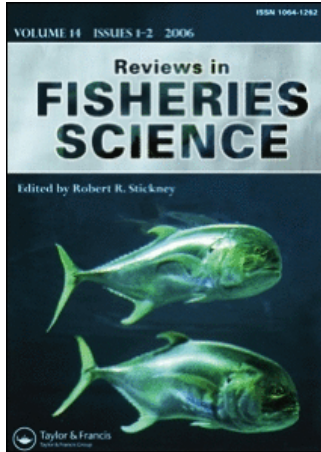


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Publisher: Taylor & Francis
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Reviews in Fisheries Science

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t713610918>

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Online Publication Date: 01 January 2008

To cite this Article: Young, Alicia C., Johnson, Eric G., Davis, Jana L. D., Hines, Anson H., Zmora, Oded and Zohar, Yonathan (2008) 'Do Hatchery-Reared Blue Crabs Differ from Wild Crabs, and Does it Matter?', Reviews in Fisheries Science, 16:1, 254 - 261

To link to this article: DOI: 10.1080/10641260701684122

URL: <http://dx.doi.org/10.1080/10641260701684122>

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Do Hatchery-Reared Blue Crabs Differ from Wild Crabs, and Does it Matter?

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*Successful use of hatchery-reared juveniles to enhance recruitment-limited populations or severely depleted stocks is contingent upon their ability to survive and grow upon release into the wild. Hatchery conditions often result in juveniles that exhibit morphological, physiological, or behavioral characteristics different from their wild counterparts. Managers of stock enhancement or restocking programs need to assess whether any such deficiencies translate into differences in performance between hatchery-reared and wild juveniles in the field. If so, the deficits may be minimized through conditioning strategies. In this review, we summarize various aspects of the morphology and behavior of cultured and wild blue crabs, *Callinectes sapidus*, and compare our work on these crabs to studies on other invertebrates. We identify similarities and differences between cultured blue crabs and wild conspecifics. In some cases where differences existed, conditioning of the hatchery-reared crabs before release rapidly mitigated the defects, and, overall, any remaining differences did not translate into decreased survival. We conclude that there are no significant impediments to the fitness of hatchery-reared blue crabs used in release programs.*

Keywords stock enhancement, restocking, *Callinectes sapidus*, blue crab, conditioning, hatchery methods

INTRODUCTION

With decreases in many important fisheries stocks (Myers and Worm, 2003), scientists and managers are increasingly turning towards new techniques which, when combined with traditional management, may be used to improve recruitment and increase productivity. One of these techniques is stock enhancement. While efforts to increase the amount or quality of habitat in cases of habitat-limited species can be considered stock enhancement; more commonly, the term is used to describe the release of juveniles to bolster recruitment-limited populations (Bell et al., 2006).

Stock enhancement has been used as a management tool for decades around the world, primarily for finfish. Compared with

finfish, which have more consistent life histories and usually have the ability to move, invertebrate stock enhancement efforts encompass a wide range of approaches. For example, invertebrate stock enhancement has included the release of hatchery-reared juveniles (e.g., Barbeau et al., 1996; Davis et al., 2005a), transplanting wild individuals to better quality habitats (Stoner and Davis, 1994), culture and release of wild caught juveniles, and thinning and relocation of dense aggregations of wild juveniles (Bell et al., 2005). Both finfish and invertebrate stock enhancement efforts face several challenges and potential criticisms, leading to some controversy over the technique (Washington and Koziol, 1993; Blankenship and Leber, 1995; Li, 1999). Some of these criticisms may be addressed with policy solutions and solid fisheries management (Bell, 2004). These include warnings that successful enhancement efforts should not excuse the need for traditional management, such as reduced fishing or habitat protection (Walters, 1986; Lichatowich, 1999), and concerns that increases in stock size due to the successes of

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release programs may provoke a rise in fishing effort, placing greater pressure on remaining wild individuals (Hilborn, 1998; Bannister, 2000). Other concerns, such as the potential reduction in genetic variability in wild populations in cases of a severely depleted species with limited broodstock (Utter, 1998), can be addressed by stringent oversight of enhancement operations and broodstock selection protocols and replenishment policies.

Concerns also exist that cultured organisms may not survive well due to deficiencies acquired during hatchery rearing (Olla et al., 1998), minimizing the potential of stock enhancement. Similarly, concerns also exist that hatchery-reared organisms may compete with wild animals and displace them (Bannister and Addison, 1998; Castro et al., 2001). These concerns about the quality and behavior of hatchery-reared organisms can be addressed, sometimes by minimal changes in rearing protocols. Such issues have led to the relatively new field of “conditioning” hatchery-reared animals, which focuses on ensuring that the cultured individuals are of a proper quality. Conditioning can be effective when differences between hatchery and wild individuals are environmentally forced and therefore potentially plastic, rather than genetic due to selection factors in the hatchery (genetic drift; Fleming et al., 1994). Both the proportion of an individual’s life spent in the hatchery and the number of generations broodstock have been held in captivity can be important in determining how divergent cultured individuals are from their wild counterparts (Fleming et al., 1994), and therefore how much conditioning is required. Identifying how hatchery-reared animals differ both morphologically and behaviorally from wild counterparts (Davis et al., 2004), and whether or not these differences contribute to decreased performance of cultured relative to wild individuals after release, is a critical step in assessing the potential of stock enhancement for any species. Laboratory and field experiments designed to identify and mitigate differences through conditioning may improve survivorship and increase the likelihood of successful releases.

Recently, we conducted small-scale field experiments (1,000–15,000 individuals released per cohort in areas of 1–8 ha) to test the feasibility of stock enhancement in the recruitment-limited fishery for the Chesapeake Bay blue crab, *Callinectes sapidus*, by raising juveniles and releasing them into nursery habitats within the Bay’s sub-estuaries. Part of this research involved assessing the quality of hatchery-reared juveniles relative to wild individuals. The goals of these studies were to test whether (1) morphological, physiological, or behavioral differences occurred between hatchery-reared and wild juvenile blue crabs of the same age and size, (2) potential differences could be eliminated through conditioning, and (3) potential deficits were translated into differences in performance of wild vs hatchery-reared juveniles after release. We used an array of laboratory and field experiments to test for potential differences in wild vs cultured juveniles. We also monitored a multi-year series of releases of hatchery-reared animals to assess potential negative interactions between wild and cultured crabs.

The purposes of this review are to (1) present key morphological, physiological, and behavioral differences between

Table 1 Summary of differences and outcomes between hatchery-reared and wild-caught blue crabs (*Callinectes sapidus*) in Chesapeake Bay

Factor	Difference Detected?	Factor Mitigated or Eliminated Through Time?	Approximate time Taken to Condition	Overall Performance Affected?
Morphological/ Physiological				
Body Shape	yes	yes	27 days	no
Color	yes	yes	2 hr–2 days	no
Growth	no			no
Behavioral				
Predator Avoidance	yes	yes	48 hr	no
Aggression	maybe	?		?
Feeding	no			no
Reproduction	no			no
Habitat Selection	no			no
Movement	no			no

hatchery-reared and wild blue crabs (Table 1), (2) identify areas in which conditioning was effective, (3) predict whether conditioning cultured individuals leads to targeted organism quality, and (4) compare our work on the blue crab to existing knowledge for other invertebrates. Our ultimate goal is to summarize these findings to identify the best approaches for future releases of hatchery-reared juveniles.

MORPHOLOGICAL AND PHYSIOLOGICAL FACTORS

Because cultured individuals are often raised in tanks with non-natural substrata, water flow, and other characteristics that vary from those experienced in natural environments, their morphology may differ from that of wild individuals. Studies spanning a wide range of marine invertebrates have made morphological or physiological comparisons between hatchery-reared and wild animals (Bell et al., 2005). Differences occur in many cases. In addition, several studies suggest that frequency of abnormalities tends to be higher in hatchery-reared organisms than in wild individuals (Ellis et al., 1997; Boglione et al., 2000; Mana and Kawamura, 2002). Some of these differences and abnormalities potentially lead to survivorship advantages or disadvantages relative to wild organisms, while others may not. Within the subset of differences and abnormalities, some that cause problems can be alleviated by conditioning, and others cannot. Below we outline the main morphological and physical attributes where deficits have been observed. This information should be useful in helping develop appropriate release strategies.

Body Shape

Body shape has implications for many aspects of an organism’s life history. Certain shapes allow better refuge use, while others facilitate improved defense from predators. One type of

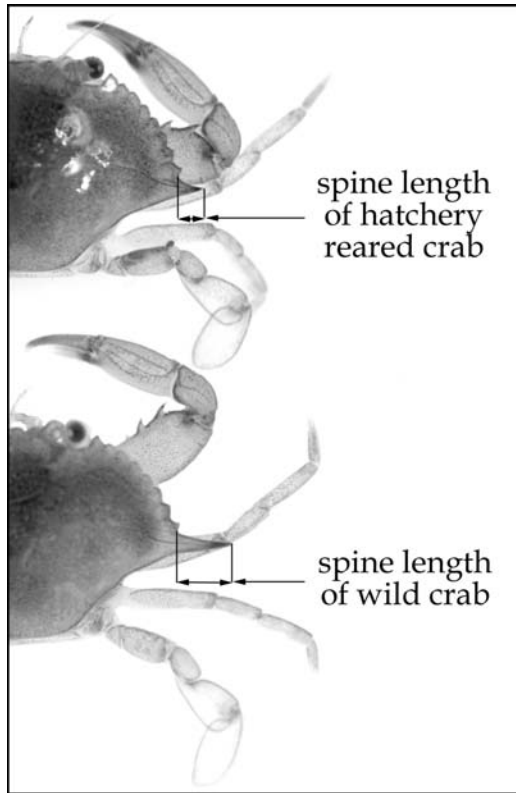


Figure 1 Differences in morphology between hatchery-reared and wild-caught blue crabs (*Callinectes sapidus*) in Chesapeake Bay.

morphological predator defense is body spines. For example, blue crabs have sharp lateral spines that require a potential fish predator to have a wider gape to ingest the crab and provide protection for individuals of smaller size. Queen conch (*Strombus gigas*) has shell spines that serve a similar purpose (Stoner and Davis, 1994). Juvenile topshell (*Trochus niloticus*) possess spines that are thought to provide effective protection from predation by allowing them to physically lock into crevices (Purcell, 2002).

We found that crabs maintained in the laboratory (both cultured and wild individuals kept for 30 days) had shorter spines than wild crabs (Davis et al., 2004, 2005b) (Figure 1). After time in the field, however, hatchery-reared crabs had spines of similar length to wild crabs, resulting from either individual spine increases (suggesting spine length is a plastic trait) or differential mortality of short-spined crabs (Davis et al., 2005b). In addition, in one experiment, cultured crabs maintained in aquaria and exposed for 27 days visually and chemically to striped bass predators increased their spine length relative to control crabs that were not exposed to predators, and to crabs that were exposed to predatory adult blue crabs. However, in another experiment, changes in spine length in response to predators were not apparent. Some tethering experiments with unconditioned hatchery-reared crabs indicated that spines do have an important effect on survival: crabs that survived had significantly longer spines than those that did not (Davis et al., 2005b). Also, crabs conditioned to have larger spines had higher survivorship than

unconditioned crabs in two field tethering experiments and one laboratory experiment (Davis et al., 2005b). While survivorship of hatchery-reared crabs was lower than wild crabs in some cases, overall survivorship of tagged cultured and wild crabs did not differ in the field.

Similar results have been reported for other invertebrates. Cultured queen conch had shorter shell spines than wild conch when they were left in the hatchery, but the spines grew to a comparable size after release (Stoner and Davis, 1994). Stoner and Davis (1994) reject differential mortality as a possible explanation, noting that shell shape is a plastic and flexible trait. Similarly, juvenile hatchery-reared topshell lack the spines on the lateral whorl of the shell that are present in wild individuals of similar size (Purcell, 2002). For both blue crabs and conch, the hatchery environment may impact shell/carapace shape by failing to provide the necessary cues or stimuli for proper development of predator defenses (Delgado et al., 2002; Davis et al., 2004). Inducible defenses, triggered by the presence of a predator, have long been noted to affect the morphology of prey species, most famously in freshwater *Daphnia* spp., where presence of a predator stimulates the lengthening of dorsal spines (Grant and Bayly, 1981). However, induction of morphological changes has not been reported in many cultured species, including penaeid shrimp and other portunid crabs.

Color

Hatchery-reared organisms often begin their lives on unnatural substrata; for example, fiberglass tanks or concrete ponds. For species whose coloration is background- or substrate-dependent, the color of the artificial substrate may lead to non-natural pigmentation. When released, these off-color individuals may be conspicuous and attract predators leading to higher mortality rates.

Under typical hatchery conditions (blue fiberglass tanks), cultured crabs were significantly bluer in hue, brighter, and less saturated in color than their wild counterparts (Davis et al., 2004). These differences, however, faded after cultured crabs were exposed to sediment for 1–2 days in the laboratory and 5 days in the field (Davis et al., 2005b). Hatchery-reared and wild crabs showed similar ability to use endocrine control of chromatophores to match their color to the background, often within 1–2 hr. A brief exposure of cultured crabs to dark backgrounds may be useful in pre-release conditioning to facilitate camouflage of hatchery-reared crabs reared on light backgrounds (Davis et al., 2005b); however, conditioned blue crabs did not survive better in the wild than non-conditioned crabs in field trials. Thus, differences in color have a negligible impact on post-release survival of hatchery-reared blue crabs and should not be a focus for conditioning programs for this species.

Differences in color or pigment pattern between cultured and wild animals have been noted in other species. For example,

hatchery-reared striped bass had a higher incidence of "broken stripedness" than wild fish (Waldman and Vecchio, 1996). Hatchery-reared sole took, in some cases, more than one month to change color to match their background as well as wild fish (Ellis et al., 1997); while other cultured flat fishes and sea horses change color rapidly. Researchers have produced several color morphs of American lobster through controlled breeding; however, survival of these individuals relative to natural colored lobsters is not known (Hughes, 1968). Albinism in hatchery-reared flatfishes is common and not simply related to dietary issues (Bolker and Hill, 2000). Variation in hatchery food may also result in color differences in hatchery-reared abalone (Gallardo et al., 2003), American lobsters (Tlusty and Hyland, 2005), and some fishes (National Research Council, 1993). While exposing cultured crabs to sediment before release did not increase survivorship relative to unconditioned control crabs in the upper Chesapeake Bay, our experiments were conducted in habitats of extremely low visibility where the dominant predators, adult blue crabs (Hines and Ruiz, 1995), locate prey using chemosensory apparatus.

Conditioning to achieve natural coloration before release, however, may be important for other species, particularly those released in high visibility habitats and for species whose main predators are visual. Conditioning for color may also have important implications in places where color raises market value, e.g., red shellfish in Asian markets or pink flesh color of salmon (Frode et al., 2006), or where color can be used as an effective "tag" e.g., color morphs in lobsters (Hughes, 1968; Irvine et al., 1991) or color marking in abalone (Gallardo et al., 2003).

Growth

Hatchery-reared individuals might be expected to have either faster or slower growth than their wild counterparts under various scenarios. Usually, hatchery organisms are fed to satiation, unlike wild organisms which must actively forage for prey under risk of predation (Gilliam and Fraser, 1987). Therefore, hatchery-reared individuals may be released in better physiological condition and with higher growth rates (Stoner and Davis, 1994; Einum and Fleming, 1997) than wild animals. In some past cases, increased growth rates may actually have been genetic in origin since individuals with the highest growth rates were often selected as candidates for broodstock (Barber et al., 1998). Alternatively, cultured organisms once released in the field are generally inexperienced at foraging and may select suboptimal prey items or have difficulty capturing live prey (see Behavioral Factors below), resulting in slower growth than wild individuals.

Laboratory experiments conducted under hatchery conditions described by Zmora et al. (2005) demonstrated that growth rates were similar between hatchery-reared and wild blue crabs (Davis et al., 2004). Initial observations from field releases (Davis et al., 2005a; Johnson et al., 2008) suggest that hatchery-reared crabs can readily adapt to natural prey (Davis et al., 2004) and grow at similar rates to wild crabs following release.

Growth rate may be difficult to control because growth rates of cultured relative to wild animals vary widely. For example, hatchery-reared Atlantic salmon, masu salmon, and brown trout had faster growth rates than wild ones in some studies (Einum and Fleming, 1997; Hedenskog et al., 2002), whereas growth of cultured conch was slower (Stoner and Davis, 1994). Other studies produced similar results to those we obtained for blue crabs, i.e., no differences in growth (Davis et al., 1992; Francescon et al., 1988).

BEHAVIORAL FACTORS

Differences in behavior of hatchery-reared individuals relative to wild counterparts have potential to affect ultimate survivorship in the field and interactions with wild individuals. Factors such as behavior towards predators, behavior towards prey, manipulation of prey, and behavior towards potential mates all influence the successful contribution of individuals to restocking and stock enhancement programs.

Predator Avoidance Behavior

Burial behavior for species like crabs and some fishes is an important predator avoidance mechanism. For example, blue crabs commonly bury themselves to escape predation from larger blue crabs and fishes. Many species use digging behavior in foraging and reproduction (e.g., egg-sticking to pleiopods of decapods). Due to the difficulty of using sediment in hatcheries, most cultured organisms never experience sediment before release and therefore may have important functional deficits.

In the laboratory, cultured crabs without prior exposure to sediment buried less often, ~25% of the time, than wild crabs, which spent ~63% of their time buried (Davis et al., 2004). After 2–4 days, however, these differences disappeared as hatchery-reared crabs gained experience with sediment. Other studies report similar differences in burial behavior and conditioning for numerous species. Hatchery-reared queen conch buried less than wild individuals, and the differences persisted for 10 months (Stoner and Davis, 1994). Cultured sole also spent less time buried than the wild fish, but only for the first 12 days after release (Ellis et al., 1997). On the other hand, hatchery-reared lobsters readily construct burrows following release, despite lacking any prior exposure to sediment (Wickins and Barry, 1996).

Conditioning experiments with cultured blue crabs indicate that it is possible to induce normal burying behavior. We exposed cultured crabs to sediment for 2 days, after which burial frequencies did not differ between hatchery-reared and wild crabs. However, survival of conditioned crabs in the field was no greater than unconditioned crabs. This suggests, at least for some species for which conditioning happens relatively quickly (in the order of just a few days), that differences in burial behavior have minimal effects on post-release survival.

In Norway, experiments with hatchery-reared European lobster (*Homarus gammarus*) have identified maladaptive behaviors that result in increased predation on hatchery-reared individuals following release. Many of these behaviors are a direct result of increased stress during transport from the hatchery to release sites. For example, ~90% of juveniles were immobile for several minutes following release, and ~10% exhibited a tail-flipping escape response (van der Meeren, 1991). Tail-flipping was particularly deleterious to survival as this attracted predatory fish and increased mortality of the vulnerable, immobile juveniles (van der Meeren, 1991). These behaviors were of short duration (15 min), however, and could be eliminated by holding lobsters in tanks at release sites. This allowed recovery from the stress of transport, and acclimation to ambient environmental conditions before release (van der Meeren, 1991). Mills et al. (2004) reported that on-grown juvenile rock (spiny) lobsters (*Jasus edwardsii*) tracked with ultrasonic telemetry behaved similarly to local wild rock lobsters with respect to selection of appropriate shelter, cohabitation with conspecifics, and predator avoidance response to divers. A similar result was reported for juvenile *J. edwardsii* in which survival of naïve (reared from wild caught puerulus larvae) and wild animals was similar at 3 of 4 release sites (Mills et al., 2006). Reduced recovery of naïve rock lobsters compared to wild counterparts at the fourth site was attributed to increased emigration, not predation.

Aggression

Aggressive behaviors play an important role in many aspects of an animal's life. To be successful, individuals need to be able to compete for mates, food, shelter, and to defend themselves against predators. However, most hatcheries are predator free, and animals are fed to excess, eliminating the need to compete for food. These conditions might produce individuals with lower levels of aggression relative to wild animals. Conversely, abnormally high densities of animals in hatcheries may increase agonistic encounters and lead to hyper-aggression.

In pilot studies, we found that wild crabs out-competed cultured crabs when presented with one prey item in a laboratory setting (Young, unpublished data). This is an example where conditioning might produce a hyper-aggressive individual with increased potential to displace wild counterparts. However, replicated releases of tagged cultured juveniles at a range of densities in small coves showed that cultured crabs did not appear to displace wild ones (Davis et al, 2005a; Johnson and Hines, unpublished data). Further experimentation is necessary to identify an optimum conditioning program.

Other hatchery-reared crustaceans have exhibited increased intra-specific aggression. Naïve lobsters (*H. gammarus*) were more likely to engage in aggressive combat than wild individuals immediately following release, increasing their susceptibility to predation (van der Meeren, 1993). Naïve lobsters also demonstrated highly aggressive responses toward conspecifics in the vicinity of their shelter (van der Meeren, 1993). Simi-

larly, hatchery-reared salmon displayed more aggressive behavior than wild conspecifics (Wessel et al., 2006).

Feeding Behavior

In many cases, cultured organisms have never encountered natural prey, so their feeding behavior may be negatively affected following release because of reduced ability to select and capture prey. Such defects could depress growth and ultimately result in reduced survivorship of cultured individuals, particularly in species such as the blue crab, in which survival is size-dependent (Hines and Ruiz, 1995; Johnson et al., 2008). However, it is also possible that cultured organisms, accustomed to constant feeding, have honed feeding skills. If so, these differences may lead to displacement of wild individuals in cases of direct competition for food resources.

Our laboratory experiments indicated that cultured blue crabs quickly adapted to new prey, feeding on infaunal clams (*Macoma* spp.) at rates equal to those of wild crabs despite having never encountered them before (Davis et al., 2004). In addition, cultured crabs targeted high-quality bivalve prey after release. In early summer releases, abundance of hatchery-reared crabs was strongly positively correlated to bivalve density (Hines et al., unpublished data), a preferred prey of wild crabs (Hines et al., 1990). We found no difference between the wet weight of stomachs from free-ranging, hatchery-reared and wild blue crabs captured from release sites, suggesting that cultured crabs can feed effectively. Multivariate analysis of stomach contents indicated hatchery-reared and wild blue crabs are generally feeding on similar prey (Rowe et al., unpublished data). However, cultured crabs may have more trouble with some prey types. After release, preliminary gut content comparisons during summer suggest that, while cultured crabs fed at higher rates on clams, wild crabs more commonly ingested fish and other blue crabs (Rowe et al., unpublished data). These differences may be related to prey mobility and need to be explored; however, differences in diet do not appear to affect growth of hatchery-reared animals following release.

Other studies on decapod crustaceans also indicate that cultured animals acclimate rapidly to foraging for natural prey in the wild. Despite being fed in daylight during culture, released rock lobsters conformed readily to the nocturnal feeding behavior of wild individuals and exhibited similar responses to predators (Oliver et al., 2005).

Reproductive Behavior

The scope of our research does not generally extend to areas where we can directly observe blue crabs brooding. However, we have observed cultured crabs mating successfully in the wild. Also, recaptured post-copulatory females returned to the hatchery have successfully produced broods of healthy larval crabs (O. Zmora, personal communication). This suggests that cultured crabs have similar reproductive behavior to wild

crabs, but further research is necessary to identify whether or not mating behaviors differ between cultured and wild animals.

Habitat Selection

The ability to select and use appropriate habitats as refuges from predation is another important behavior that may affect survival. Again, the absence of natural conditions in the hatchery might limit the capability of juveniles to select appropriate habitat. Although hatchery managers frequently place artificial structures in rearing tanks, this "habitat" is seldom equivalent to that used by crabs in the wild. Thus, adaptive behaviors observed in wild juveniles, such as selection of appropriate refuge, may be lacking in hatchery-reared individuals, resulting in reduced survival and growth after release. Coarse woody debris in shallow near-shore water is the primary refuge for wild blue crabs in areas like the Rhode River in the upper Chesapeake Bay, particularly following ecdysis, when crabs are soft and vulnerable to predation (Everett and Ruiz, 1993; Hines and Wolcott, unpublished data). In field experiments, patterns of habitat use by cultured crabs were similar to those of wild crabs. Both cultured and wild crabs used structured habitats more often than nearby unvegetated habitats, consistent with reported patterns of habitat use for juvenile blue crabs in Chesapeake Bay. More late pre-molt and early post-molt individuals than other molt stages were found in structured habitats, indicating that crabs preferentially used structured habitats as a refuge from predation during molting. Overall, hatchery-reared blue crab juveniles used the same habitats as wild juveniles and are probably not disadvantaged with respect to habitat selection relative to wild conspecifics.

Cultured and wild crabs behaved similarly in laboratory and field experiments designed to test dispersal and distance moved, patterns of bottom use and bathymetry, and use of structural refuges. Although other cultured and wild species show similar habitat preference (e.g., Ellis et al., 1997), a greater number of studies report lower use of refugia by hatchery-reared than wild individuals (e.g., Einum and Fleming, 1997; Stunz and Minello, 2001).

ULTIMATE IMPACT ON STOCK ENHANCEMENT SUCCESS

Unlike several other studies for fishes (Bolker and Hill, 2000; Kellison et al., 2000) and invertebrates (Ray et al., 1994; Stoner and Davis, 1994), which found reduced fitness of cultured animals, our tethering experiments revealed few differences in survival of hatchery-reared and wild juveniles. Simultaneous field releases of free-ranging wild and hatchery-reared blue crabs showed that, while juveniles sometimes suffered higher mortality than wild crabs, there were usually no differences in survival.

This suggests that, whereas some differences between cultured and wild crabs can be mitigated through conditioning, the negligible effect on post-release survival observed in our field experiments do not warrant the cost and effort.

Although some studies report no differences (e.g., Maeda-Martinez et al., 2000), most focus on contrasts between cultured and wild animals. Two explanations exist for this: (1) cultured and wild animals are truly more different than similar, or (2) researchers tend to report differences and de-emphasize reporting of non-significant results. It is important to keep the latter hypothesis in mind when interpreting these studies.

We encourage researchers to present non-significant differences between cultured and wild organisms to enable the best analysis of the situation, and to develop conditioning programs where necessary. Conditioning programs should not focus on deficits that take only a few days to rectify, as their impact will be negligible unless the deficits result in increased mortality immediately after release. Neither should they focus on differences that take a long time to reverse because the cost may be prohibitive. Instead, the focus should be on factors that take an intermediate amount of time to address, combined with a cost:benefit analysis.

ACKNOWLEDGMENTS

We thank the many undergraduate students and technicians for their assistance in the field and laboratory experiments. Special thanks to M. Goodison, M. Kramer, and R. Aguilar for their assistance with laboratory and field studies. We also thank the researchers and technicians at COMB for raising the cultured crabs used in this study; in particular, B. Bystry, without whom this research would not have been possible. We are also grateful to two reviewers, whose comments and suggestions significantly improved the article. Funding for this research was provided to BCARC by NOAA, Phillips Seafood, the Maryland Watermen's Association, the Smithsonian Environmental Studies Program, and the Smithsonian Internship Program.

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