

Importance of Blue Crab Life History for Stock Enhancement and Spatial Management of the Fishery in Chesapeake Bay

ROBERT AGUILAR, ERIC G. JOHNSON, ANSON H. HINES,
MARGARET A. KRAMER, and MICHAEL R. GOODISON

Smithsonian Environmental Research Center, Edgewater, Maryland, USA

*Due to over-harvesting and habitat degradation, spawning stock abundance and biomass of the Chesapeake Bay blue crab (*Callinectes sapidus*) has declined over 80% in the last 15 years. In addition, only a small portion (11–22%) of the spawning stock migrates successfully to the historic spawning areas of the lower estuary. As a result, recent management goals to decrease harvests and increase spawning stock biomass have been adopted by the different Chesapeake Bay regulatory agencies. The crisis has also prompted an experimental assessment of the potential for stock enhancement to increase the number of spawners. While much of the current stock enhancement work has focused on assessing the competency of hatchery-reared individuals and identifying key processes that optimize survival and growth of juveniles to maturity, less attention has been paid to examining factors that influence the long-term efficacy of stock enhancement efforts. Here we discuss important interactions between blue crab life history, stock enhancement efforts, and management options available to increase the standing stock of mature females in Chesapeake Bay. We propose the establishment of migration corridors to protect female blue crabs when they undergo the long-distance migration after mating to lower Bay spawning areas.*

Keywords *Callinectes sapidus*, marine sanctuary, corridor, migration, overharvest, restocking

INTRODUCTION

Successful rebuilding of depleted stocks through stock enhancement can occur only when the factors responsible for stock decline are addressed concurrently through sound fishery management (Hilborn, 2004; Purcell, 2004). Stock enhancement must be carefully integrated with traditional fisheries management to protect both remaining wild stocks and stocked individuals if the targeted populations are to be augmented successfully (Bell et al., 2006). Connectivity between juvenile and adult spawning habitats is also vital for conservation and management of wild stocks (Gillanders et al., 2003) and equally important for maximizing the potential benefits of releasing hatchery-reared individuals (see Lipcius et al., 2008). However, difficulties may arise in maintaining connectivity when target species undergo

long-distance migrations over multiple habitats and regulatory jurisdictions. Life history traits, such as migrations, need to be considered when developing optimal stock enhancement strategies. During the migration period, large numbers of individuals may be concentrated at high densities. Consequently, migrants may incur increased mortality owing to greater vulnerability to overharvesting, predation, or episodic deleterious environmental conditions. All these risks may vary spatially and temporally within and outside areas supplemented with hatchery-reared juveniles and could severely impact the efficacy of stock enhancement efforts.

One species currently being investigated for the feasibility of stock enhancement (Zohar et al., 2008) that undergoes a long-distance spawning migration is the blue crab (*Callinectes sapidus* Rathbun) (Van Engel, 1958; Aguilar et al., 2005). The blue crab is a commercially and ecologically important brachyuran crab that occurs from Nova Scotia to northern Argentina. Within the United States, the blue crab is most common south of Cape Cod, where it supports a major fishery and is a dominant

Address correspondence to Robert Aguilar, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037. E-mail: aguilar@si.edu

predator in many estuarine systems. However, the Chesapeake Bay blue crab population has declined drastically in recent years most likely due to overharvest and habitat degradation and loss. From 1992 to 2000, the spawning stock abundance and biomass declined 81% and 84% (Lipcius and Stockhausen, 2002), respectively, and remain at record low levels (Bi-state Blue Crab Technical Advisory [BBTAC], 2006). Furthermore, larval abundance and post-larval recruitment have declined precipitously in the same period (Lipcius and Stockhausen, 2002). These population declines, along with evidence of recruitment limitation, have identified the blue crab as a possible candidate for stock enhancement. Since 2001, the Blue Crab Advanced Research Consortium (BCARC) has been conducting laboratory and field release experiments to determine the feasibility of blue crab stock enhancement in Chesapeake Bay (see Zohar et al., 2008, for an overview). However, while considerable attention has been placed on evaluating blue crab stock enhancement by assessing the competency of hatchery reared individuals (e.g., hatchery vs wild comparisons, genetic considerations; see Young et al., 2008) and by identifying key processes that optimize survival and growth of juveniles to maturity (see Hines et al., 2008), less attention has been focused on processes affecting hatchery-reared mature females following recruitment to the fishable stock. An understanding of how the female spawning migration (Aguilar et al., 2005) that is subject to intense harvest (Miller et al., 2005) interacts with release strategies is a critical component of the ultimate success of blue crab stock enhancement in Chesapeake Bay. Such consideration of stock enhancement within the larger framework of fishery management is often lacking (Bell et al., 2006).

In this article, we discuss the effects of potential management options for establishing a migration corridor to protect mature females during migration on strategies for stocking juvenile blue crabs in Chesapeake Bay. We explain the risks of migration in the context of over-exploitation, female migration in the blue crab life cycle, strategic elements of current blue crab fishery management, and environmental factors affecting migration. Particular attention is paid to the need to consider the complex blue crab life cycle, the high degree of environmental variation within Chesapeake Bay, and the dynamic nature of the blue crab fishery in assessing the potential benefits of stock enhancement and other management strategies. We view primary and secondary migration corridors as key components of a stock enhancement strategy integrated with fishery management for the Chesapeake blue crab stock.

BLUE CRAB LIFE HISTORY AND FEMALE MIGRATION

Blue crabs in Chesapeake Bay have a complex life cycle which involves a unidirectional long-distance female migration from lower salinity mating areas to higher salinity spawning grounds. Mating of blue crabs typically occurs from May to

October in mesohaline and oligohaline areas (Van Engel, 1958). Males couple with females before the terminal molt to maturity. Following ecdysis, mating occurs while the females are soft and males continue to guard females (Van Engel, 1958) for a period of hours to 3 days (Jivoff, 1997). After the mating pair separate, males remain in these lower salinity areas, whereas most females eventually move to high salinity areas within the lower estuary to spawn (Van Engel, 1958). Periods of peak spawning along the Mid-Atlantic Bight have typically been documented from late July to August (McConaughy et al., 1983; Epifanio, 1995).

The migration of mature female blue crabs is characterized by two distinct phases (Tankersley et al., 1998). Phase I involves the movement of post-copulatory females from mating areas to the lower estuary. The majority of mature females (at least from upper Chesapeake Bay) appear to delay Phase I migration until fall (Turner et al., 2003; Aguilar et al., 2005). This most likely allows recently molted females to begin to accrue energy required for oogenesis and the muscle mass and hepatopancreas reserves necessary for migration (Turner et al., 2003). During Phase I migration, females appear to use areas near the deep channel, particularly the eastern shoulder, of Chesapeake Bay as a migration corridor to the spawning areas of the lower estuary (Aguilar et al., 2005; Figure 1). Phase II migration entails movement of late-stage ovigerous females to the estuary mouth or into adjacent coastal waters (Figure 1). During Phase II, females use selective-tidal-stream-transport (STST) on nocturnal ebb tides to move seaward to release their larvae at or near nocturnal high tides (Tankersley et al., 1998; Forward et al., 2003). After spawning, most females return to the estuary, but do not move back into lower salinity areas (Hines et al., 1987; Medici et al., 2006). If conditions allow, females may produce more than one brood within a year and produce further broods in successive years (Hines et al., 2003).

Strong evidence indicates that hatchery-reared blue crabs released in the wild as juveniles are reproductively competent as adults (e.g., complete the spawning migration). Hatchery-reared blue crabs mate and produce viable offspring in the laboratory, including those recaptured as adults from release sites (Hines et al., 2008; Zohar et al., 2008). Moreover, there are negligible long-term differences in behavior of hatchery-reared and wild blue crabs (Young et al., 2008).

STRATEGIC MANAGEMENT ISSUES AND ENVIRONMENTAL FACTORS CONCERNING BLUE CRAB MIGRATION AND STOCK ENHANCEMENT

Blue Crab Harvest

The Chesapeake Bay blue crab stock has recently experienced overfishing (Miller et al., 2005). From 1998 to 2002, over 60% of the fishable population was harvested, well above the rate estimated to conserve 10% of the spawning stock. In response to these data and recommendations from the BBCAC, Maryland

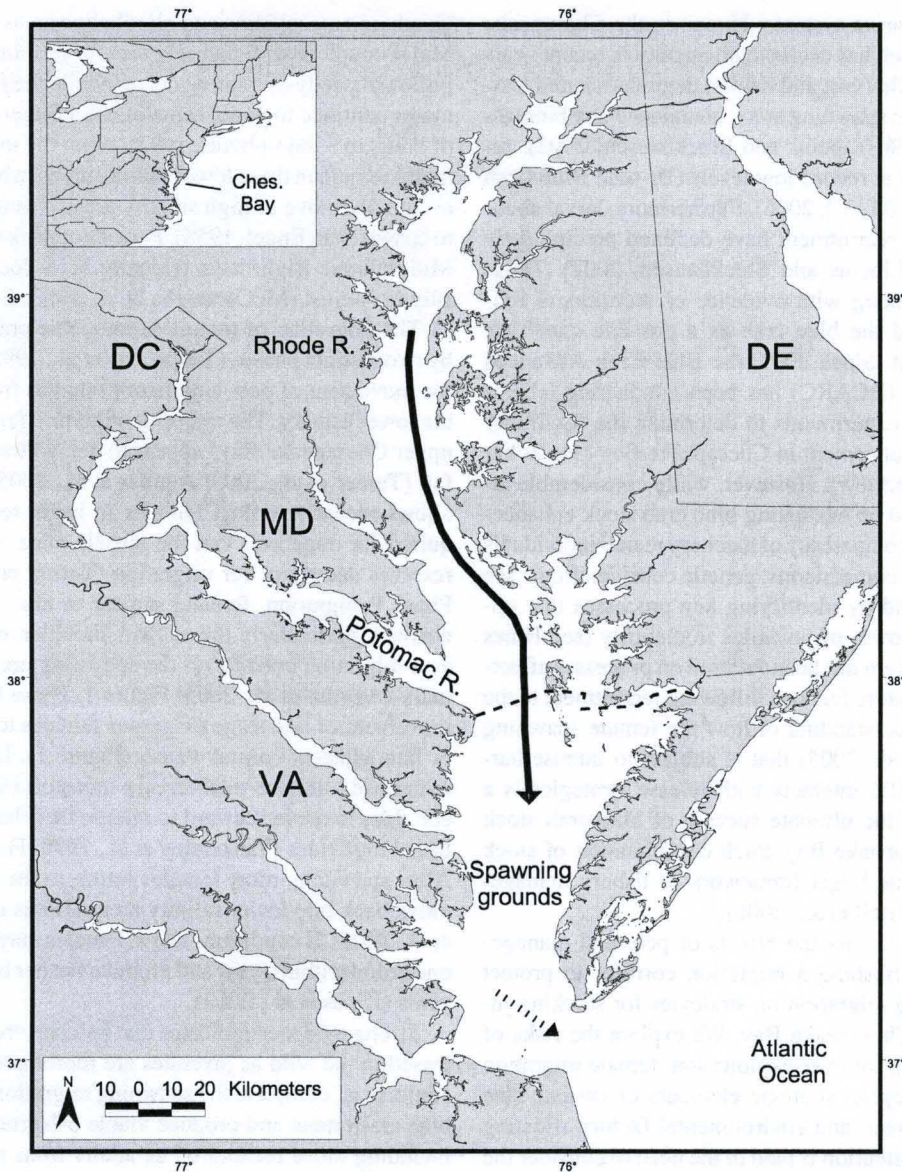


Figure 1 Migration of mature female blue crabs from mating to spawning areas in Chesapeake Bay. The solid line represents Phase I migration: The movement of post-copulatory females to the spawning grounds of the lower estuary (typically using shoulder areas near the main channel, particularly those along the eastern shore). The dashed line represents the Phase II migration: The movement of late-stage ovigerous females to the estuary mouth or adjacent coastal waters to release larvae.

and Virginia implemented new regulations to reduce harvest pressure and double the size of the blue crab spawning stock from the 1997–1999 average level. In 2005, for the first time in eight years, exploitation was below the target rate estimated to conserve 20% of the spawning stock (BBTAC, 2006). However, despite increasingly restrictive management in both states, the spawning stock biomass has not increased, and concerns still remain about the resilience of the blue crab stock to natural perturbations and further high levels of harvest.

Once recruited to the fishery, blue crabs are targeted by a varied array of gear at multiple life stages almost year-round throughout Chesapeake Bay. Male crabs, specifically large indi-

viduals, are highly prized and are captured by most gears types (crab pot, trotlines, etc.) throughout the main crabbing season (April–November). Although current regulations aim to protect the spawning stock, mature females continue to be captured and are often a majority of the catch during the fall migration period. Intense fishing in Chesapeake Bay results in only 11–22% of the potential spawning stock reaching the spawning grounds in the lower Bay (Seitz et al., 2001). Mature females are also a major component of the Virginia winter dredge fishery. Much of the dredge fishery occurs in spawning areas of the lower Bay (i.e., within the summer spawning sanctuary), where females generally remain after spawning. Pre-molt (peeler crabs) and recently

molted (soft crabs) crabs are targeted with scrapes in the grass beds of southern Maryland and Virginia. Pre-pubescent females are specifically targeted in peeler pots, which are baited with reproductively active male crabs. After capture, crabs in imminent molting condition (soft and peeler crabs) are held until they molt because the value of soft crabs is ~6 times greater than that of hard crabs.

Bi-State Management

One of the major issues regarding blue crab management in Chesapeake Bay is multi-jurisdictional regulation. Historical and geographical differences between Maryland and Virginia, in combination with blue crab life history traits, have led to differing harvesting practices and management strategies (Table 1). However, in recent years there has been recognition of the importance of cooperation in the management of blue crabs. In 2001, BBCAC issued a report on the status of the blue crab population and management recommendations to increase the stock in Chesapeake Bay (Chesapeake Bay Commission, 2001). The goals set forth in the BBCAC report were recognized and addressed, with new regulations adopted by the three major Chesapeake Bay regulatory agencies.

Hypoxia

Chesapeake Bay is prone to chronic hypoxia (<2 mg l⁻¹ dissolved oxygen) and anoxia (0 mg l⁻¹ dissolved oxygen) during summer. Low oxygen conditions may force crabs into shallower, more spatially restricted areas of the Bay, increasing their vulnerability to predation or capture. Prolonged hypoxia may limit food resources (mainly infaunal bivalves) in affected areas even after normoxic conditions resume (Holland et al., 1987). Wind-induced upwelling can also result in seiching of hypoxic waters into shallower areas, which may last for several hours to days

Table 1 A subset of current blue crab commercial harvest regulations in Chesapeake Bay. The tidal portion of the Potomac River is managed by the Potomac River Fisheries Commission, which contains representatives from Maryland and Virginia. Please note there are special provisions for some limited areas within certain jurisdictions (e.g., Worcester County, Maryland, and Tangier Island, Virginia)

Criterion	Jurisdiction		
	Maryland	Virginia	Potomac River
"Sponge" female harvest	Prohibited	Allowed	Prohibited
Crab dredging	Prohibited	(Dec 1–Mar 31)	Prohibited
Crab pots in tributaries	Prohibited	Allowed	Allowed
Commercial week	6 d ^A	5–6 d ^B	7 d
Spawning sanctuary	N/A	(June 1–Sep 15)	N/A

Note: ^A Commercial fishers must take either Sunday or Monday off. ^B All commercial crabbing is prohibited on Sundays, except fishing peeler pots and tending other gear (shedding facilities, floats, nets, etc.). In addition, dredging is prohibited on Saturdays.

(Buzzelli et al., 2002). This may contribute directly to mortality of free-ranging blue crabs, which attempt to avoid hypoxia but are often unsuccessful (Bell et al., 2003). It also increases "by catch" mortality by killing crabs of all sizes trapped in passive fishing gear. Many fishers in Chesapeake Bay have reported entire dead catches (of up to 50 bushels) from crab pots set for ~24 hr during episodic hypoxic events. Hypoxia can also result in spatial compression as blue crabs move from hypoxic areas to restricted normoxic waters (Eby and Crowder, 2002). This can increase the catch efficiency of fishermen who respond to intermittent hypoxic events by concentrating their gear in normoxic areas (Selberg et al., 2001).

Most crabs from upper Chesapeake Bay appear to begin the spawning migration in the fall (Aguilar et al., 2005) and may avoid the bulk of hypoxic conditions. Stock enhancement strategies (e.g., release site, timing, and size) should attempt to maximize the number of mature females migrating after normoxic conditions have resumed (i.e., fall). Additionally, local and meso-scale propensity for areas to experience chronic and episodic hypoxia should be an important factor in selection of sites for releasing crabs—areas with high levels of sustained or episodic hypoxia are unsuitable. Similarly, sites with a high tendency for hypoxia should be also avoided, as episodic hypoxia may force large crabs from deeper water into shallower nursery areas and increase juvenile mortality (Eggleston et al., 2005).

Overwintering Mortality

Winter mortality can be an important source of blue crab loss (Rome et al., 2005). Blue crabs, like all members of the genus *Callinectes*, are a tropical species by origin, and Chesapeake Bay is at the upper latitudinal limit of their geographic range. Thus, individual crabs may not be well adapted to the most extreme winter conditions typical of northern areas. Blue crab winter-induced mortality risk appears to be affected by three synergistic factors: temperature, salinity, and life stage (Tagatz, 1969; Rome et al., 2005). Blue crab osmoregulation efficiency decreases at low temperature and salinity (Tagatz, 1971). In laboratory experiments and field surveys, blue crabs have generally showed increasing mortality risk with decreasing temperature and salinity and increasing size. The highest mortality occurs for mature females (Tagatz, 1969; Rome et al., 2005) when temperatures drop below the February average of 3.4°C (Rome et al., 2005). After spawning, mature females generally avoid low-salinity waters and do not return to mating areas. However, migrating females that do not arrive in the lower estuary prior to the onset of winter conditions may suffer considerable mortality during extremely cold and wet years.

Consideration of overwintering mortality is important in determining optimal spatial and temporal release strategies of stock enhancement efforts in Chesapeake Bay. Many subestuaries of the upper Bay appear to be ideal release locations based on habitat characteristics, i.e., they are recruitment limited and have abundant food resources and low levels of fish predation

(Johnson et al., 2008). However, crabs released there may suffer increased mortality due to lower salinities during winter if they do not migrate to spawning grounds beforehand. This impact may be lessened or eliminated by releasing hatchery-reared juveniles at specific times of year or sizes. For example, crabs released in spring avoid winter mortality since they grow rapidly, reach maturity, and migrate from upper Bay nursery areas by fall to higher salinity and temperatures of the lower Bay before the onset of harsh winter conditions (Davis et al., 2005; Hines et al., 2008; Johnson et al., 2008).

CONSIDERATIONS FOR STOCK ENHANCEMENT

Consideration of the spatial linkages between release sites and spawning grounds has important implications for stock enhancement of blue crabs in Chesapeake Bay. Optimal release strategies (e.g., season, size, habitat, location) must not only consider post-release survival of hatchery-reared juveniles in shallow release habitats as they grow to maturity (Davis et al. 2004, 2005; Hines et al., 2008), but also losses of mature females due to environmental conditions and harvest regimes before they reach spawning areas. For example, the potential benefits of releases of hatchery-reared blue crabs into recruitment limited areas of upper Chesapeake Bay may be mitigated if mature females are exposed to hypoxia or extreme winter conditions, or subjected to intense fishing pressure as they migrate from release sites to the spawning sanctuary. Release strategies should also consider factors that might affect reproductive potential of released individuals, such as geographic variation in size at maturity. Female blue crabs in the upper portions of the Bay generally reach maturity at larger sizes than crabs in the lower estuary (R. Aguilar, unpublished data), most likely related to differences in temperature and salinity (Fisher, 1999). Larger size is an advantage because the number of eggs within a brood is positively related to carapace width (Hines, 1982; Prager et al., 1990). Under normal conditions, the greater fecundity of large crabs does not result in higher total annual reproductive output than small female crabs over the course of a season because the interval between broods is shorter for smaller crabs (i.e., they probably produce more broods). However, under high rates of exploitation or natural mortality that remove females before they can spawn multiple times, hatchery-reared and wild crabs originating from the upper Bay may provide a greater per capita reproductive contribution.

NEED FOR A MIGRATION CORRIDOR

The existing Virginia Spawning Sanctuary Complex (VSSC) has proven effective in preserving mature female blue crabs in Chesapeake Bay during the summer months (June 1–September 15), when fishing within the sanctuary is prohibited (Lipcius et al., 2001; Seitz et al., 2001). As many as 70% of mature females entering the sanctuary are protected until they spawn (Lip-

cius et al., 2003). Further evidence for the efficacy of the VSSC are the results of a recent tag-return study, in which mature females outside the spawning sanctuary were 2.8 to 6.3 times more likely to be captured than females within the sanctuary (Lambert et al., 2006). However, females are still vulnerable to harvest en route to the sanctuary during their fall migration and within sanctuary boundaries during winter when fishing is permitted.

Due to the timing and route of the blue crab migration (Turner et al., 2003; Aguilar et al., 2005), establishment of a Maryland Migration Corridor (MMC; Figure 2, even for the limited period of the fall migratory season, could ease fishing pressure. Reduced fishing on migrating females would increase the number of post-copulatory crabs reaching the spawning grounds from recruitment limited areas in upper Chesapeake Bay, and still allow acceptable levels of harvest (from the perspective of fisheries managers and commercial fishers) from other areas in the Bay. Moreover, the current spawning sanctuary in Virginia may increase the likelihood of acceptance of the MMC by commercial fishers in Maryland. The placement and timing of closures are critical for effective protection of migrating females. The MMC would only need to encompass a spatially limited area (depths >8 m) along the mainstem channel during a focused season within the main migration period (late September through November) to provide effective protection for mature females (Figure 2; Turner et al., 2003; Aguilar et al., 2005).

A series of secondary corridors would link the mainstem migration corridor to individual subestuaries which serve as nurseries (Gillanders et al., 2003) and places where females forage on abundant prey following mating (Figure 2). We suggest that secondary corridors should be established in subestuaries where cultured juveniles are released. Indeed, selection of optimal sites for stock enhancement should include consideration of the configuration and enforcement of such secondary corridors. These corridors could also be shifted spatially and temporally to support release strategies in other suitable subestuaries as needed. The multiple years of mark-recapture data for the Rhode River subestuary in upper Chesapeake Bay and other locations (Aguilar et al., 2005; R. Aguilar, unpublished data) provide a good starting point for identifying the location of migration corridors. However, further research is needed to refine knowledge about the movement of females as they depart the nursery subestuaries.

Other options could be considered as supplements or alternatives to establishing migration corridors. For example, the duration of the existing VSSC could also be extended until November (Lambert et al., 2006) to preserve a sizable portion of females that arrive after the spawning period. A gauntlet fishery may preserve spawners by allowing only the harvest of immature individuals (Simfendorfer, 1999). However, this would be impractical and ineffectual with such a short-lived, quick-growing crustacean as the blue crab. Moreover, both male and female crabs mature at small sizes (Jivoff, 2003) undesirable to the fishery, and for males there is no morphologically obvious indication of sexual maturity as there is for females. Although recently mated female crabs are directly targeted in the peeler

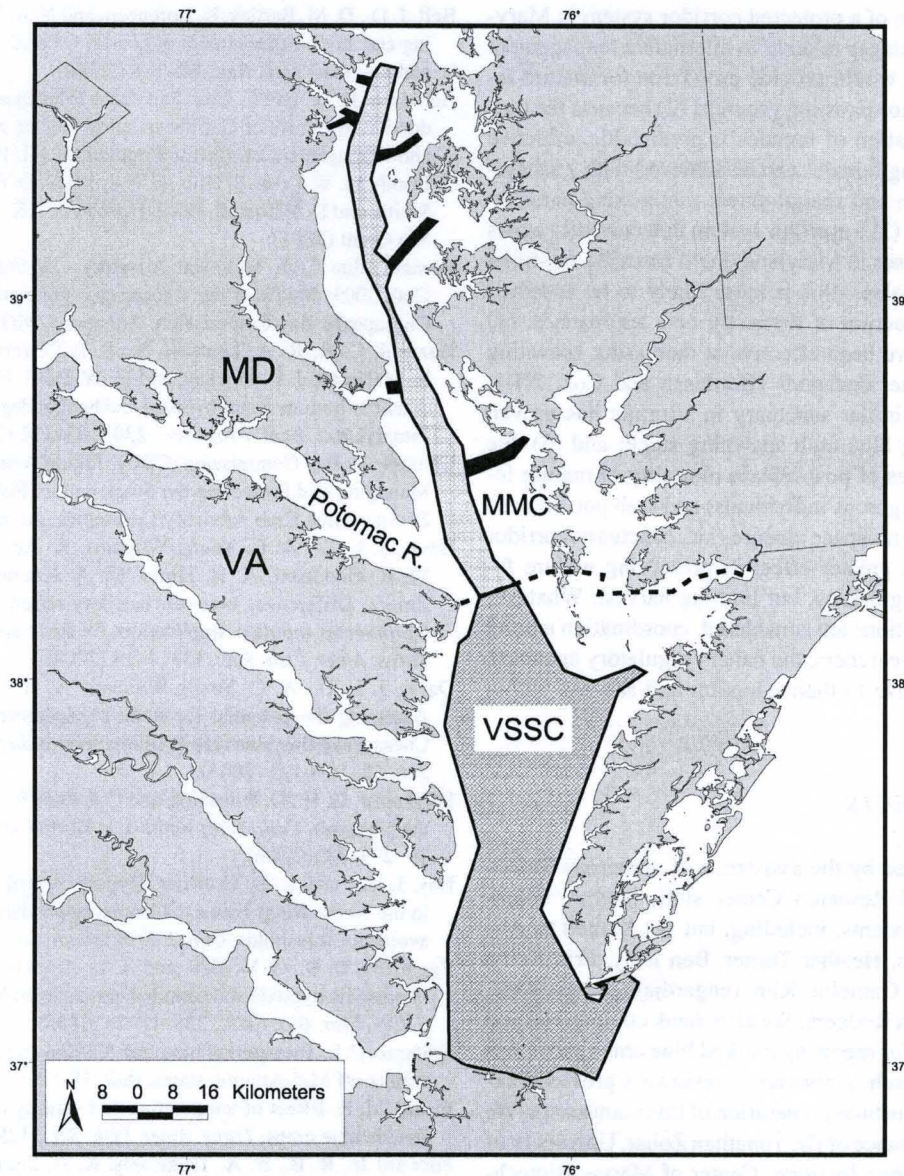


Figure 2 The hypothetical Maryland Migration Corridor (MMC; light shaded area) for Chesapeake Bay, with secondary corridors (dark shaded areas) and the Virginia Spawning Sanctuary Complex (VSSC; grey shading).

fishery, such that restrictions placed on the soft crab and peeler fisheries may increase the numbers of mature females reaching the spawning grounds, they represent only a small percentage (<9%) of the total Chesapeake Bay harvest by weight, but fairly large percentage (~15–30%) of the total value (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD, USA). Due to the high demand and price for soft crabs, restrictions on this life stage may be difficult to implement and enforce.

Another option would be to prohibit harvest of females for the 2- to 3-month period during peak migration. However, during fall mature female blue crabs are specifically targeted by commercial fishers and form a major component of the total catch. Similarly, mature females are a large component of the Virginia

winter dredge fishery. Consequently, there may be reluctance to enact restrictions perceived to severely impact commercial fishers. Furthermore, recent evidence indicates that a sanctuary/corridor complex that limits all fishing may have a greater effect in preserving mature females than mandating release of female crabs because of the capture stress induced by fishing. Dickinson et al. (2006) reported that ovigerous females caught by crab pots incurred considerable levels of “sponge” damage (30–50%), either through mechanical abrasion or egg removal by crabs. Mature females (particularly ovigerous individuals) may also suffer considerable levels of post-release mortality after release from fishing gear (R. Aguilar, personal observation; R. N. Lipcius, Virginia Institute of Marine Science, unpublished data).

The implementation of a protected corridor system in Maryland has several advantages relative to alternative management options: (1) the MMC would provide protection for mature females as they migrate to spawning grounds; (2) because the timing and route of migration of females is predictable, effective protection for spawning females can be achieved with a sanctuary of limited duration and spatial extent minimizing hardship to commercial fishers; (3) a corridor system that currently exists for navigational purposes in Maryland could be easily modified to protect mature females—this is more likely to be accepted by fishers than introduction of distinctly new approaches; (4) marine sanctuaries have been effective at increasing spawning stock biomass for other decapods (Bertleson and Cox, 2001; Rowe, 2002), and a similar sanctuary in Virginia has proven effective in protecting blue crab spawning stock; and (5) due to potentially high rates of post-release mortality of mature females (particularly ovigerous individuals) and crab pot-induced “sponge” damage, a time-space closure (i.e., sanctuary/corridor complex) may have a greater effect in preserving mature females than by allowing fishing, but limiting harvest. Whatever future management options are considered, coordination among stock enhancement researchers, the fishery regulatory agencies, and fishers is imperative to their adoption and success within Chesapeake Bay.

ACKNOWLEDGEMENTS

This work was aided by the assistance of numerous Smithsonian Environmental Research Center staff, interns, volunteers, and graduate students, including, but not limited to Alicia Young, Jana Davis, Heather Turner, Ben Daly, Erin Kelly, Kathryn Chop, Emily Gamelin, Kim Tengardjaja, James Wolf, Anna Miller, and Paula Rodgers. We also thank commercial and recreational crabbers for reporting marked blue crabs and cooperating with our research. Anonymous reviewers provided extensive comments in the final preparation of this manuscript. We acknowledge the assistance of Dr. Yonathan Zohar, University of Maryland, Biotechnology Institute, Center of Marine Biotechnology (COMB). This research was supported by funds from NOAA Chesapeake Bay Program Office to the Blue Crab Advanced Research Consortium (BCARC), Maryland Sea Grant College Program, and Smithsonian Environmental Science Program.

REFERENCES

- Aguilar, R., A. H. Hines, T. G. Woolcott, D. L. Woolcott, M. A. Kramer, and R. N. Lipcius. The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, **319**: 117–128 (2005).
- Bell, G. W., D. B. Eggleston, and T. G. Wolcott. Behavioral responses of free-ranging blue crabs to hypoxia: I. Movement. *Mar. Ecol. Prog. Ser.*, **259**: 215–225 (2003).

- Bell, J. D., D. M. Bartley, K. Lorenzen, and N. R. Loneragan. Restocking and stock enhancement of coastal fisheries: Potential, problems and progress. *Fish. Res.*, **80**: 1–8 (2006).
- Bertleson, R. D., and C. Cox. Sanctuary roles in population and reproductive dynamics of Caribbean spiny lobster. In: *Spatial Processes and Management of Marine Populations* (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, Eds.). Fairbanks, AK: University of Alaska Sea Grant (2001).
- Bi-state Blue Crab Technical Advisory Committee (BBTAC). Blue Crab 2005: Status of the Chesapeake population and its fisheries. Chesapeake Bay Commission. Annapolis, MD (2006).
- Buzzelli, C. P., R. A. Leuttich, Jr., S. P. Powers, C. H. Petersen, J. E. McNinch, J. L. Pinckey, and H. W. Paerl. Estimating the spatial extent of bottom-water hypoxia and habitat degradation in a shallow estuary. *Mar. Ecol. Prog. Ser.*, **230**: 103–112 (2002).
- Chesapeake Bay Commission (CBC). Taking Action for the Blue Crab. Managing and Protecting the Stock and its Fisheries. Report of the Bi-State Blue Crab Advisory Committee, Annapolis, MD (2001).
- Davis, J. L. D., A. C. Young-Williams, R. Aguilar, B. L. Carswell, M. R. Goodison, A. H. Hines, M. A. Kramer, Y. Zohar, and O. Zmora. Differences between hatchery-raised and wild blue crabs (*Callinectes sapidus*): Implications for stock enhancement potential. *Trans. Amer. Fish. Soc.*, **133**: 1–14 (2004).
- Davis, J. L. D., A. C. Young-Williams, A. H. Hines, and Y. Zohar. Assessing the potential for stock enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*). *Can. J. Fish. Aquat. Sci.*, **62**: 109–122 (2005).
- Dickinson, G. H., D. Rittschof, and C. Latanich. Spawning biology of the blue crab, *Callinectes sapidus*, in North Carolina. *Bull. Mar. Sci.*, **79**: 273–285 (2006).
- Eby, L. A., and L. B. Crowder. Hypoxia-based habitat compression in the Neuse River Estuary: Context-dependent shifts in behavioral avoidance thresholds. *Can. J. Fish. Aquat. Sci.*, **59**: 952–965 (2002).
- Eggleston, D. B., G. W. Bell, and A. D. Amavisca. Interactive effects of episodic hypoxia and cannibalism on juvenile blue crab mortality. *J. Exp. Mar. Biol. Ecol.*, **325**: 18–26 (2005).
- Epifanio, C. E. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off Mid-Atlantic states. *Bull. Mar. Sci.*, **57**: 713–725 (1995).
- Fisher, M. R. Effect of temperature and salinity on size at maturity of female blue crabs. *Trans. Amer. Fish. Soc.*, **128**: 499–506 (1999).
- Forward Jr., R. B., R. A. Tankersely, K. A. Smith, and J. M. Welch. Effects of chemical cues on orientation of blue crab, *Callinectes sapidus*, megalopae in flow: Implications for location of nursery areas. *Mar. Biol.*, **142**: 747–756 (2003).
- Gillanders, B. M., K. W. Able, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. Evidence of connectivity between juvenile and adult habitats for mobile fauna: An important component for nurseries. *Mar. Ecol. Prog. Ser.*, **247**: 281–295 (2003).
- Hilborn, R. Population management in stock enhancement and sea ranching. In: *Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities*, pp. 201–209 (K. M. Leber, S. Kitada, H. L. Blankenship, and T. Svasand, Eds.). Oxford, UK: Blackwell (2004).
- Hines, A. H. Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.*, **69**: 309–320 (1982).
- Hines, A. H., P. R. Jivoff, P. J. Bushmann, J. van Montfrans, S. A. Reed, D. L. Wolcott, and T. G. Wolcott. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bull. Mar. Sci.*, **72**: 287–210 (2003).
- Hines, A. H., E. G. Johnson, A. C. Young, R. Aguilar, M. A. Kramer, M. Goodison, O. Zmora, and Y. Zohar. Release

- strategies for estuarine species with complex migratory life cycles: Stock enhancement of Chesapeake blue crabs. *Rev. Fish. Sci.*, **16**: 175–185 (2008).
- Hines, A. H., R. N. Lipcius, and M. A. Haddon. Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **36**: 55–64 (1987).
- Holland, A. F., N. K. Mountford, and J. A. Mihursky. Temporal variation in upper Bay mesohaline benthic communities I: The 9-m mud habitat. *Chesapeake Sci.*, **18**: 370–378 (1987).
- Jivoff, P. The relative roles of predation and sperm competition on the duration of the post-copulatory association between the sexes in the blue crab, *Callinectes sapidus*. *Behav. Ecol. Sociobiol.*, **40**: 175–185 (1997).
- Jivoff, P. Summary Paper: Reproduction and Embryonic Development Session, Blue Crab Symposium 2000. *Bull. Mar. Sci.*, **72**: 265–272 (2003).
- Johnson, E. G., A. H. Hines, M. A. Kramer, and A. C. Young. Importance of season and size of release to stocking success for the blue crab in Chesapeake Bay. *Rev. Fish. Sci.*, **16**: 243–253 (2008).
- Lambert, D. M., R. N. Lipcius, and J. M. Hoinig. Assessing effectiveness of the blue crab spawning stock sanctuary in Chesapeake Bay using tag-return methodology. *Mar. Ecol. Prog. Ser.*, **321**: 215–225 (2006).
- Lipcius, R. N., R. D. Seitz, W. J. Goldsborough, M. M. Montane, and W. T. Stockhausen. A deepwater dispersal corridor for adult female blue crabs in Chesapeake Bay. In: *Spatial Processes and Management of Marine Populations*, pp. 643–666 (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, Eds.). Fairbanks, AK: Alaska Sea Grant College Program. AK-SG-01-02 (2001).
- Lipcius, R. N., and W. T. Stockhausen. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab in the Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **226**: 45–61 (2002).
- Lipcius, R. N., W. T. Stockhausen, R. D. Seitz, and P. J. Geer. Spatial dynamics and value of a marine protected area and corridor for the blue crab spawning stock in Chesapeake Bay. *Bull. Mar. Sci.*, **72**: 453–470 (2003).
- Lipcius, R. N., D. B. Eggleston, S. J. Schreiber, R. D. Seitz, J. Shen, M. Sisson, W. T. Stockhausen, and H. V. Wang. Importance of metapopulation connectivity to restocking and restoration of marine species. *Rev. Fish. Sci.*, **16**: 101–110 (2008).
- Medici, D. A., T. G. Wolcott, and D. L. Wolcott. Scale dependent movements and protection of the female blue crab, *Callinectes sapidus*. *Can. J. Fish. Aquat. Sci.*, **319**: 117–128 (2006).
- McConaugha, J. R., D. F. Johnson, A. J. Provenzano, and R. C. Maris. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. *J. Crust. Biol.*, **3**: 582–591 (1983).
- Miller, T. J., S. J. D. Martell, D. B. Bunnell, G. Davis, L. Fegley, A. Sharov, C. Bonzek, D. Hewitt, J. Hoinig, and R. N. Lipcius. Stock Assessment of Blue Crab in Chesapeake Bay 2005. Final Report to NOAA, Silver Spring, MD. 163 pp. (2005).
- Purcell S. W. Management options for restocked *Trochus* fisheries. In: *Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities*, pp. 233–243 (K. M. Leber, S. Kitada, H. L. Blankenship, and T. Svasand, Eds.). Oxford, UK: Blackwell (2004).
- Prager, M. H., J. R. McConaugha, C. M. Jones, and P. J. Greer. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay. Biological, statistical, and management considerations. *Bull. Mar. Sci.*, **46**: 170–179 (1990).
- Rome, M. S., A. C. Young-Williams, G. R. Davis, and A. H. Hines. Winter mortality of Chesapeake blue crabs (*Callinectes sapidus*). *J. Exp. Mar. Biol. Ecol.*, **319**: 129–145 (2005).
- Rowe, S. Population parameters of American lobster inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Fish. Res.*, **56**: 167–175 (2002).
- Selberg, C. D., L. A. Eby, and L. B. Crowder. Hypoxia in the Neuse River Estuary: Responses of crabs and crabbers. *N. Amer. J. Fish. Manag.*, **21**: 358–366 (2001).
- Seitz, R. D., R. N. Lipcius, W. T. Stockhausen, and M. M. Montane. Efficacy of blue crab spawning sanctuaries in Chesapeake Bay. In: *Spatial Processes and Management of Marine Populations*, pp. 607–626 (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, Eds.). Fairbanks, AK: Alaska Sea Grant College Program. AK-SG-01-02 (2001).
- Simpfendorfer, C. A. Demographic analysis of the dusky shark fishery in southwestern Australia. In: *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. Proceedings of the Symposium on Conservation of Long-Lived Marine Animals*, pp. 149–160 (J. A. Musick, Ed.). Monterey, CA (1999).
- Tagatz, M. E. Some relations of temperature acclimation and salinity to thermal tolerance of the blue crab, *Callinectes sapidus*. *Trans. Am. Fish. Soc.*, **98**: 713–716 (1969).
- Tagatz, M. E. Osmoregulatory ability of blue crabs in different temperature-salinity combinations. *Chesapeake Sci.*, **12**: 14–17 (1971).
- Tankersley, R. A., M. G. Wieber, M. A. Sigala, and K. A. Kachurak. Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: Evidence for selective tidal-stream transport. *Biol. Bull.*, **195**: 168–173 (1998).
- Turner, H. V., D. L. Wolcott, T. G. Wolcott, and A. H. Hines. Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay blue crabs, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.*, **295**: 107–130 (2003).
- Van Engel, W. A. The blue crab and its fishery in Chesapeake Bay: Part I. Reproduction, early development, growth and migration. *Comm. Fish. Rev.*, **20**: 6–17 (1958).
- Young, A. C., E. G. Johnson, J. L. D. Davis, A. H. Hines, O. Zmora, and Y. Zohar. Do hatchery reared blue crabs differ from wild crabs, and does it matter? *Rev. Fish. Sci.*, **16**: XX–XX (2008).
- Zohar, Y., A. H. Hines, O. Zmora, E. G. Johnson, R. N. Lipcius, R. D. Seitz, D. B. Eggleston, A. R. Place, E. Schott, J. S. Chung. The Chesapeake Bay blue crab (*Callinectes sapidus*): A multidisciplinary approach to responsible stock replenishment. *Rev. Fish. Sci.*, **16**: 24–34 (2008).