recovery or recapture rates (Stoner and Glazer 1998), which aid in economic analyses but are inherently linked to the amount of sampling effort. This effort is usually variable even across studies based on fishery-independent data. As a result, recapture rates only provide a minimum survivorship rate over a minimum period of time. In addition, if recovery rates are calculated from fishery landings rather than research surveys, those values become mortality rates, providing little information about the number of individuals that survive to contribute to the brood stock.

Some reports do provide difficult-to-calculate survivorship rates for hatchery-produced individuals. However, because survivorship values for wild individuals in many cases are not known (Davenport et al. 1999), assessing the relative quality of these survivorship rates is not possible. In addition, comparisons across taxa are complicated by differences in life history or fishery patterns. For example, one might compare survivorship rates for two species over similar periods of time, but it might make more sense to compare survivorship rates over equal proportions of time to maturity or time to harvest. Most European lobsters (*Homarus gammarus*) take 4–5 years to reach maturity and legal size (Bannister et al. 1994; Bannister and Addison 1998), whereas blue crabs take 0.5–1.5 years. Comparisons of enhancement efforts must therefore account for this life-history difference.

Table 4. Contribution values (proportion of all individuals composed of hatchery-raised individuals) reported in other studies.

	Contribution (%)	Time (years)[a]	Reference
American lobster	0	1	Castro et al. 2001
Topshell	0	1.5	Crowe et al. 2002
Masu salmon	10.6	Recruitment to fishery	Masuda and Tsuakamoto 1998
Barramundi	15–20	3	Rimmer and Russell 1998
European lobster	10–35	4–8	Bannister et al. 1994
European lobster	26	4–8	Bannister and Addison 1998; van der Meeren et al. 1998
Scallops	40–50		Bull 1993
Red sea bream	0–50		Tsukamoto 1989; Imai et al. 1994; Masuda and Tsukamoto 1998
Threadfin	0–64	0.67	Leber et al. 1998
Chum salmon	90		Kaeriyama 1996

[a]Time after release at which contribution was measured, where available.

Attempting to judge success

Despite the challenges posed to assessment, comparisons with other efforts suggest that our experiments provided relatively high levels of enhancement. We estimated 5%–20% survivorship to maturity for blue crabs, higher than that reported for several other species. Survivorship was estimated at 0.0007% for released cod (*Gadus morhua*) larvae resampled after 1 year, a period shorter than the time to maturity (Svåsand 1998). Only 1%–3% of hatchery-produced abalone, *Haliotis rufescens* (which mature after 2–3 years), survived after 1 year (Tegner and Butler 1985, 1989). Survivorship of queen conch (*Strombus gigas*), which mature after 3 years, was 0.0005%–1.4% per year (Stoner and Glazer 1998). Of stocked panaeid shrimp, 2.8%–3.5% survived to fishable size at the age of 6 months (Davenport et al. 1999). After 1 year, survival of topshell, *Trochus niloticus*, which reach maturity at 2–3 years, was 4.4% (Crowe et al. 2002).

Some studies provide survivorship values equal to or higher than those we estimated for blue crabs. In Texas, 21% of red drum, which recruit to the fishery at the age of 1–2 years, survived to age 2 (McEachron et al. 1998). At least 10–30% of Japanese flounder survived to fishery size (Masuda and Tsukamoto 1998). Though recapture rates in European lobster fisheries, when hatchery individuals were 4–8 years old, were only <2% (Cook 1995; Bannister and Addison 1998), survivorship of these hatchery individuals was estimated at 37%–80% (Bannister et al. 1994; Bannister 2000). The discrepancy between recapture rate and survival rate indicates that a large proportion of hatchery individuals escaped fishing mortality and potentially contributed reproductively to the population.

Quantifying survivorship is only a piece of determining enhancement success, as in many cases, baseline survivorship rates of wild juveniles are not known. Determining the degree to which hatchery individuals contribute to the total population can help, despite the fact that because a second density estimate is required (that of wild individuals), these values can be very variable (Table 4). Both terms, survivorship and contribution, have merits and negatives and should be considered together when assessing success. There are cases in which survivorship of hatchery animals is low, but because wild densities are also low, contribution is high. There may also be cases in which survivorship of hatchery animals is high, but because few hatchery individuals are released, contribution may be low. In our experimental releases, densities of hatchery and wild crabs were generally relatively balanced as a result of substantial hatchery crab survivorship, resulting in a high contribution.

Large-scale stock enhancement of the swimming crab in Japan may provide the best available comparison with the blue crab (summarized in Secor et al. 2002). During the 1990s, Japanese hatchery releases ranged from 700 000 to 1 400 000 juveniles per year in three bay systems ranging from 10 000 to 100 000 ha. Harvest recapture rates ranged from 1.2% to 31.3%, and hatchery contribution to the fishery catch ranged from 9% to 59% (Ariyama 2000; Secor et al. 2002). However, despite the large scale of hatchery releases, experimental analysis to quantify survival and contribution of hatchery swimming crabs to the wild population has been limited by lack of replication (Secor et al. 2002).

Carrying capacity

When assessing enhancement success, ultimate effect on population size must also be considered. If populations are limited not by recruitment but by resource availability, hatchery individuals may survive and appear in significant proportions in populations, but this may not lead to larger population sizes. Instead, they may be displacing wild individuals, either through direct competition or by indirectly using limited resources. Displacement can be assessed, as in our study, with paired measurements of densities in both enhanced and control areas coupled with tagging of hatchery individuals (Heppell and Crowder 1998; Hilborn 1998; Crowe et al. 2002).

Our results indicate that replacement of wild crabs by hatchery crabs did not occur. Lack of displacement of wild crabs and low dispersal of hatchery crabs away from release sites suggest that total crab densities in enhancement coves were below carrying capacity. Rather than serving the role of out-competitor, hatchery crabs may instead have served the role of potential prey for wild crabs, as blue crabs are highly cannibalistic. Wild crabs appeared to be drawn into our enhancement sites immediately after release of hatchery crabs, perhaps attracted to our released hatchery crabs as prey.

Others have suggested that current blue crab population levels are below carrying capacity in many areas of the Chesapeake Bay (Lipcius and Stockhausen 2002). Wild densities measured in our enhancement coves ranged from 0.004

to 0.07 crabs·m^{-2} (40–720·ha^{-1}), much lower than the densities reported for similar types of systems during historical highs of blue crab abundance in the Chesapeake Bay (Hines et al. 1987). Our enhancement efforts resulted in an initial increase in density by 0.07–0.33 crabs·m^{-2} (700–3300 ha^{-1}), which, even when added to the wild populations already present, falls below probable carrying capacity densities.

In conclusion, our experimental enhancements of local blue crab populations met several of the criteria for success articulated in recent years (Hilborn 1998; Leber 1999). Tagging enabled us to determine that hatchery crabs contributed to the populations of our small embayments, doubling, on average, the number of crabs in the hatchery crab size range and increasing the total wild population by a third. Tagging also enabled us to determine that hatchery crabs released earlier in the summer matured in a much shorter period than expected for wild crabs. The use of control sites enabled us to determine that hatchery crabs did not displace wild crabs, which suggests that these areas are below carrying capacity.

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