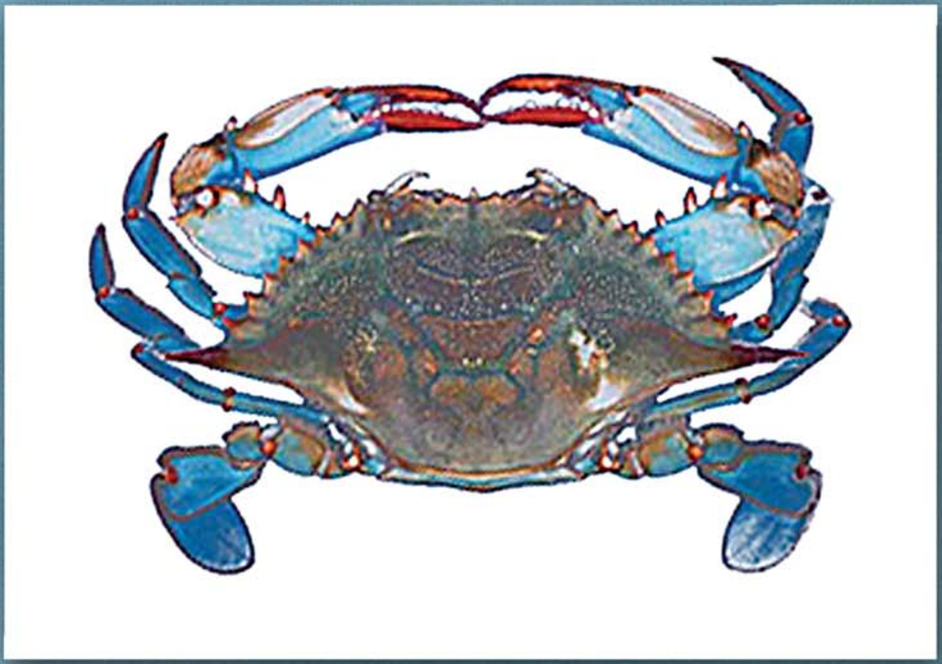
ECOSYSTEM BASED FISHERIES MANAGEMENT FOR CHESAPEAKE BAY

Crab Species Team Background and Issue Briefs



Blue Crab Species Team
Background and Issue Briefs

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Introduction

Eric Johnson, Chair, Blue Crab Species Team

The blue crab, *Callinectes sapidus*, is perhaps the Bay's most iconic species. Blue crabs exhibit a complex life history with large-scale dispersal between estuarine and marine habitats during larval, juvenile and adult phases. Within Chesapeake Bay, blue crabs utilize key nearshore habitats including seagrass, tidal salt marshes and woody debris that are particularly vulnerable to a suite of anthropogenic stressors. The blue crab is an integral component of the complex estuarine foodweb, and serves important roles as both predator and prey in the Chesapeake Bay ecosystem (Baird and Ulanowicz 1989). The blue crab supports both a thriving recreational fishery and Chesapeake Bay's most lucrative commercial fishery. The fishery is complex with commercial and recreational sectors, regional variation in fishing gear and effort, multi-jurisdictional management, and a variety of markets including "live hard crab", "soft and peeler" and "processed crab meat" industries (Kennedy et al. 2007). Recent declines in blue crab populations, female spawning stock and harvest have resulted in coordinated single-species management efforts. However, given the ecological, economic and sociological importance of the blue crab to the region, this species is perhaps the ideal candidate for ecosystem-based fishery management (EBFM) in Chesapeake Bay.

Fisheries researchers, managers and policy makers have become increasingly aware of the importance of adopting multi-species and EBFM in Chesapeake Bay (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006). These approaches provide a more holistic framework that recognizes the complex interactions among species, habitat and environment that combine to regulate the population dynamics of exploited fishery stocks. Further, EBFM approaches recognize that the biological and socioeconomic systems to be managed are inexorably linked. Despite this awareness, effective development and implementation of EBFM plans have been hampered because this approach requires not only traditional fisheries data sources such as standardized surveys of abundance, effort and harvest, but a detailed knowledge of multi-species interactions, complex ecological processes and the impacts of environmental stressors. In Chesapeake Bay, the need for multi-species and EBFM approaches has been acknowledged for more than a decade (Miller et al. 1996; Houde et al. 1998; CBFEAP 2006). As a critical step towards advancing EBFM in Chesapeake Bay, Maryland Sea Grant assembled teams of experts to develop detailed background and issue briefs for five of the bay's most important fishery species including the blue crab.

Herein, we provide briefing documents that summarize the major ecological, environmental, and socioeconomic issues facing managers seeking to develop an EBFM plan for the blue crab in Chesapeake Bay.

Issue briefs are subdivided into five major sections:

1. **Biological Background** (Larval Biology, Post-larvae and Young Juveniles, Late Juveniles and Adults)

2. **Habitat** (Climate Change, Habitat Degradation, Fishing Pressure, Disease)

3. **Food Web** (Predation, Cannibalism, Prey, Fishing Pressure, Invasive Species, Disease)

4. **Stock Assessment** (Population Dynamics, Connectivity, Recruitment Variability, Environmental Drivers, Mortality, Exploitation)

5. **Socioeconomics** (Ecosystem Services, Competition With Imports, Equitable Management Alternatives, Regional and National Economic Value, Aquaculture, Management Options and Models)

The background and issue briefs developed by the blue crab species team will be provided to the fisheries managers and Quantitative Ecosystem Teams (QETs) and used to identify relevant EBFM metrics and generate appropriate target and threshold reference points for the blue crab fishery in Chesapeake Bay.

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Acknowledgments

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Maryland Sea Grant would like to thank the Blue Crab Species Team members for their contributions. We also acknowledge and are grateful for the efforts of the many other contributors who provided insights and materials needed for completion of the Ecosystem Issue Briefs.

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Maryland Sea Grant and the Blue Crab Species Team would also like to thank Rochelle D. Seitz for her contributions to the Background and Ecosystem Issue Briefs.

BLUE CRAB BACKGROUND AND ECOSYSTEM ISSUE BRIEFS

BLUE CRAB BACKGROUND BRIEFS

Section	Authors
1. Early Life History	
a. Larval Biology	McConaugha
b. Post-larvae and young juveniles	Ralph/Lipcius/van Montfrans/Seitz
2. Late Life History (Late Juveniles/Adults)	Hines

BLUE CRAB ECOSYSTEM ISSUE BRIEFS

QET	Authors	Issue Brief	Issues	Metric/Indicator Needed	Reference Points Needed
Habitat Suitability	**Hines/Johnson**	3. Climate Change (Direct and Indirect)	Reproduction	Broods per season, Fecundity, Time to Maturity, Egg Development Time	
			Survival - Cold Winter	Growing and Reproductive Seasons, Reduced Winter Mortality	
			Loss of SAV and Marsh Habitat	SAV acreage, Decreased Shoreline and Salt Marsh, Increased eelgrass and widgeon grass	
			Mangroves and Oyster Reef	Expanding Ranges	
			Dead Zones		
			Larval Recruitment/Larval Survivorship	Changes in Current Systems	
			Storm Impacts	Storm Frequency and Intensity	
	vanMontfrans/Lipcius	4. Habitat Degradation	Eutrophication/Hypoxia	HABs, SAV loss, Extent and Duration of Hypoxia, DO level, Habitat Suitability, Nutrient Concentration	
			Destruction of Habitat	Fragementation, Larval Transport, Shoreline Development/Hardening, SAV abundance	
			Loss of oyster reefs		
			Shoreline Development		
			Pollution/Contamination	Degraded Nursery, Restriction on Human Consumption, Mosquito Spraying in Marshes	
	Johnson/Hines/Lipcius/Ralph	5. Fishing Pressure	Trophic cascades	Loss of Marsh Habitat	
			Derelict Fishing Gear	Mortality, Habitat Degredation	
			Dredge Fishery Habitat Impact	Trawls, Dredges, Bycatch	
	Schott/Messick	6. Disease	Eelgrass,Oyster, Salt Marshes, Oysters, Muddy and Sandy Bottom	Habitat Loss through disease agents, Spatial and Temporal Trends, Salt march/seagrass/oyster bed acreage, soil composition, sea level	
			Open Ocean and Coastal Zone	HAB blooms, potential reservoir monitoring	
Foodweb	**vanMontfrans/Johnson/Lipcius**	7. Predation	Changes in relative abundance and composition	Trawl/WDS data	
			Increase forage demand	Trophic Supply/Demand	
				ChesMMAP trawl survey	
	Hines/Kahn/Johnson	8. Cannibalism	Relative Abundance of Life Stages	Baywide Index of Recruitment	
	Ralph/Lipcius/Seitz/vanMontfrans	9. Prey	Health of the benthic system	Extent of Hypoxic Areas	
				benthic 2^o production k-selected spp	
				extent hardened shoreline/dredge areas	

Foodweb, continued	**Johnson/Miller**	10. Fishing Pressure	Relative Abundance of Life Stages	removals and trophic impacts (predators, prey, juvenile crabs)	
			Coordinated Baywide Index	multi-species interactions	
	Hines/vanMontfrans	11. Invasive Species	Invasive Predators/Prey	Abundance - Blue catfish, Pragmites australis, Competitors	
				Zebra Mussels	
	Messick/Schott/Shields	12. Disease	Disease impacts on Predators/Prey	Abundance - Str bass, Atl. Croaker, Weakfish, Spot, N Puffer, Am Eel	
				Eastern Oyster, clams	
Stock Assessment	**Miller/Johnson/Ralph/Messick/**	13. Population Dynamics	Population Connectivity	Regional/Local Connectivity	Center of Mass of Distribution
	Hines/Kahn/ Lipcius/McConaugha/		Population Structure	Spatial Considerations	
	Schott/Shields/van Montfrans	14. Recruitment Variability	Population Abundance	Stock and Recruitment	Time series - Fishery Independent
				Abundance conversions	Intra-seasonal data
		15. Environmental Drivers of Recruitment		Index of Recruitment (all size ranges)	
				Post hoc analysis of surveys	
		16. Juvenile and Adult Mortality	Environmental Drivers of Mortality	Density-dependent processes	
			Disease	Health Assessment Monitoring	
			Natural Mortality	Scale, variability and pattern - integrated	
		17. Fishery Impacts	Status and Trend of the Stock	Landing Est Reliability	Variance Estimates
			Exploitation Rates	Uncertainty	Sector, stage, spatially specific
				Stock - Recruit Models	Compensatory Ability
Socio-economics	**To be addressed**	Ecosystem Services	Existence Value, Social Value		
		Competition with imports			
		Equitable management alternatives	Comp. different state systems, Comm and Rec		
		Regional and National Economic Value			
		Aquaculture			
		Management Options and Models	Spatial Management, Corridors, ITQs, Stock Augmentation		
			Description of Stakeholders		

BACKGROUND

Early Life History: The Larval Phase of a Complex Life History

John R. McConaugha

The vast majority of marine benthic invertebrate species have a complex life history with a pelagic larval stage (Thorson 1950; Thorson 1966). The life history of *Callinectes sapidus* includes an estuarine adult phase and a pelagic, planktotrophic larval phase that develops in coastal waters (Sandifer 1975; Provenzano et al. 1983; McConaugha 1988; Epifanio 1988; Epifanio 2007 - detailed review). The estuarine adults and juveniles range from Brazil to New England and are extremely adaptable to a broad range of environmental conditions. The larval stages are restricted to a narrow range of temperature and salinity that is characteristic of tropical to sub-tropical oceanic waters (Costlow and Bookhout 1965; Epifanio 2007). Female C. s*apidus* mature and mate throughout the Bay before migrating to the higher salinities of the estuarine mouth. Mating and migration starts in the late summer and fall after the molt to maturity. The fall migration, known as the fall run by watermen, results in a large percentage of mature females congregating in the lower Bay (Hampton Roads area) during the winter (Van Engle 1958; Turner et al. 2003). Others over-winter along the main stem of the Bay. Females constrained in their migration by low winter temperatures arrive on the spawning grounds during the following spring and throughout the summer (Jones et al. 1990; Prager et al. 1990).

The spawning season generally starts in mid-May and continues through early September (Van Engle 1958; Jones et al. 1990; Wells 2009). The spawning ground is roughly defined as the area from the mouth of the York River to the Virginia Capes (Van Engle 1958; Jones et al. 1990; Prager et al. 1990). As eggs develop (10-14 days), females migrate from the spawning ground to the Virginia Capes and out onto the inner continental shelf (McConaugha 1992a). Females in temperate waters have the ability to produce 7 or more egg masses during the spawning season (Dickinson et al. 2006) but under natural field conditions only 1-3 broods are produced. Brood size has historically ranged from 0.7 to 6.0 x 10^6; mean 3.2 x 10^6 eggs per brood (Van Engel 1958; Prager et al. 1990; Hines 2007). In recent years (2002-2006) fecundity per brood has dropped, ranging from 0.1 to 4.5 x 10^6; mean 0.8 x 10^6; eggs per brood (Wells 2009). After releasing their larvae, females may remain on the continental shelf, even migrating south toward Albemarle Sound or return to the lower Bay between broods (McConaugha 1992b). Peak spawning in Chesapeake Bay occurs in mid-July (McConaugha 1988).

Larvae of *C. sapidus* (zoeae) are released on a nighttime ebb tide near the south side of the mouth of the estuary (Dittel and Epifanio 1982; Provenzano et al. 1983; Epifanio et al. 1984). Newly hatched zoeae are negatively geotactic and positively phototactic (Sulkin 1984; Sulkin et al. 1980; Forward 1989). These behaviors assure that zoeae are entrained in the outward flowing plume (a thin layer of warm, lower saline water, flowing south along the Virginia coast (Boicourt

1982; Reiss and McConaugha, 1999)) and are transported southward along the Virginia coast (Provenzano et al. 1983; McConaugha 1988). The width and speed of the plume is determined by the flow from the Bay, wind speed and direction. During the spawning season upwelling favorable wind patterns predominate, resulting in a wider and slower plume that tends to mix with the shelf water as the plume moves southward (Figure 1a, 1b) (Boicourt 1982). Upwelling favorable winds cause the surface layers of the inner shelf and the entrained zoeae to move northeast from the coast (Johnson et al. 1984; Johnson 1985; Garvine et al. 1997; Reiss and McConaugha 1999) (Figure 2).

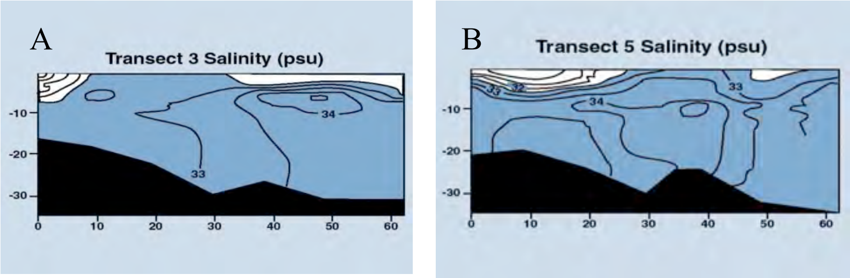


Figure 1 (A and B). Hydrological sections across the Chesapeake Bay plume and coastal waters, August 1988. A is an offshore transect from Cape Henry Virginia. Note the inner edge of the plume and some low salinity water of plume origin offshore. B is a transect off of Duck, NC. Note the increased width of the bay plume and a smaller area of low salinity water offshore. From Reiss and McConaugha (1999).

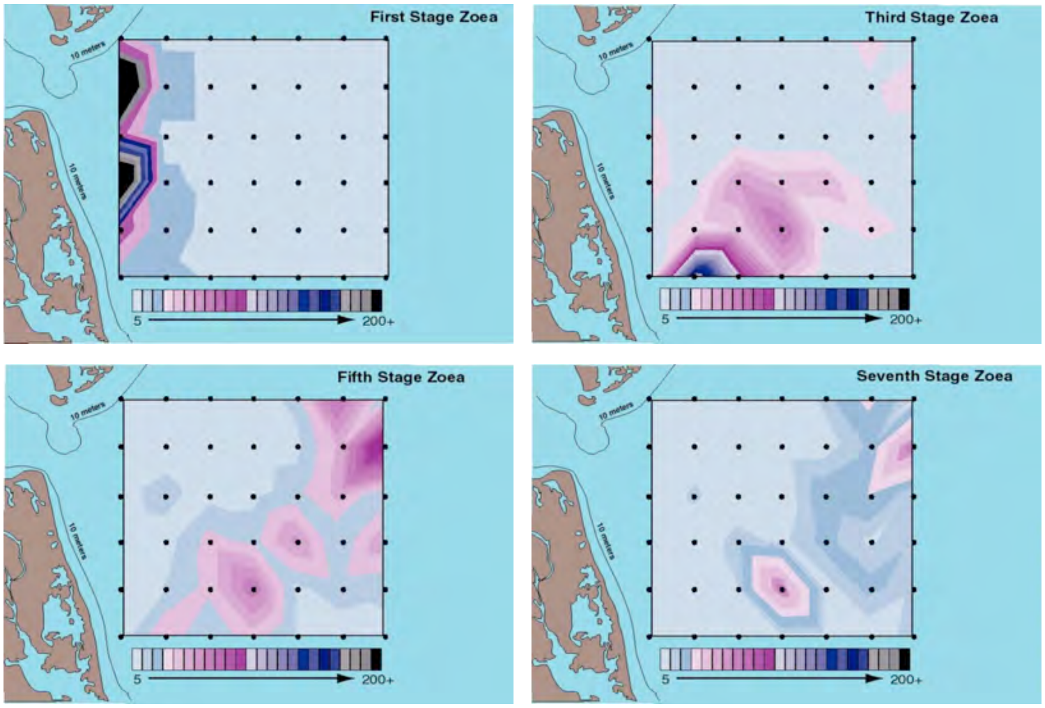


Figure 2. Snapshot of the distribution of zoeal stages 1, 3, 5, and 7 from a 4 day grid sampling effort in August 1988. Due to downwelling favorable winds the 3 days prior to the cruise, the bay plume was moving inshore of its expected position, resulting in the truncation of the distribution of stage 1 zoeae. Note the initial progression of larval stages southward, then offshore and toward the North (McConaugha, unpublished data).

The larval phase consists of 7 zoeal stages requiring approximately 30 days before metamorphosing into a post-larval megalopa stage (Costlow and Bookhout 1959). Variations in the number of larval stages have been reported and may represent an additional developmental stage or intermediates of the standard 7 zoeal stages (Costlow 1967; Costlow and Bookhout 1965; McConaugha, personal observation). Later zoeal stages and the post-larval megalopa stage remain positively phototactic and negatively geotactic in offshore water (Sulkin et al. 1980; Forward et al. 1994). These behaviors place 80% of the larval stages and the megalopae in the upper 3 m of the water column with a preference for the neuston layer (McConaugha 1988). This preference for the near surface coupled with upwelling favorable winds, results in Ekman transport of larvae offshore and toward the north resulting in larval retention near the parental estuary (Hester 1983; Johnson et al. 1984; Garvine et al. 1997) (Figure 3). Inter-annual variability in transport processes and distribution of larvae on the shelf is related to differences in wind speed and direction during the spawning period (Varnell 1989). Comparison of the inter-annual wind data for the Virginia coast with lagged Chesapeake Bay harvest data suggests that 35 to >50% of the observed inter-annual variation in harvest is due to larval transport processes (Hester 1983; Johnson et al. 1984).

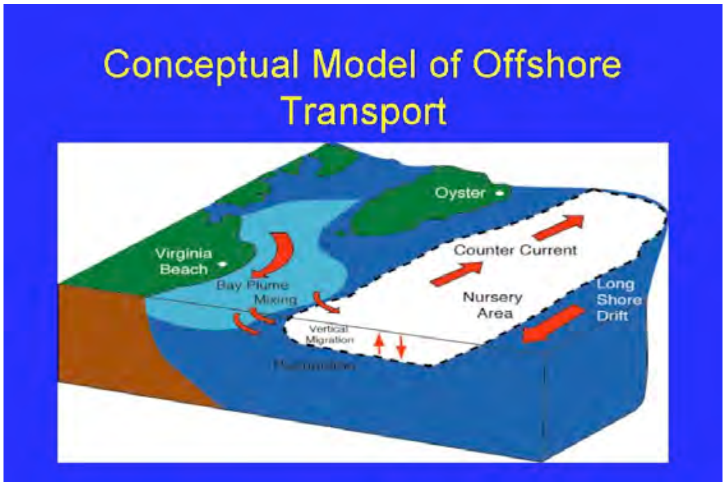


Figure 3. Conceptual model of offshore transport processes for Callinectes sapidus *larvae. Larvae are transported via the Bay plume, subsequently mixed offshore and transported northeast by Ekman transport. Larvae are in the upper 3 m of the water column (McConaugha, unpublished).*

Environmental variables (temperature and salinity) can affect larval and megalopa durations (Costlow and Bookout 1965; Sulkin and Epifanio 1975; Sulkin and Van Heukelem 1986). Low temperature delays larval development in all stages while high salinity greatly extends the duration of megalopae (60 days or longer) (Costlow 1967). Cooler temperature early in the spawning season can delay zoeal development by 10-15 days (Costlow 1967). Salinity-induced extension of the megalopa stage appears to be critical for enhancing the likelihood of on-shore transport and recruitment to the estuary under highly stochastic shelf conditions. Megalopae retained offshore in high saline water will delay molting to the first crab stage. As the reproductive season progresses (July to October) the incidence of weather systems that produce downwelling favorable winds increases in the mid-Atlantic Bight. Periodic down-welling favorable winds result in shoreward cross-shelf transport of post-larval megalopae (Goodrich et al. 1989). When megalopae in surface waters approach an estuary, environmental signals (water soluble chemicals) promote behavioral changes (Forward et al. 1997; Tankersley and Forward 1994) that facilitate transport into the estuary. During daylight and ebbing tides, megalopal preference is to remain near the bottom (Dittel and Epifanio 1982; Brumbaugh 1994; Olmi 1994; Olmi 1995; Forward et al. 1997). During nighttime flood tides, the megalopae move up into the water column and are transported into the estuary (Brumbaugh 1994; Olmi 1994; Tankersley and Forward 1994). Megalopae respond to declining turbulent flow at the end of the flood tide by settling to the bottom (Welch et al. 1999). These processes have been called selective tidal transport (STT) (Forward and Tankersley 2001) and facilitate retention and settlement of megalopae in the estuary. Water-borne chemical cues and decreased salinity also initiate the molt cycle in megalopae (Forward et al. 1994; Forward et al. 1996). Molting to the first crab stage occurs within 24-48 hours after entering the estuary (Brumbaugh and McConaugha 1995), further insuring retention in the estuary.

The larval and post-larval phase of the life history of the blue crab, *Callinectes sapidus*, plays a key role in the population dynamics of this species. Wind forced larval transport can alter recruitment success by 35->50% as seen in long-term harvest statistics. Factors that affect larval survival and recruitment and a significant stock-recruitment relationship are key components in understanding the population dynamics of the Chesapeake Bay blue crab population (Lipcius and Stockhausen 2002; Olmi 1994). The abundance of post-larval megalopae recruiting to the estuary is the first quantitative estimate of annual recruitment in the Bay. The availability of juvenile habitat and juvenile survival is critical to the next life history phase.

Early Life History: Post-larvae and Young Juveniles

Gina Ralph, Romuald N. Lipcius, Jacques van Montfrans, and Rochelle Seitz

Introduction

The current model of the early life history of blue crabs involves the colonization of structured coastal habitats by megalopae from the continental shelf, followed by settlement and metamorphosis into the first juvenile instar crab. Post-larval settlement, recruitment of young juveniles, and post-settlement processes are significantly influenced by the quantity and quality of available nursery habitat, particularly seagrass beds, coarse woody debris, certain types of macroalgae, and the food resources available (Seitz et al. 2003a). Young juveniles range from approximately 3- 25 mm in carapace width (Figure 4). Growth in blue crabs and other crustaceans with rigid exoskeletons occurs through the discontinuous process of ecdysis (Smith and Chang 2007). The diet of small juvenile blue crabs appears to follow prey availability, and, in general, consists of smaller prey items than that of larger juveniles that are typically used in diet studies. Finfish are the primary predators of the early life history stages of blue crab in the Chesapeake Bay, though other crustaceans and larger blue crabs also prey upon these stages (Lipcius et al. 2007). The juveniles tend to remain within the colonized habitats until reaching the seventh to ninth instar at which time they may disperse to less structured habitats such as mud or sand flats.

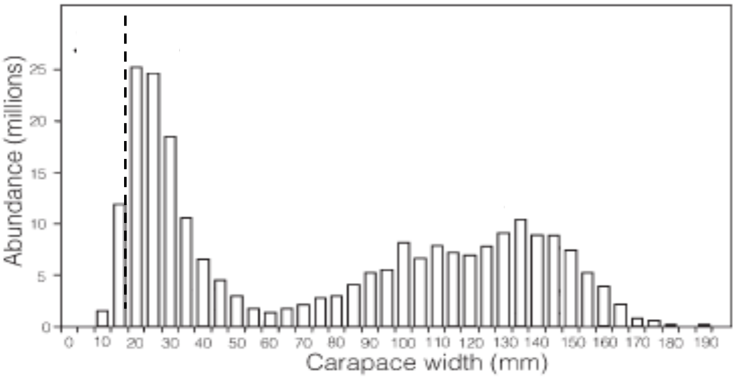


Figure 4: Size-frequency estimated from a dredge survey in Chesapeake Bay during the winter of 1990-1991 (Rothschild et al. 1992, cited in Smith and Chang 2007). The dotted line represents the approximate carapace width at which young juveniles leave nursery habitat.

Settlement

The megalopal stage invades structured, primary nursery habitat from the continental shelf, aided by a combination of wind-driven, geostrophic currents and vertical migration behaviors. Though there is much debate as to which processes are most important, both physical and behavioral mechanisms influence settlement. Wind-driven exchange in the surface waters may be the mechanism most important for post-larvae to enter the Chesapeake Bay (Goodrich et al. 1989), while vertical migration behaviors in response to changing pressure and salinity may influence up-estuary transport once the megalopae have entered the Bay (Olmi 1994; Tankersley et al. 1995; Forward et al. 2003).

In the current conceptual model (Figure 5), megalopae either colonize and settle in the preferred primary nursery habitat, such as seagrass beds, or into alternative nursery habitat such as coarse woody debris, salt marshes, or other structured habitat. Generally within 3-5 days of finding suitable habitat, the megalopae metamorphose into the 1st juvenile instar (Lipcius et al. 2007). The juveniles tend to remain within the colonized habitats until reaching the 7th-9th instar, unless high densities drive them out prematurely in search of less populated nurseries. This phenomenon is termed secondary dispersal, whereby younger juveniles leave the nursery habitat to avoid density-dependent cannibalism and predation. At approximately 20-25 mm carapace width, they disperse to less structured habitats such as shallow mud or sand flats, where they have now reached a relative size refuge.

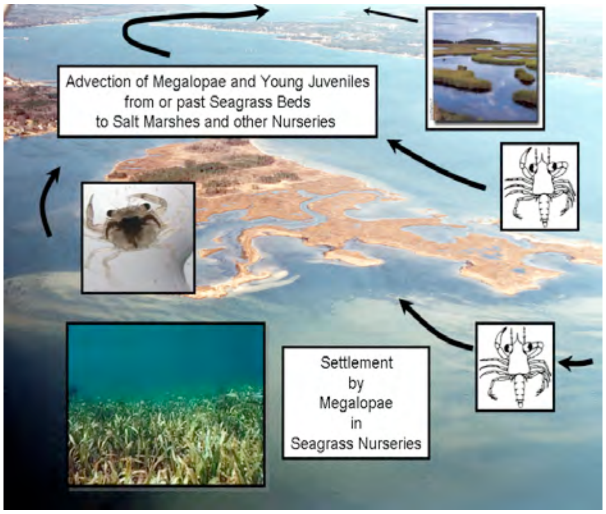


Figure 5. Conceptual model of the early life history, including settlement into primary and secondary nursery habitat. From Lipcius et al. 2007.

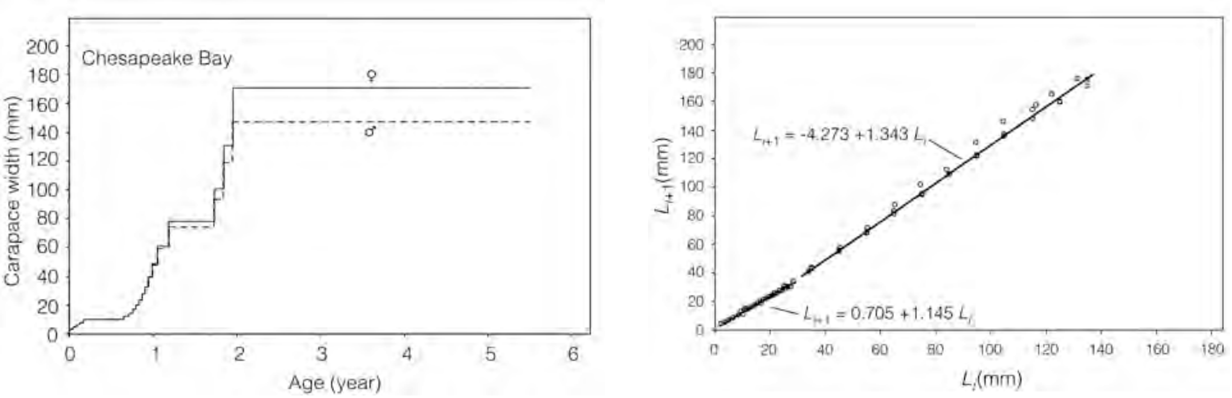
Nursery habitat

The types and role of nursery habitat for blue crab development is still unsettled. The nursery role hypothesis began with observations of higher densities of juveniles in seagrass than adjacent unstructured areas (Orth and van Montfrans 1987; Heck et al. 2003). However, the term nursery suggests that these areas should increase the probability that an individual reach the adult stage. This could occur via increased protection from predators, which would increase survival, or more abundant prey, which would increase specific growth rates, than non-nursery habitats (Heck et al. 2003). Heck and Thoman (1984) suggest that seagrass beds, particularly eelgrass *Zostera marina*, support larger numbers of juvenile blue crabs, most of which are female, but that this is more evident in the lower Bay than the upper Bay. Coarse woody debris habitats had higher densities of many invertebrate species, including blue crab, and were shown to provide refuge from predation for grass shrimp (Everett and Ruiz 1993). It is likely that these regions of coarse woody debris may act as alternative nursery habitat for blue crabs. Lipcius et al. (2005) concluded that mud and sand flats near salt marshes and in marsh coves can be important nursery grounds as well.

The metamorphosis of megalopae into the first benthic juvenile instar can be delayed in offshore waters and accelerated in estuaries, particularly near seagrass beds (Forward et al. 1994, Lipcius et al. 2007). Habitat-specific responses by megalopae to these chemical and physical cues upon settlement may be important in ensuring that blue crabs encounter preferred nursery habitats, such as seagrass beds, salt marshes, and mud flats. However, conflicting evidence has been reported by other investigators. Morgan et al. (1996) concluded that the ability of megalopae to discriminate between three types of experimentally transplanted vegetation (*Ruppia maritima*, *Spartina alterniflora*, and *Juncus roemerianus*) was inconclusive due to low statistical power, and Diaz et al. (1999) suggested that the chemical and visual cues may be related to predator avoidance rather than habitat selection.

Growth

Crabs grow by molting, a discontinuous process, that has prevented efforts to accurately model the growth of an individual throughout its lifetime. However, Smith and Chang (2007) created a molt-process length-age model for blue crabs that represents the growth of the average blue crab, using approximate annual temperature regimes from the Chesapeake Bay (Figure 6). Recent research has transformed the previous opinion that molting was a brief interruption to a cycle of physiological and biochemical events that an individual spends much of the intermolt period recovering from and preparing for (Smith and Chang 2007). There are two main components to the mathematical description of growth, intermolt period and molt increment. Both of these components change ontogenetically; the frequency decreases and increment increases with time. For early juveniles <30mm CW, the intermolt period, in degree days, can be modeled by: $IP_{dd}(i) = \gamma(L_i) + \beta(L_i)$, where $\gamma(L_i) = 43.5+1.74(L_i)$ and $\beta(L_i) = 53.18 + 2.82L_i$, and the molt increment by: $L_{t+1} = 0.705 + 1.145(L_i)$ (Figure 7).



Figures 6 and 7. (6) Molt-process length-age model for blue crab females (solid line) and males (dashed line). (7) Blue crab molt increment functions for early juvenile males and females (Li</= 30mm) and late females (Li> 30mm), from Smith and Chang (2007).

Foodweb

The current model of the juvenile blue crab foodweb suggests that polychaetes, isopods, amphipods, plants and detritus may be the most important food sources for blue crabs, while finfish predation may be the most important source of mortality (Figure 8). However, there have been few studies that characterize the diet of young juveniles <25 mm carapace width. Typically, however, young juvenile diets have been inferred from diets of juveniles past the ninth instar, 25 to 60 mm carapace width (Mansour 1992). The diet of these larger juveniles basically follows prey availability, which is directly dependent on habitat type. They primarily eat benthic infauna and epifaunal invertebrates, especially bivalves, crabs, shrimp, amphipods, isopods, polychaetes, gastropods. Fish remains, and some plant and detrital matter have also been found (Mansour 1992). Seitz et al. in an unpublished manuscript analyzed gut contents of juveniles <20 mm and between 20 and 40 mm carapace width and Fantle et al. (1999) used stable isotope compositions to determine the importance of marsh detritus in the diets of young juveniles in the Delaware Bay. These studies suggest that smaller juveniles ingest different, and smaller, prey items, such as polychaetes, amphipods, and plant material, than older juveniles (Seitz et al., unpublished manuscript). In addition, no conspecifics were found in the guts of juveniles <40 mm carapace width, suggesting that young juveniles do not cannibalize (Lipcius et al. 2007).

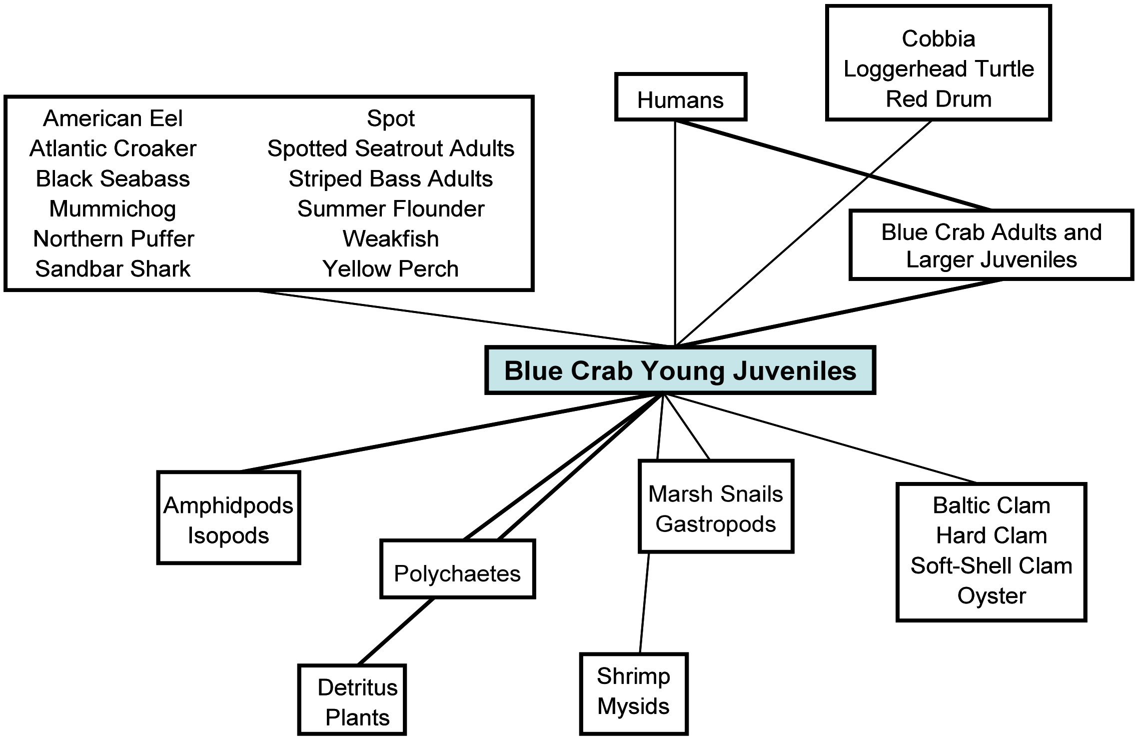


Figure 8. Food web of the blue crab, focusing on only those linkages with juvenile blue crab as either predator or prey. Thicker lines indicate stronger connections, as determined from stomach contents studies. Derived from Lipcius (2005), Lipcius et al. (2007), Seitz et al. (unpublished manuscript), van Montfrans (unpublished data).

Laboratory studies suggest that intra-cohort cannibalism by larger juveniles upon megalopae and smaller juveniles can be a major source of mortality among newly settled crabs, especially in sandy habitats, and up to the 5th instar in seagrass habitats (Moksnes et al. 1997). As post-larvae and early juveniles, blue crabs are very susceptible to predation, which can have an enormous impact on the abundance and distribution of later life stages. Both sand shrimp *Crangon septemspinosa* and grass shrimp *Palaemonetes pugio*, common in the Chesapeake Bay, are capable of consuming large quantities of megalopae (Olmi and Lipcius 1991). Predation by the mummichog *Fundulus heteroclitus* on megalopae and three sizes of juvenile crabs was also intense in experimental mesocosms but was moderated by habitat structure, life-history stage and juvenile crab size (Orth and van Montfrans 2002). Numerous fish species consume juvenile blue crabs, depending on numerous factors including the size and species of predator, life-history stage of the crab, feeding habits, residency within an estuary, and a host of environmental characteristics (Van Engel 1987). Striped bass is the top predatory fish on blue crabs in Chesapeake Bay (van Montfrans et al. unpublished), possibly because striped bass, unlike other predatory species, are cold-tolerant and feed in the shallows during the fall. Other important fish predators on juvenile crabs include Atlantic croaker *Micropogonias undulatus*, weakfish *Cynoscion regalis*, spot *Leiostomus xanthurus*, and northern puffer *Sphoeroides maculates* (van Montfrans et al. unpublished).

In summary, post-larval settlement, recruitment of young juveniles, and post-settlement processes are significantly influenced by the quantity and quality of available nursery habitat. In general, the diet of small juvenile blue crabs appears to follow prey availability. Finfish are the primary predators of the early life history stages of blue crab in the Chesapeake Bay, though cannibalism can account for a large percent of natural mortality.

Life History of Late Juveniles and Adults

Anson H. Hines

Introduction to Life Cycle

Newly settled blue crabs (*Callinectes sapidus*) generally grow through a series of early juvenile instars (developmental stages punctuated by ecdysis) within seagrass and other settlement habitats of the lower estuary (Orth and van Montfrans 1987; Williams et al. 1990; Olmi and Lipcius 1991; Perkins-Visser et al. 1996; Pile et al. 1996; Pardieck et al. 1999). They may also move upstream to settle in soft-bottom areas (Seitz et al. 2003a; Lipcius et al. 2005). Upon attaining the 5th to 7th crab instar and ~20 mm carapace width (cw), juveniles typically disperse from their settlement site to exploit an array of habitats throughout the estuary (Pile et al. 1996; Moksnes et al. 1997; Pardieck et al. 1999; Etherington and Eggleston 2000, 2003). Dispersed juveniles use a variety of micro-habitats in lower salinity nursery areas of tributaries, where they forage on diverse food resources and grow for a typical period of 0.5 to 1.5 y (depending on temperature and food availability) until they reach sexual maturity in the 16th to 20th crab instar at ~110 to 180 mm cw (Van Engel 1958; Tagatz 1968; Rugulo et al. 1998). After mating, inseminated mature females cease molting and migrate back to the lower estuary, produce broods, and incubate eggs until larvae are released and transported out of the estuary onto the continental shelf (Jivoff et al. 2007; Epifanio 2007). By contrast, mature males may continue to molt and grow for 1 to 3 additional instars (typical large size is 180 to 200 mm, but occasionally some grow to >250 mm cw) (Van Engel 1958; Smith and Chang 2007). Unlike females, mature males tend to remain dispersed in the upper estuary without migrating directionally along the salinity gradient (Van Engel 1958; Hines et al. 1990, 1995).

Timing of life history events is regulated by seasonal fluctuations in temperature. Settlement occurs in summer and fall, with dispersal of juveniles into nursery areas in fall. Small juveniles remain in shallow nurseries over winter, while larger juveniles and adults move into deeper water in channels and the main stem of the Bay to over-winter. Winter in Chesapeake Bay is a period of dormancy, with movement, feeding, and molting proceeding slowly if at all, especially at temperatures below 9° or 10°C. Maturation typically occurs in the second season after settlement in Chesapeake Bay (e.g., see Ju et al. 2003; Smith and Chang 2007). Most blue crabs are thought to die after a lifespan of about 3 y, with mortality in the Chesapeake stock ensuing from a combination of intense fishing pressure and senescence. In Chesapeake Bay, only a small portion of the population lives to be 4 to 5 y old, with individuals rarely (<1%) living to 6 to 8 y (Sharov et al. 2003; Fogarty and Lipcius 2007).

Ecological interactions of juvenile and adult blue crabs begin when juveniles disperse out of their settlement habitat and continue through the 1 to 3 y period of growth, maturation, and adulthood (e.g., Gillanders et al. 2003). The interactions typically involve crabs that range in size from 20 to 200+ mm cw. This range includes crab instars 7 to 22 and ages of about 2 months to 3+ years post-settlement.

Habitat Use

Habitat use after post-settlement dispersal varies by size, sex, and molt stage, such that densities of blue crabs vary greatly among habitats. Thus, a wide range of estuarine habitats is required to complete the life cycle, typically involving sequential use of a series of habitats along the salinity gradient (e.g., Gillanders et al. 2003). Juveniles use an array of structural habitats that provide them with refuge from predation and cannibalism and with food resources. Small juveniles (<25 mm cw) utilize seagrass species, especially *Zostera marina* (eel grass) and *Ruppia maritima* (wigeon grass) in Chesapeake Bay (Heck and Orth 1980; Penry 1982; Heck and Thoman 1984; Heck and Wilson 1987; Wilson et al. 1987; Williams et al. 1990; Perkins-Visser et al. 1996). Juveniles also obtain refuge in other vegetated habitats, especially drifting algae, salt marshes and coarse woody debris. Algal mats and drifting algae (Heck and Orth 1980), e.g., *Ulva lactea* sea lettuce (Wilson et al. 1990a, b; Sogard and Able 1991) and *Gracilaria vermiculophylla* (Lipcius, pers. comm.), may create important structured habitat for juveniles in some areas. Juveniles also utilize salt marshes and associated marsh creeks throughout Chesapeake Bay. Salt marshes and associated creeks in the lower estuary support variably high abundances of blue crabs (up to 13 crabs m^{-2}), particularly juveniles that move between marsh creeks and the marsh edge during the tidal cycle (Orth and van Montfrans 1987; Ryer et al. 1990). However, densities measured on various marsh interiors are low and use of the marsh surface in many places appeared to be limited mainly to the edge habitat (Lin 1989; Fitz and Wiegert 1991; Micheli 1997). Up-estuary habitats associated with, and adjacent to, salt marshes may be as important as seagrasses for blue crab nursery habitat, due to availability of food and lower predation levels (Seitz et al. 2003b; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Eastern oyster (*Crassostrea virginica)* reefs are used by juveniles over a wide range of salinities in Chesapeake Bay (Van Engel 1958; Galtsoff 1964). However, some reports indicate relatively low abundances of blue crabs in oyster reef habitats (e.g., Lehnert and Allen 2002; Coen et al. 1999), so the role of this habitat for blue crabs is not well defined. Coarse woody debris, which is especially common in shallow waters of forested shorelines of upper Chesapeake Bay, has provided still another structured habitat for juvenile blue crabs (Everett and Ruiz 1993).

Non-structured soft-bottom habitats are typically characterized by low crab abundances, with summer peak estimates on muddy and sandy bottoms ranging from 0.08 to 0.63 crabs m^{-2} for larger juveniles (>20 mm cw) and adults in upper Chesapeake Bay (Hines et al. 1987, 1990), 0.02 to 0.36 crabs m^{-2} in lower Chesapeake Bay (Seitz et al. 2003a). Recent studies (Seitz et al. 2003b; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005) indicate that shallow muddy habitats adjacent to salt marshes in the low salinity reaches of subestuaries are of great value to juvenile blue crabs, probably because of their higher food resources (infaunal bivalves) and lower predator abundance. Soft-bottom habitats >1 m deep are frequently used by large, adult crabs. In subestuaries, these habitats are the primary habitat for foraging males and females in the summer (Hines et al. 1987, 1990, 1995; Wolcott and Hines 1989a, 1990). Deeper (>10 m) soft-bottom habitats of the Chesapeake main stem are used extensively by females during fall migration (Aguilar et al., 2005, 2008) and by adult males and females for burial over-winter (Van Engel 1958; Schaffner and Diaz 1988; Sharov et al. 2003) and by mature females during the summer spawning season (Lipcius et al. 2003).

During summer, habitat use by blue crabs varies with size, sex, and molt stage as they feed, grow, molt to maturity, and mate, as illustrated within the Rhode River, a subestuary of Chesapeake Bay (Hines et al. 1987, 1995). There, large, intermolt crabs (>100 mm cw) primarily use non-structured soft bottom habitat in deeper (1-4 m) water of estuarine channels and basins when foraging on infaunal prey, whereas small juveniles (30-70 mm cw) primarily use shallow (>70 cm) water along the shoreline, where they escape predation or cannibalism by large crabs (Hines et al. 1987, 1990, 1995; Ruiz et al. 1993; Hines and Ruiz 1995). Juveniles seek woody debris primarily along the shoreline as refuge for molting (Hines et al. in prep.). As prepubertal males approach their molt to maturity, they move up into tidal creeks, where >90% of the crabs are male and in active molt stages (Hines et al. 1987). These males select the shallow tidal marsh edge along the creek as the microhabitat for molting (Wolcott and Hines 1990). After molting to maturity, males move back out into the subestuarine basin to forage and mate. In contrast, prepubertal females molt to maturity within the estuarine basin, where they couple with intermolt mature males. Mated females remain to forage in deeper waters in and/or near the subestuary through the summer until the fall migration (Turner et al. 2003; Aguilar et al. 2005). During migration to the spawning area in the lower estuary, females tend to use habitat along the deep channel of the mainstem of Chesapeake Bay (Aguilar et al. 2005; Hines et al. 2008). Thus, the deeper waters of the mainstem of the estuary form a migration corridor for females (Lipcius et al. 2003; Hines et al. 2008). In lower Chesapeake Bay, over-wintering blue crabs are mostly mature females that are least abundant in shoal and spit habitats, at intermediate abundance in deep channels, and most abundant in basin habitats of the mainstem, especially at depths >9 m in sediments composed of 40 to 60% sand (Schaffner and Diaz 1988). In contrast, wintering juveniles and males bury into sediments of deeper channels and the mainstem of the middle and upper estuary (Sharov et al. 2003). During the summer spawning season in Chesapeake Bay, mature females exhibit peak abundance in the mainstem at depths of 6 to 14 m, with nearly half of all adult females in the lower Bay found deeper than 10 m (Lipcius et al. 2003).

Blue crab abundance varies along the salinity gradient, with small juveniles forming highest densities in the settlement habitats of the polyhaline zone (Orth and van Montfrans 1987; Fitz and Wiegert 1991; Moksnes et al. 1997; Zimmerman et al. 2000; King et al. 2005). After they disperse from their settlement habitat, the abundance of juveniles and males tends to be more evenly distributed across a broad range of salinities from polyhaline to mesohaline waters. Juvenile blue crabs in Chesapeake Bay can be abundant up-estuary in nursery areas of lower salinity (Seitz 1996; King et al. 2005), which harbor fewer large crab and fish predators and afford reduced mortality (Ruiz et al. 1993; Hines and Ruiz 1995; Seitz et al. 2003b; Posey et al. 2005), especially in mud and sand flats associated with fringing salt marshes (King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Juvenile blue crabs also may be abundant in oligohaline salinities and tidal freshwater marshes (Haefner and Shuster 1964; Ettinger and Blye 1981; deFur et al. 1988; Rozas and Odum 1987). Thus, low salinity zones may provide good nursery areas because of lower predator abundance and reduced mortality, as well as good food resources for juvenile blue crabs. Crab densities are diminished in hypoxic areas because crabs may move into very shallow waters during hypoxic events, such as nocturnal hypoxia in summer or during plankton blooms (e.g., Loesch 1960; Pihl et al. 1991).

Habitat configuration and connectivity also interact to affect habitat use and value for blue crabs. The combined effects of multiple habitat loss and fragmentation creating a mosaic of refuges are complex, because juvenile blue crabs, their prey, and their predators may respond differentially and with fluctuating densities to such habitat changes (Irlandi 1997; Eggleston et al. 1998a, b; Micheli and Peterson 1999; Hovel and Lipcius 2001; Hovel et al. 2002; Hovel 2003; Hovel and Fonseca 2005). The interaction of transport processes, movement, and habitat value at multiple scales indicates that landscape-level factors should be considered in analyses of habitat use (e.g., Stockhausen and Lipcius 2003; Hovel 2003). Habitat value for blue crabs also depends interactively on patch size and complexity (i.e., density of structural elements within the patch) (Heck and Orth 1980; Irlandi 1997; Hovel et al. 2002; Hovel and Fonseca 2005). Blue crab abundance is related to the interaction of salinity zone, presence of adjacent salt marsh habitat, and watershed land use (King et al. 2005). Juveniles are most abundant in higher salinities and in areas adjacent to salt marshes of subestuaries with watersheds that are predominantly forested or in agriculture, whereas suburban and urbanization of watersheds have lower juvenile densities. Thus, sites with connection to marsh habitats providing detritus sources for blue crab food, especially deposit feeding bivalves like the Baltic macoma *Macoma balthica*, favor blue crab abundance, whereas human development of watersheds appears to reduce blue crab abundance, albeit through indirect ways (Seitz et al. 2003a; King et al. 2005).

Feeding

Blue crabs are epibenthic generalist predators that forage on a diversity of sessile infaunal and epibenthic invertebrates and on motile fish and crustaceans, as well as feeding omnivorously on plant material and detritus and scavenging carrion (Darnell 1958; Tagatz 1968; Laughlin 1982; Alexander 1986; Ryer 1987; Hines et al. 1990; Hsueh et al. 1992; Mansour 1992; Meise and Stehlik 2003; Stehlik et al. 2004). Blue crab diet includes at least 99 species from several phyla, especially mollusks (typically 20-40% of stomach content weight or volume), arthropods (10-26%), chordates (fishes; 5-12%) and annelids (polychaetes; 1-7%). Stomach contents also often include detritus and unidentified, partially digested matter, as well as sediment that may be ingested incidentally. Juvenile blue crabs have the digestive enzymes to utilize plant detritus, but the importance of such low quality food is not evident for blue crabs except, perhaps, when restricted to certain refuge habitats (McClintock et al. 1991). Xanthid crabs, blue crabs themselves, and fish are important secondary components of the diet. In a trophic web analysis of Chesapeake Bay (Baird and Ulanowicz 1989), the diet of blue crabs was described as consisting of about 60% bivalve mollusks, with the remainder comprising polychaetes, amphipods, dead fish, and juvenile blue crabs (Darnell 1958; Tagatz 1968; Virnstein 1977; Nelson 1981; Paul 1981). Although blue crabs certainly exhibit a broad diet, quantitative studies show that bivalve mollusks are dominant prey that consistently comprise the largest volume or weight of juvenile and adult diet in many habitats (Laughlin 1982; Hines et al. 1990; Eggleston et al. 1992; Mansour 1992; Meise and Stehlik 2003). Importantly, however, the diet of blue crabs exhibits significant ontogenetic, temporal, and spatial variation.

Two major foodweb models place blue crabs at a central position of the Chesapeake Bay trophic dynamics: (1) Baird and Ulanowicz (1989) considered blue crabs as the foremost benthic scavenger or predator in a carbon flow foodweb for Chesapeake Bay. The indirect carbon flows indicated that the blue crab is at the hub of carbon recycling and transfers for the benthic subsystem of the foodweb, and accordingly blue crabs were grouped into a “Benthic Deposit Feeder” category that is dominant in a simplified foodweb for the Chesapeake mesohaline ecosystem. Although rates of carbon flow in the foodweb model varied greatly on a seasonal basis, the overall structure of the foodweb did not change much seasonally. (2) Using “Ecopath with Ecosim" modeling software that emphasized fishery species in the foodweb also placed blue crabs in a central position (NOAA Chesapeake Bay Program, H. Townsend, pers. comm. 2004). The portion of the foodweb model that includes the species and trophic groups with direct interactions with adult and young-of-the-year blue crabs shows hard clams, soft clams, and eastern oyster as prey species with commercial importance. It lumps all other prey species as "other infauna and epifauna" and "other suspension feeders", also includes "benthic algae" as a food source. This foodweb illustrates predation by adult blue crabs on juveniles (young-of-the-year), as well as by Atlantic croaker, migratory and resident striped bass (*Morone saxatilis*), sandbar shark (*Carcharhinus plumbeus*), American eel, "littoral forage fish", and "piscivorous birds".

Predation

A diverse array of at least 101 species have been documented to prey upon blue crabs, including 72 species of fishes (especially eels, rock fish, croaker, weakfish, red drum), 3 species of reptiles (alligator, Kemp's Ridley sea turtle, loggerhead sea turtle) 18 species of birds (especially great blue heron), 3 species of small mammals (especially raccoons and perhaps river otters), some invertebrates, and blue crabs themselves (Hines 2007). Although it is clear that blue crabs may be important in the diet of some fish and other vertebrates, and that some species are effective predators on blue crabs, there is little quantitative data demonstrating rigorously that predation by fish or other vertebrates directly regulates blue crab populations at life stages >20 mm cw. Cannibalism by large blue crabs upon smaller crabs and molting crabs appears to be a major source of mortality that is common throughout most estuarine habitats. Of course, effects of human fishing on large crabs also may be very great, affecting abundance, population size structure, sex ratio, and habitat distribution.

Vulnerability of blue crabs to predation varies greatly by size and molt stage. Generally, small crabs are subject to a wider range of predators and predator effects, and several studies have shown that crab vulnerability to predation decreases markedly with increasing size (Moody 1994, 2001, 2003; Dittel et al. 1995; Hines and Ruiz 1995). Blue crabs are especially vulnerable at the time of ecdysis when they are soft and relatively immobile (Shirley et al. 1990, Ryer et al. 1997). Soft, post-molt crabs are often used for bait in sport fisheries, and soft crabs have been documented in the stomach contents of several fish species, including striped bass (Orth et al. 1999) and American eel (Shirley et al. 1990).

Blue crabs obtain refuge from predation by use of key habitats that provide structural complexity or are inaccessible to predators. Refuge habitats with structural complexity include seagrass, oyster reefs, emergent marsh vegetation, mangrove prop roots, and coarse woody debris from terrestrial trees. Habitats with structural refuges are especially important to small juveniles and molting blue crabs. Submerged aquatic vegetation beds have received extensive research, which found increased abundance and higher survival of juvenile and molting blue crabs in vegetated than in adjacent unvegetated habitat (Heck and Orth 1980; Heck and Thoman 1981; Wilson et al. 1987, 1990b; Pile et al. 1996; Ryer et al. 1997). Edges of salt marshes and drift algae also provide refuge structure (Heck and Orth 1980; Wilson et al. 1990a), as does coarse woody debris in many parts of Chesapeake Bay (Everett and Ruiz 1993). Shallow water (<70 cm) along the shoreline, even in the absence of structure in the environment, is a crucial refuge habitat for 0+

age class juveniles (30 to 70 mm cw) in Chesapeake Bay (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995).

Summary

- Habitat use after post-settlement dispersal varies by size, sex, and molt stage, such that densities of blue crabs vary greatly among habitats.

- A wide range of estuarine habitats is required by juvenile and adult blue crabs, typically involving sequential use of a series of habitats along the salinity gradient.

- Blue crabs play a key role in the trophic dynamics of the Chesapeake Bay and are considered the foremost benthic consumer in the Bay foodweb.

- Juvenile and molting adult blue crabs obtain refuge from predation by use of key habitats that provide structural complexity or are inaccessible to predators

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HABITAT

Predictions for Climate Change Effects on Blue Crabs

Anson H. Hines and Eric G. Johnson

Climate change is predicted to have a wide range of effects on the blue crab in Chesapeake Bay, including direct effects on blue crab demography, indirect effects on habitat and ecosystem attributes, and weather effects on recruitment dynamics.

Direct Effects on Demography

Blue crab populations extend over a broad range of latitude from the species' tropical origins into the temperate zone. Hines et al. (in review) reviewed and projected demographic effects of latitude to serve as a surrogate for the effects of climate change. They suggested that climate change could have a major effect on seasonal temperature variation, primarily causing warmer winters and longer warm seasons, rather than simply increasing temperatures uniformly across all seasons. Demographic impacts were based on analyses of survival, reproduction, growth and maturation of populations in Florida, North Carolina and Chesapeake Bay (Maryland and Virginia).

Reproduction is accelerated and extended over a longer reproductive season at lower latitudes and with the warmer temperatures due to global warming. Brooding in populations at lower latitudes begins 3-4 months earlier than at high latitudes, allowing more broods per season (Jivoff et al. 2007; Hines 2007). Blue crabs in Chesapeake Bay now produce 1-3 broods per year, crabs in North Carolina 3-5 broods per year, and crabs in Florida 3-8 broods per year (Hines et al. 2003; Dickinson et al. 2006; Hines et al., in review).

Cold winter temperature restricts the growing season and causes a prolonged period of suspended activity compared to lower latitudes, where juveniles grow rapidly to mature in one season rather than two at higher latitudes. However, tethering experiments indicate predation and cannibalism on juveniles is much higher during the warm season than fall through spring. Although there are not clear trends across latitude, size at maturity is inversely correlated with temperature within a site, when salinity is held constant (Hines et al., in review). While small females may molt to maturity and mate sooner, small size increases vulnerability to predation and diminishes fecundity per brood.

Field surveys and laboratory experiments indicate that harsh winters (especially February temperatures $< 3^{o}$C in areas of low salinity < 8 ppt) cause significant mortality in small (10 mm carapace width) juveniles and mature females in Chesapeake Bay (Rome et al. 2005; Bauer and Miller, in press). Predicted survival was highest in the warmer, saline waters of the lower Bay and decreased with increasing latitude up Bay. There was also significant inter-annual variation with survival being lowest after the severe winters of 1996 and 2003. Similar patterns of survival were observed in a Bay-wide fisheries independent survey; however experimentally derived survival estimates are consistently lower than survival observed in the field. Thus, severe winters can cause high mortality (as much as 70%) of blue crabs in certain areas of Chesapeake Bay.

Cold winter temperature and a short growing and reproductive season restrict the species' northward distribution from its tropical origins. If climate change reduces the severity of winters, it is predicted to increase winter survival and to promote rapid growth and brood production. However, warmer temperatures may also increase juvenile mortality due to predation and reduce the size at maturity. Demographic schedules for fishery models will need to consider these complex effects of warming.

Indirect Effects on Habitat and Ecosystem Attributes

Climate change is predicted to affect many habitats and ecosystem attributes that influence blue crab population dynamics. These indirect effects are likely to be complex and interactive.

Submerged Aquatic Vegetation (SAV)

Eelgrass (*Zostera marina*) and, to a large degree, widgeon grass (*Ruppia maritima*) exhibited a major defoliation throughout lower Chesapeake Bay in 2005, which was attributed to high summer temperatures and poor water quality (R. J. Orth and K. A. Moore, personal communication). Since then widgeon grass and eelgrass appear to be recovering. Localized declines in juvenile blue crab abundance, food and survival may have been related to the loss of SAV as critical habitat (R.N. Lipcius, personal communication). There is some speculation that southern species may move northward to replace *Zostera* if warming prevents its recovery. There is also speculation that, if water quality improves, other species of SAV such as widgeon grass could recover sufficiently to compensate for eelgrass losses in Chesapeake Bay.

Salt Marshes

The unvegetated bottom adjoining salt marshes provides crucial resources for juvenile blue crabs (King et al. 2005; Seitz et al. 2005). Marshes provide detritus that fuels infaunal prey in juvenile crab nursery habitat. With sea-level rise, 161,000 acres of salt marsh are predicted to be lost in Chesapeake Bay by 2100. However, given the complex ecological and environmental interactions regulating the dynamics of coastal wetlands there is considerable uncertainty regarding this projection. Recent experimental work suggests that elevated CO_2 stimulates marsh elevation rise serving to counterbalance potential rises in sea level due to global warming (Langley et al. 2009). Conversely, the migration of marshes to higher elevations may be precluded by various forms of shoreline hardening (e.g., bulkhead) which prevent shoreward movement in the face of rising sea level. Moreover, subsidence of many marshes of the Eastern shore may accelerate loss in those regions.

Mangroves

Along tropical (e.g. Caribbean) and subtropical (e.g. Florida) shorelines, mangroves serve as important structural habitat. In Florida, cold winter temperatures (freezing) limit the northern distribution of mangroves along the east coast, whereas warming is promoting the northward spread of mangroves, which now extend beyond Cape Canaveral. Establishment of mangroves as far north as Chesapeake Bay is, however, not a likely scenario and need not be considered at present for future management considerations.

Oyster Reefs

There is very little empirical or experimental evidence that oyster reefs *per se* are utilized extensively by blue crabs (Hines 2007). Rather, epifaunal and infaunal organisms associated with oyster reefs seem to provide food resources, especially for larger crabs. Oysters are at record low levels in Chesapeake Bay, with almost no viable oyster populations remaining as they have been decimated by overfishing, by reef degradation associated with fishing, and by disease. Oyster disease in Chesapeake Bay is especially intense at higher salinities, however, restoration of a viable spawning stock of oysters remains a major objective for ecological recovery of the Bay. In lower latitude estuaries, oysters in the intertidal zone often have less disease due to warm temperatures and sustained exposure. In the upper parts of Chesapeake Bay, intertidal oysters are killed by low winter temperatures. With warming, intertidal oysters will persist and provide a spawning stock that may help restore reefs as a habitat.

"Dead Zones" and Low Dissolved Oxygen

Low dissolved oxygen (DO) develops in the dense, deeper waters of eutrophic estuaries that are stratified by differences in water temperature and salinity. Stratification and eutrophication are both promoted by freshwater runoff. Thus, in estuaries like Chesapeake Bay and the Neuse River in North Carolina (warming, higher rainfall), stratification and low DO will increase in extent and duration. This will reduce foraging resources and distribution of blue crabs (Aumann et al. 2006). Duration of low DO may also interfere with the dispersal of juvenile blue crabs up the estuary (Johnson and Hines, unpublished), and mature females migrating down the estuary (Aguilar et al. 2005; Hines et al. 2008; in review).

Effects of Weather on Larval Recruitment

Changes in coastal currents and weather patterns along the East Coast may have marked effects on blue crab recruitment due to three processes.

Shifts in Current Systems

Oceanic currents, especially the Gulf Stream, which appear to advect most blue crab larvae away from lagoon systems (Indian River Lagoon) in eastern Florida, may experience substantial alterations. If the Gulf Stream weakens, then recruitment may be favored. In Chesapeake Bay the Gulf Stream is far off shore but can have major effects on inshore current patterns. Nearshore southward flowing current often seems to provide counter-current flows, which advect larvae to neighboring estuaries southward. If this pattern is disturbed, we cannot be certain of the nature of the broad-scale effects that will ensue.

Storm Impacts

The effects of increased storm activity associated with global warming will be primarily on larvae during the settlement season in late summer and fall for northern estuaries. If storm intensity increases during the hurricane season, which coincides with the settlement season, this can cause major disturbances not only offshore, but also inshore due to major run-off and flushing problems within the estuaries (see also “Dead Zones” above). In the lagoonal Croatan-Albemarle-Pamlico Estuarine System (CAPES) of North Carolina, increased storm activity expanded blue crab nursery capacity through increased enhanced delivery of megalopae to settlement habitats (Eggleston et al. 2010). However, the benefits of storms in this system appear to be mitigated by heavy rainfall and extreme flooding events that accompany many storms which can exacerbate runoff and hypoxia, cause mass mortality of recruiting megalopae and increase freshwater outflow disrupting secondary dispersal of early juveniles (Paerl et al. 2001; Eggleston et al. 2010). The impacts of storms in the tidally-dominated Chesapeake Bay system remain unknown; however the system-wide negative impacts of previous storms (e.g., Hurricane Agnes in 1972) are well documented.

Continental Pattern of Weather Fronts

Weather fronts moving across North America may have both direct and indirect effects. Northerly fronts moving across from Canada in spring promote species that spawn in springtime in tributaries (striped bass, *Morone saxatilis* and white perch, *Morone americanus*). Southerly fronts moving across the Gulf of Mexico may promote fall spawners on the continental shelf (Sciaenids such as spot, *Leiostomus xanthurus* and croaker, *Micropogonias undulatus*). These species can be important predators on juvenile blue crabs, depending on size and habitat. Also, blue crabs in Chesapeake Bay are primarily a late summer and fall spawner whose larvae are advected onto the continental shelf, so southern fronts may have important effects.

Habitat Degradation and Blue Crabs

Jacques van Montfrans and Romuald N. Lipcius

Habitat degradation is a major concern in Chesapeake Bay and around the world. With populations increasing along the shoreline and in watershed areas, the human footprint is having an ever-increasing impact on Chesapeake Bay biota. Hypoxia, habitat destruction, shoreline development, chemical toxicants and global warming are among the most pressing influences, which either directly or indirectly affect the blue crab population in Chesapeake Bay.

Hypoxia

One of the most widespread threats to estuarine and marine ecosystems is caused by low DO; anoxia (0 mg O_2 L^{-1}) and hypoxia ($\leq$ 2 mg O_2 L^{-1}), which has occurred with increasing frequency and aerial cover historically in Chesapeake Bay (Diaz and Rosenberg 2008). Low DO events can arise daily (diel cycling due to nighttime respiration of autotrophs, particularly algae; Tyler et al. 2009), seasonally (after the spring phytoplankton bloom through autumn) or periodically (in relation to weather events or spring-neap tidal cycles; Diaz and Rosenberg 2008). Typically, hypoxic and anoxic zones of the Chesapeake Bay mainstem and major tributaries are associated with areas deeper than 10 m (Pihl et al. 1991).

Responses by blue crabs to low DO are determined in part by the severity of such events and their tolerances to low oxygen levels. Blue crabs circumvent anoxic areas and readily detect and avoid hypoxic waters < 4 mg O_2 L^{-1} (Das and Stickle 1994; Bell et al. 2003). Thus, crab densities are zero in anoxic waters and are greatly diminished in hypoxic areas. Typically, blue crabs move out of deeper water affected by low DO and into shallow areas during hypoxia or anoxia. In doing so, they become more concentrated in the shallows and are more susceptible to fishing gear, density-dependent predation and agonistic interactions.

Female crabs migrating to the spawning grounds may also be affected by low DO since they utilize deep (13 to 25 m) water to reach their destination (Lipcius et al. 2003; Turner et al. 2003; Aguilar et al. 2005). During the summer spawning season, mature females exhibit peak abundance in the Chesapeake Bay mainstem at depths of 6 to 14 m and about half of the impregnated females in the lower Bay are found deeper than 10 m (Lipcius et al. 2003). When deeper waters of the mainstem are affected by low DO, these areas become inaccessible to migrating crabs and thus, normal migration patterns might be disrupted.

The responses of crab prey to low DO are also influenced by species-specific tolerances to low oxygen levels and the duration, severity and areal extent of such events (Pihl et al. 1991; Seitz et al. 2003 a, b; Diaz and Rosenberg 2008). Many infaunal organisms move to the surface of the sediments during periodic hypoxia (Jorgensen 1980; Pihl et al. 1991; Long and Seitz 2008). Such responses render redistributed moribund prey more vulnerable to mobile predators such as blue crabs which move into affected areas to exploit the benthos during return to normoxia (Pihl et al. 1991; Nestlerode and Diaz 1998; Long and Seitz 2008). The escape response (burial rate) of a primary blue crab prey, *Macoma balthica*, is also severely compromised under hypoxic conditions (Tallqvist 2001), thereby increasing the potential for predation by blue crabs. Severe hypoxic events of long duration destroy entire populations of benthic prey, thereby excluding them entirely from exploitation by mobile predators (Holland et al. 1987).

Overall, low DO affects the distribution of crabs and concentrates them in the shallows, increasing mortality rates via exploitation and predation and enhances agonistic encounters. Effects on blue crab prey communities can either enhance access to moribund prey under periodic and less severe low DO events, while entire prey populations are destroyed and unavailable to exploitation under conditions of long lasting severe hypoxia.

Seagrass Habitat Destruction

Seagrass habitats in Chesapeake Bay provide structural complexity that protects newly settled blue crabs from predation and cannibalism. Two primary species of seagrasses occur in lower Chesapeake Bay: eelgrass, *Zostera marina,* a Boreal species, and widgeon grass, *Ruppia maritima*, of sub-tropical origin. Beds of submerged aquatic vegetation (SAV) are considered the most important primary nurseries in Chesapeake Bay for settling megalopae and newly settled 1st to 7th instar juvenile blue crabs (Orth and van Montfrans 1987; Pile et al. 1996; Lipcius et al. 2007). Marginalized water clarity from phytoplankton blooms caused by agricultural chemical runoff, waste water treatment plant discharges and other nutrient sources, and sediment-induced turbidity from excessive soil erosion have caused substantial historical declines in SAV habitat areal distribution (Orth and Moore 1983; Moore et al. 2000). These anthropogenic influences reduce solar radiation reaching SAV and cause beds to shrink or disappear from upriver and deeper areas of the bay and tributaries (Moore et al. 1996, 1997).

Seagrass loss limits primary nurseries in Chesapeake Bay and potentially affects blue crabs by concentrating recruiting individuals in limited nursery habitats, thereby exacerbating competition for resources, escalating cannibalism and amplifying density-dependent dispersal to less favorable habitats at an early age. Habitat loss also occurs via biotic interactions. When cownose rays invade Chesapeake Bay in mid-summer and search for infaunal bivalve prey in SAV beds, their excavations uproot eelgrass shoots and create bare patches, thereby increasing overall eelgrass edge habitat (Orth 1975; Hovel and Lipcius 2001). Such activities often produce a mosaic of seagrass patches of varying size and complexity interspersed with areas of bare sand.

Seagrass patch size and structural complexity affect habitat value for blue crabs of different sizes (Heck and Orth 1980; Hovel et al. 2002; Hovel and Fonseca 2005). Small patches (~ 0.25 m^2), when compared to bare sediment, support elevated densities (Orth and van Montfrans 1987), higher growth (Perkins-Visser et al. 1996), and greater survival (Pile et al. 1996; Eggleston et al. 1998a, b; Hovel and Lipcius 2001) of juvenile blue crabs. Interactive effects of patch size and landscape configuration result in higher survival in small (1-3 m^2) rather than in large (> 100 m^2) patches, and higher survival in patchy rather than in continuous seagrass beds (Hovel and Fonseca 2005). Thus, the mosaic effects in SAV beds caused by cownose ray feeding may positively affect blue crab populations, though this assertion has not been tested in the field.

Other effects of habitat fragmentation may also occur. The higher ratio of edge to interior in smaller patches likely increases habitat encounter rates by recruiting crabs, food supply transported by currents, and predator confrontation rates while foraging around patch edges (Eggleston et al. 1998a, b; Blackmon and Eggleston 2001). Mobile predators (e.g. large blue crabs) may more readily encounter prey such as small blue crabs, which utilize patch interiors as a refuge when edge to interior ratios progressively decrease in larger patches (Eggleston et al. 1998a, b, 1999; Hines 2007), thereby increasing cannibalism rates.

Effects of SAV patch size vary temporally with seasonal changes in blue crab recruitment and predator or cannibal use of patches (Hovel and Lipcius 2001; Hovel et al. 2002). The interaction of transport processes affecting recruitment, secondary dispersal, and habitat value at multiple spatial scales (Stockhausen and Lipcius 2003; Hovel 2003) suggests that landscape-level factors should be carefully considered when evaluating effects of habitat destruction on blue crabs.

Peak densities of 50-90 newly settled juvenile blue crabs per m^2 in Chesapeake Bay SAV beds exceed those found in surrounding unvegetated habitats by a factor of 10 or more (Orth and van Montfrans 1987; Pile et al. 1996; Perkins-Visser et al. 1996; Pardieck et al. 1999). Seagrass habitats also harbor high densities of larger pre-molt and molting blue crabs because of the refuge provided from predators (Heck and Orth 1980a, b; Heck and Thoman 1981; Wilson et al. 1987, 1990; Pile et al. 1996; Ryer et al. 1997). In fact, commercial soft-crab fishers target SAV beds exclusively when “scraping” for “peeler” and “soft” crabs (Oesterling 1995).

Thus, recovery and restoration of SAV has often been considered vital to sustaining blue crab populations and fisheries (Anderson 1989) and has prompted conservation measures (Beck et al. 2001) of these habitats. However, global warming threatens the persistence of boreal *Zostera marina*, which exists at the southern extent of its range in Chesapeake Bay and North Carolina. As oceanic temperatures rise, *Z. marina* will likely be displaced northward from these areas. Conversely, subtropical widgeon grass, *Ruppia maritima*, will be favored and extend its temporal and spatial cover throughout the Bay during global warming. These changes could have major consequences for the carrying capacity of remaining Chesapeake Bay habitats and future blue crab population levels.

Oyster Reefs, Coarse Woody Debris and Marsh Habitats

Blue crabs seek structurally complex habitats for protection from predators while they are small or about to shed. In addition to SAV, those complex habitats in Chesapeake Bay include marshes, oyster reefs, and coarse woody debris originating from terrestrial environments. Many of these habitats serve as secondary nurseries for crabs that depart SAV after attaining a size of 25 mm CW. Survivorship of tethered juvenile blue crabs is higher in each of these habitats than in bare sediment (Hines 2007). Coarse woody debris in the central portion of the bay also serves as a refuge for molting juveniles (Everett and Ruiz 1993; Hines et al. 2007). Each of these habitats has also undergone substantial declines because of coastal development (Mann et al. 1991; Everett and Ruiz 1993; Rothschild et al. 1994). Collectively, these declines, though difficult to quantify at the population level, likely have a negative affect overall.

Shoreline Development

Natural marshes stabilize shorelines while concurrently providing detrital input and dampening wave action. Collectively such functions promote the establishment and persistence of benthic communities upon which blue crabs forage. These important Chesapeake Bay water edge habitats have suffered historically from residential and commercial development and the replacement of emergent marsh edges by inert structures like bulkheads and riprap to stabilize shorelines. Reductions in primary sources of detrital input and increased wave-generated scouring have precluded or altered the establishment of benthic communities in the nearshore subtidal zone, depriving blue crabs of potential prey such as the Baltic macoma, *Macoma balthica* (Hines and Comtois 1985; Hines et al. 1990; Seitz and Lipcius 2001; Seitz et al. 2003a, b, 2005). Wave scouring can also increase water depth in the nearshore zone thereby reducing a critical shallow water (< 40 cm deep) refuge, even when structure is absent, for 0^+ age class (30-70 mm CW) juvenile blue crabs (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995). The consequences of such effects are manifested in lower abundances of juvenile blue crabs in urbanized than in natural marsh watersheds (Seitz et al. 2003a; King et al. 2005).

The alteration of natural watersheds via human development has likely reduced overall blue crab abundance in Chesapeake Bay by subtle and intangible processes. The long-term overall effects, however, may be important in the continuing decline of the blue crab in Chesapeake Bay and along the Atlantic and Gulf of Mexico coasts. Fringing salt marsh habitats should therefore be designated essential blue crab nursery habitat and restored or protected from development as a conservation measure (Beck et al. 2001; Heck and Spitzer 2001; Heck et al. 2003; Minello et al. 2003).

Chemical Contaminants: Pollution and Toxicants

Blue crabs are important components of the Chesapeake Bay estuarine food web. Their omnivorous feeding behavior and benthic habitat requirements make them prone to bioaccumulation of various toxicants (Brouwer and Lee 2007) including heavy metals and chemical pollutants also known as anthropogenic xenobiotics. These chemicals reach the hemolymph via the stomach or gills and are transported to the lipid-rich hepatopancreas where they often bioaccumulate or are metabolized. In Chesapeake Bay, the multitude of contaminants to which blue crabs are exposed each have very different effects depending upon their physical-chemical properties and how these compounds are processed, accumulated, biotransformed and eliminated.

Organic xenobiotics, including metals and various pesticides, may potentially affect crab growth, reproduction, and development. In excess, naturally occurring trace metals such as cobalt, copper, and selenium, which are essential for various physiological processes including digestive enzyme synthesis and secretion, nutrient uptake and accumulation of nutrient reserves (Gibson and Barker 1979; Wright and Ahearn 1997), may become toxic.

Organometallic compounds commonly found in the blue crab's environment include tributyltin (TBT) and methylmercury. The anti-fouling chemical TBT has extensive toxicity to most marine invertebrates. In blue crabs, TBT is rapidly metabolized by the hepatopancreas and eliminated. Tributyltin inhibits growth of blue crab oocytes and reduces successful embryonic hatching by 50% (Lee et al. 1996). Limb regeneration and ecdysis are delayed in fiddler crabs exposed to TBT, and regenerated limbs are deformed; similar results are likely in blue crabs also. Lab studies demonstrated numerous effects of heavy metals (e. g. methylmercury) at the cellular level and also a reduction of limb regeneration in fiddler crabs; however, concentrations used in these studies exceed those typically found in contaminated locations. Thus, limited information exists regarding the effects of methylmercury on crustaceans in nature.

Organophosphate and organochlorine compounds developed as insect pesticides are also inherently toxic to blue crabs and other crustaceans. These compounds may be of potential concern when insect eradication efforts occur in habitats that overlap with those of blue crabs (e.g. mosquito control activities in salt marshes). Insect pesticides impair nervous system function (Hodgson and Levi 1987) and have far greater effects on crustaceans than on marine fishes by several orders of magnitude (Eisler 1969; Odenkirchen and Eisler 1988). Organochlorine compounds in contaminated estuaries affect blue crab growth, reproduction and development (Nimmo et al. 1975; Bookhout et al. 1976, 1980; Koenig et al. 1976; Schimmel et al. 1979), and may inhibit limb regeneration.

Polycyclic aromatic hydrocarbons (PAHs) are also of great concern worldwide. Decreases in shrimp populations along the southeastern United States have been correlated with increased concentrations of PAHs, and in areas where farms border estuaries, population decreases are also correlated with the presence of various pesticides (Finley et al. 1999). Recent studies demonstrated that PAHs effect molt hormone production and cell proliferation. In juvenile blue crabs, PAHs seem to act as endocrine disrupters as evidenced by the inhibition of growth and molting. However there is no evidence of how such effects translate to the population level.

Blue crabs occupying habitats adjacent to development cannot escape effects of chemical toxicants. Since blue crabs have such a complex life cycle involving many stages of development, it is crucial to assess the effects of xenobiotics on growth, development, molting, and reproduction at the population level. Collectively though, population-level consequences of exposure to contaminants remain unknown. Brouwer and Lee (2007) postulated that greater threats "to blue crab populations may be posed by increased nutrient loading, alterations of freshwater inflow, and physical destruction of estuarine and coastal habitats that accompany increasing human population densities and development near the coast (Engel and Thayer 1998)."

Effects of Fishing Pressure on Habitat

Eric G. Johnson, Anson H. Hines, Romuald N. Lipcius, and Gina M. Ralph

Fishery exploitation can alter trophic interactions among species resulting in direct impacts on food web dynamics and indirect effects on biogenic structured habitats (e.g. salt marsh, seagrass, oyster reefs) for blue crabs in Chesapeake Bay. Herein, we summarize the major potential direct and indirect impacts of fishery exploitation on blue crab habitat in Chesapeake Bay.

Trophic Cascades

Fishery exploitation can alter the abundance of predator and prey, but can also often initiate cascading effects that travel through multiple trophic levels and ultimately affect habitat value. The importance of unstructured shallow muddy coves surrounded by fringing marshes as juvenile nurseries in Chesapeake Bay is becoming increasingly understood (King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Further, the value of these habitats as secondary nurseries for juveniles may be increasing, particularly for early juvenile instars, as primary nursery habitats in the lower Chesapeake Bay, such as seagrass beds, decline. Recent evidence suggests that salt marshes may be threatened by a top-down trophic cascade initiated by the overharvest of blue crabs, which serve as predators in these systems (Silliman and Bertness 2002). Blue crabs are a key predator on marsh snails, *Littoraria irrorata*, in tidal salt marshes, and limit snail populations directly through predation. The marsh snails (periwinkles) are the dominant grazer in these systems, and can reduce a productive, healthy salt marsh to unvegetated mudflat in the absence of natural predators (Silliman and Bertness 2002). One hypothesis to explain die-offs of salt marshes in many coastal Atlantic and Gulf of Mexico estuaries posits that die-offs are driven by cascading effects of precipitous declines in blue crab abundance resulting from overharvesting. At present, while ecological experiments clearly demonstrate the mechanism for top-down regulation of primary productivity in salt marshes, the relative role of such cascades in observed losses of salt marsh habitat in coastal ecosystems is unknown.

Overharvesting of large predatory sharks has reduced abundances of these species in coastal ecosystems (Myers et al. 2007). In response, populations of elasmobranch prey species on which they feed, including the cownose ray, *Rhinoptera bonasus*, have increased exponentially with potentially significant impacts to blue crab primary nursery habitat in Chesapeake Bay. Seagrass beds are the primary settlement habitat for blue crabs in Chesapeake Bay, providing structured refuge from predation and abundant prey for enhanced growth (Heck and Thoman 1984; Orth and van Montfrans 1987, 1990; Pile et al. 1996). Foraging by cownose rays for infaunal bivalves within submerged aquatic vegetation can uproot and destroy important seagrass nurseries for juvenile crabs (Orth 1975).

Cownose rays are voracious predators on an array of bivalve species including the Eastern oyster, *Crassostrea virginica* (Smith and Merriner 1985), which serves as structured habitat and prey for blue crabs (Eggleston 1990; Posey et al. 2005). Foraging by schools of cownose rays can result in top-down effects on oyster prey populations. These trophic impacts can be significant and bivalve prey populations can be driven to local extinction. For example, predation by cownose rays nearly extirpated a restored oyster bar within Chesapeake Bay, and rays have been cited as a major impediment to oyster restoration (Blue Ribbon Oyster Panel 2007). The impact of cownose rays on natural oyster populations; however, may be diminished on three-dimensional reefs with vertical relief because the structure and arrangement of oysters on three-dimensional reefs appears to reduce feeding efficiency. The indirect impact on blue crabs remains uncertain since the historical importance of oyster reefs as blue crab habitat is not well understood. However, blue crabs are found in oyster reefs, and these habitats may increase in importance as nursery areas decline in seagrass and other structured habitats such as fringing salt marshes.

Derelict Fishing Gear

The blue crab fishery in Chesapeake Bay employs crab pots as the primary method for harvest (Miller et al. 2005). Crab pots are generally large cubes (2’ × 2’ × 2’) constructed from galvanized or coated vinyl meshes. The pots are baited to attract blue crabs, which enter the pot through four funnel-shaped entrances. Pots are fitted with mandatory cull rings that allow for undersize crabs to escape. A buoy attached to the pot via a sinking line is used to recover the pot after deployment. It has been estimated that 10-20% of each watermen’s pots may be lost annually due to strong currents, storms, line chafing and boat propellers. These derelict blue crab traps are called “ghost pots”. Recent estimates are that 42,000 of these ghost pots have been lost in the Maryland portion of Chesapeake Bay (Giordano et al. 2009). Ghost pots are also a major problem in Virginia, and efforts are currently underway to estimate the number of derelict fishing traps in the Virginia portion of the Bay (Havens et al. 2009). Ghost pots may be a major issue since they have ecological and environmental impacts for blue crabs and finfish. Untended, ghost pots remain in the water and continue to actively trap blue crabs and finfish. On average, 17 blue crabs will be captured and die in each ghost pot over the course of a single fishing season (Giordano et al. 2009).

Direct Effects of Fishing Gear on Habitat

Fishing with mobile fishing gears such as trawls and dredges not only removes target and non-target fishery species, but also represents an important source of human disturbance to natural environments. These gears can negatively impact blue crab habitat by reducing complexity and refuge value of biogenic habitats (e.g. seagrass, oyster reefs: Auster 1998; Watling and Norse 1998; Auster and Langton 1999), by reducing overall productivity, and by altering the diversity and composition of infaunal benthic communities that serve as prey for blue crabs (Thrush et al. 1998). Fishing impacts on oyster reefs are well studied. Destructive gears eliminate vertical relief in these habitats reducing the height of reefs, lessening their habitat value and increasing oyster mortality through direct and indirect effects of hypoxia and disease (Lenihan and Petersen 1998; Lehihan et al. 1999). Historically, hydraulic dredges used to harvest clams from within seagrass have resulted in severe damage to this habitat (Manning 1957; Petersen et al. 1987); however, current regulations in both Maryland and Virginia prohibit this method of harvest in seagrass.

The impact of trawling and dredging on the value of unvegetated habitats to blue crabs remains poorly understood; however the blue crab winter dredge fishery, which until its closure in 2009, scoured a considerable area of lower Bay and likely impacted the benthic communities and decreased water clarity through the resuspension of soft sediments.

Summary

Fishery exploitation can alter trophic interactions, resulting in direct and indirect impacts on blue crab habitat quality. Derelict crab traps may have major ecological and environmental impacts for blue crabs. A variety of fishing gears can negatively impact blue crab habitat by reducing complexity and refuge value of biogenic habitats.

Diseases and Blue Crab Habitat

Eric Schott and Gretchen A. Messick

Blue crabs occupy diverse habitats (Hines 2007; Lipcius et al. 2007). In Chesapeake Bay, the full life cycle of blue crab makes use of the coastal ocean, submerged aquatic vegetation, oyster reefs, salt marshes, and unstructured shallows and benthos. Larval stages and females carrying mature egg masses are restricted to the lower Chesapeake Bay and coastal zone by the physiological requirement of larvae for high salinity. Following settlement as megalopae, small juvenile crabs disperse northward and into subestuaries to forage, utilizing structured environments that provide refuge from predators and cannibalism.

In Chesapeake Bay, virtually all structured habitat is comprised of various kinds of organisms: submerged aquatic vegetation (especially eelgrass), salt marshes (predominantly *Spartina* spp.) and oysters. There are well-described diseases that affect these species, and they can have significant impacts. Unstructured habitats, the coastal ocean (occupied by zoea) and open bay bottom (exploited by adult predatory crabs) may also harbor organisms harmful to blue crab.

Progress in understanding disease in the environment has been accelerated by the interplay of new concepts and new technologies. Molecular technologies that allow disease-causing organisms to be tracked in non-host organisms or in the environment have raised the possibility of disease forecasting, disease reservoir tracking, and retrospective studies on archived animal or environmental samples. These abilities will, hopefully, catalyze development of testable hypotheses about origins and fates of disease-causing organisms, and allow a more thorough understanding of their role in blue crab habitats.

Submerged Aquatic Vegetation

Seagrass beds in high salinity coastal lagoons and the lower Chesapeake Bay are the preferred nursery habitat for megalopae and first crabs settling out after ingress from the coastal zone. The dominant angiosperm in this habitat is eelgrass (*Zostera marina*). The restricted range of eelgrass beds is considered one of several limiting factors for survival of early stage blue crabs in Chesapeake Bay, as it provides refuge from cannibalism during the molting cycle (Ryer et al. 1997). While climate effects, eutrophication and sediment are obvious factors in the annual fluctuations of eelgrass beds, diseases may be an exacerbating factor or one that strikes sporadically in isolated coastal bays (for review, see Muehlstein 1989). The slime mold pathogen, *Labyrinthula zosteracea*, is now firmly believed to be the cause of eelgrass “wasting disease”, first described in the 1930s when it struck along the Atlantic coast (Ficher-Piette et al. 1932). The disease has been a recent concern in New England (Muehlstein 1989), but appears not to be the cause of current eelgrass loss in the Mid-Atlantic or Chesapeake Bay.

Though dominated by eelgrass in high salinity, SAV includes a variety of angiosperm species that inhabit salinity ranges from oceanic to fresh water. Other plants include Redhead grass (*Potamogeton perfoliatus*), widgeon grass (*Ruppia maritima*), Sago pondweed (*Stuckenia pectinata*), and several Naiads (*Najas* spp.). Like *Zostera*, and every terrestrial plant studied, each of these species has diseases that affect their growth, reproductive success, or dispersal. As early as 1997, the Atlantic States Marine Fisheries Commission released a policy paper addressing the need for member states to monitor SAV diseases and develop better science to understand the effects of disease on SAV (Atlantic States Marine Fisheries Commission, Submerged Aquatic Vegetation Policy, 1997). Given the crucial role of SAV to crab juvenile populations, and the many reports of long term declines in blue crab abundance (Lipcius and Stockhausen 2002; Miller et al. 2005) this need persists.

Salt Marshes

As mentioned in other briefs, salt marsh is prominent among the essential habitats for blue crab. This habitat consists of one primary species (cordgrass, *Spartina alternifolia*) and other species that vary depending on region, but may include salt hay (*Spartina patens*), saltgrass (*Distichlis spicata*), and needle rush (*Juncus* sp.). While coastal development appears to be a significant threat to salt marsh, this decade has seen a sudden spike in reports of marsh dieback. The phenomenon of sudden wetland dieback (SWD) has been of increasing concern in New England, and struck the mid-Atlantic in 2006. Similar in appearance to the earlier brown dieback in the Gulf of Mexico, it is also of unknown etiology. In Delaware inland bays, SWD is of urgent concern, and reports of SWD in Maryland inland bays are starting to come in (Isle of Wight; Bason et al. 2007). Given the role that salt marsh plays in carbon input into estuaries, even interior dieback could have effects on productivity, and thence crab foraging success.

Although SWD has characteristics of a phenomenon caused by an infectious disease, there is no specific infectious agent that has been identified. There have been no obvious correlations of SWD with fungus, nematode, or toxic metals (Bason et al. 2007). An oft-cited alternative explanation ties SWD to climate: McKee et al. (2004) hypothesized that SWD in southern states is caused by drought-initiated changes in sediment chemistry (oxidation and acidification). However, a more recent review of the phenomenon nationwide does not support a link between drought and dieback in the mid-Atlantic (Alber et al. 2008), even as it supports the hypothesis for the Southeast. It is clear that marsh dieback is in need of further study and monitoring.

Oyster Reefs

Oyster reefs are utilized by blue crabs for their provision of food as well as refuge from predators (Eggleston 1990; Posey et al. 2005; Kellogg et al. 2006). In the past half century, the effects of two protozoan diseases, *Perkinsus marinus* (a.k.a. Dermo) and *Haplosporidium nelsoni* (a.k.a. MSX), have significantly altered population dynamics of oysters from the Gulf of Mexico to the Mid-Atlantic. The effects of dermo and MSX on the food resource that oysters represent is covered in the food web brief. In Chesapeake Bay, where Dermo still limits some oyster populations to a 2 or 3 year life span, it is likely that the paucity of oyster reefs has exacerbated the blue crab population decline indirectly: changes in the way that oysters were harvested (more destructive to reefs), and a shift of fishing effort from oystering to crabbing, as oyster populations declined. Genetically-based resistance to MSX arose both in oyster breeding programs and in wild populations some decades after the disease was first described. Dermo resistance has been elusive, but breeding programs have proven useful for production of seed destined for aquaculture.

Open Ocean and Coastal Zone

Crab larvae are released from mature egg masses in high salinity water, where they persist in the coastal zone (McConaugha, this series; DeVries et al. 1994). While disease may not have a direct effect on this coastal habitat, it is reasonable to hypothesize that biotic factors can change this environment to the benefit or detriment of crab larvae. Responding to climate change, altered freshwater input, and anthropogenic nutrient loading, harmful algal blooms (HABs) have shown global decade-long increases. These blooms may harm zoea, which are grazers of phytoplankton and zooplankton (which feeds on phytoplankton). Perez and Sulkin (2005) found that larvae of *Cancer* spp. will graze on certain species of toxic dinoflagellates, leading to accelerated mortality in at least one instance. Maryland's coastal bays harbor a number of toxic HABs (Wazniak and Hall 2005).

Muddy and Sandy Bottoms

In sandy and muddy bottoms of coastal lagoons from Delaware to the Gulf of Mexico, blue crabs periodically suffer large mortalities due to infection with *Hematodinium* sp., a parasitic dinoflagellate (Messick and Shields 2000). The recurrence of crab disease in certain hotspots has led to the hypothesis that the parasite, as a dinoflagellate, may produce cysts that create a pathogen reservoir in sediment, similar to what is observed for some HAB species (Frischer et al. 2006). PCR-based tools have been developed to monitor *Hematodinium* sp. in crabs, other invertebrates, and in sediment (Nagle et al. 2009; Donaldson et al. 2009). These tools are being used to investigate the sediment reservoir hypothesis (Donaldson et al. 2009). The foraging of blue crabs in sediment would put them in close contact with other infectious agents present. As detailed in the diseases brief, there are many such organisms. It has not been investigated whether the sediment can be a reservoir for these as well.

Issues

Three critical biogenic habitats (eelgrass, oyster, salt marsh) for juvenile blue crab are impacted by disease. Monitoring of oyster diseases is straightforward and is done comprehensively by those involved in the fishery and restoration. As these monitoring programs are carried out, investigators should be vigilant and watch for emerging diseases. The MD DNR Shellfish lab at Oxford currently does this as part of its annual surveys. The known disease of eelgrass has hallmark symptoms (Meuhlstein 1989), so monitoring not only the extent, but health of eelgrass should be pursued. Attention to spatial and temporal trends may allow detection of disease-related declines that could signal a new pathogen. It may be important to measure not just extent, but also health of SAV species. Recent reports of salt marsh dieback in coastal bays along the Atlantic and Gulf coasts are a sign that careful monitoring of salt marshes is needed. There is little or no understanding of the effects on crab larvae populations of HAB blooms in the coastal zone. Field sampling can inform us as to whether HABs and crab larvae co-occur. Laboratory studies can be pursued to investigate whether larvae graze on, and are harmed by, HAB species. There is a lack of knowledge about the dynamics of crab disease-causing organisms in the benthos. Molecular tools are available or can be developed to detect viruses, bacteria and protozoans in environmental samples.

Indicators

1. Salt marsh acreage, soil composition, and sea level

Salt marshes supply both carbon input to estuaries and refuge for blue crab, and are therefore thought to affect blue crab abundance. Baseline and comparative data on salt marsh soils, paired with climate monitoring, marsh composition and marsh extent would assist in developing predictions for salt marsh health.

2. Seagrass acreage

Because eelgrass beds are of intense interest to many researchers of Chesapeake Bay ecology, there are detailed ongoing surveys of this species (Orth et al. 2007). It will continue to be essential to distribute the findings of such surveys to stakeholders. Specific regional reductions in eelgrass or any other SAV species could signal the effects of a pathogen. Like eelgrass wasting disease, emerging diseases would be expected to cause characteristic symptoms on the plants.

3. Oyster bed acreage

In locations that have natural spatfall, oyster reefs have made advances, such as in the Lynnhaven River and the Great Wicomico (Schulte et al. 2009). In Maryland, after decades of planting oysters (bar restoration) primarily for the fishery, recent efforts to restore oysters are anticipated to pursue a dual approach of emphasizing aquaculture which allows for the establishment of large oyster sanctuaries that would be closed to harvest for decades at a time (MD OAC 2009). The scale of these activities is anticipated to be an order of magnitude larger than current efforts. The sanctuaries may result in a significant increase in structured habitat for blue crab juveniles. As they are constructed and monitored, these sites will provide an opportunity to study long term effects of habitat enhancement on local crab abundance. One goal of sanctuaries is to develop genetically-based disease resistance for production of natural spatfall. If successful, the wild recruits will add to the structured habitat.

4. Coastal HAB blooms

It has not been specifically investigated whether HAB blooms co-occur in time and space with blue crab larvae. Current surveys for HABs and crab larvae should include detection of the reciprocal species, through sharing of samples by researchers engaged in these surveys.

5. Potential benthic reservoirs of blue crab disease

Do benthic sediments serve as a reservoir for disease-causing organisms? Synergy with studies of potential HAB reservoirs in coastal bays should be exploited.

Summary

Structured habitats for blue crab depend on living resources (SAV, oysters, salt marsh) that may be susceptible to disease. Known diseases of eelgrass (wasting disease) and oyster (Dermo, MSX) are under surveillance. There is a need to monitor marshes throughout the region, given the possibility of dieback. There are current restoration efforts for SAV, oysters and salt marshes. The influence of HABs and sediment-derived pathogens on blue crab mortality is not known. Molecular tools are available and can be developed to address such questions.

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FOODWEB

Predation

Jacques van Montfrans, Eric G. Johnson, Romuald N. Lipcius

Predation can be an important determinant of blue crab population size in Chesapeake Bay. Predation has the greatest effect on the smallest and most numerous early life history stages and decreases with increasing crab size (or age: i.e., predation mortality on larvae > postlarvae > juveniles > adults). These impacts on blue crabs vary seasonally (predation in spring < summer > fall with virtually no predation-induced mortality occurring in winter) in relation to variation in water temperature that affects crab and finfish distribution and activity. Predation intensity also varies within and among habitats (generally, predation in structured habitats < unstructured habitats). Strong latitudinal gradients in predation intensity also exist throughout the range of blue crab populations with higher rates occurring at lower (i.e., subtropical and tropical) than at higher (temperate) latitudes (Heck and Wilson 1987; Orth and van Montfrans 1990). This pattern of predation is also evident along the south to north latitudinal gradient in Chesapeake Bay (Johnson et al., unpublished data). Blue crabs are challenged by many predators during various stages of their complex life cycle (Figure 1) which impact population dynamics, and determine, in part, survival to the reproductive stage.

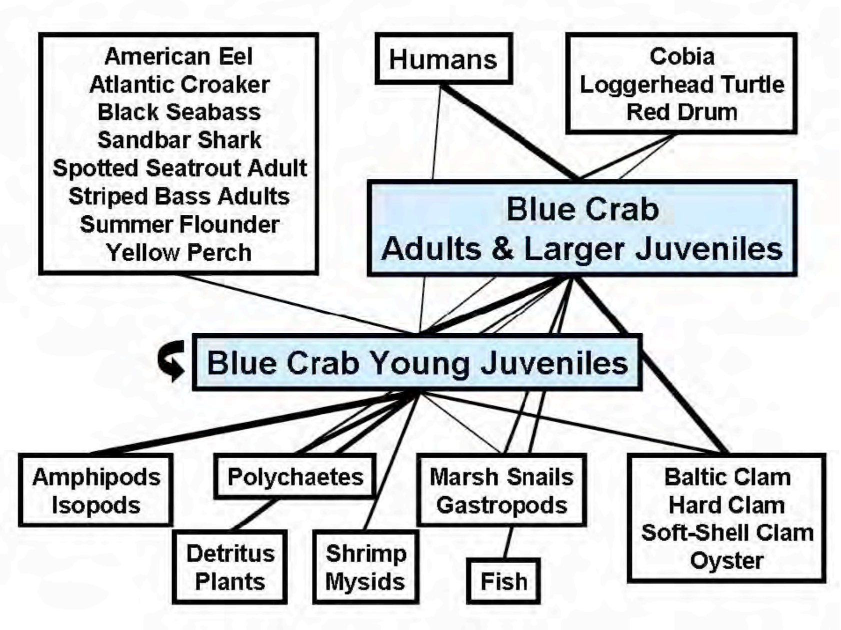

Figure 1. The blue crab foodweb illustrates that many predators consume blue crabs in nature. Cannibalism is a major source of natural mortality and several species of finfish also consume juvenile crabs. Adult and sub-adult blue crabs are preyed upon by only a small suite of predators, including humans.

Predation mortality in blue crabs occurs as early as the egg stage, primarily by the symbiotic nemertean, *Carcinonemertes carcinophila* (Shields and Overstreet 2007). This egg predator lives in the gill chambers and feeds on blue crab embryos once eggs have been extruded onto the abdomen or "apron". Unlike in other crab species (e.g., Alaskan king crabs), *C. carcinophila* occurs in relatively low abundance in the Chesapeake Bay blue crab population, and likely has a minor effect on crab survival. Highest mortality from predation most likely occurs during the pelagic phase of larval development, though the magnitude of the effect has not been quantified. Morgan (1987) demonstrated that blue crabs, whose larvae are exported from Chesapeake Bay for optimal development in high salinity coastal waters, are more vulnerable to predation because the dorsal and lateral spines in zoeal stages are significantly shorter than in other estuarine-dependent crab species which complete larval development within the Bay. He postulated that: a) longer spines reduce predation by constraining the suite of gape-limited estuarine fish predators that consume planktonic crab larvae, and b) predation pressure on crab larvae is higher within the Bay than in coastal waters.

After metamorphosis to the megalopa (postlarval) stage, ingressing megalopae exhibit adaptive behaviors that reduce predation during their search for suitable settlement habitat. Tidally-mediated diel vertical migration behavior results in megalopal distributions near or on the bottom in the daytime and during ebbing tides. Megalopae migrate vertically and are neustonic only during nocturnal flood tides. Such behavior enhances up-estuary transport while concurrently reducing daytime mortality by visual predators (Olmi 1994, 1995) such as crustaceans and fishes.

Blue crabs in Chesapeake Bay recruit as megalopae during summer and fall (van Montfrans et al. 1990, 1995) when many predatory fish migrate out of the bay, except for striped bass and seagrass residents (van Montfrans et al. 2005). Some of the resident fish in primary blue crab settlement habitat (seagrass, SAV) consume megalopae and recently settled juvenile crabs early in the fall prior to migrating into deeper water. Silver perch (*Bairdiella chrysoura*), spot (*Leiostomus xanthurus*), pipefish (*Syngnathus fuscus*), striped cusk eel (*Ophidion marginatum*), black sea bass (*Centropristis striata*), Bay anchovy (*Anchoa mitchilli*) and Atlantic silverside (*Menidia menidia*) consume megalopae during recruitment peaks. Newly settled juveniles (J1 – J4) are consumed by black sea bass, striped cusk eel, spot, silver perch, and northern puffer (*Sphoeroides maculatus*; van Montfrans et al., in preparation).

Experimental evidence from mesocosms demonstrated intense predation by mummichog (*Fundulus heteroclitus*) on megalopae and early juvenile crabs, with the effects moderated by habitat structure (mortality in SAV < sand), life-history stage (predation on megalopae > juveniles) and crab size (consumption of small crabs > larger juveniles; Orth and van Montfrans 2002). Crustacean predators including sand shrimp (*Crangon septemspinosa*) are voracious predators on blue crab megalopae, while grass shrimp (*Palaemonetes pugio*) also consumed megalopae (Olmi and Lipcius 1991).

Predation on megalopae and early juveniles (J1–J4) may also occur via intra-cohort cannibalism (Moksnes et al. 1997). In mesocosm experiments, cannibalism on megalopae during settlement was dependent upon molt stage such that increased cannibalism occurred when megalopae molted to the first juvenile instar. Mortality was significantly higher in sand than in *Zostera marina* (Moksnes et al. 1997) attesting to the nursery role of SAV habitats. Furthermore, when megalopae were exposed to juvenile crabs, mortality via inter-cohort cannibalism was significant, though moderated by habitat type (seagrass < sand) and crab density (low < high) for crabs smaller than J5. Juvenile crab predators exhibited an inversely density-dependent (type II) functional response in sand, causing high mortality at low prey (i.e., megalopal) densities (Moksnes et al. 1997). In contrast, juvenile crab predators in *Zostera marina* displayed a weak density-dependent (type III) functional response with significantly lower proportional mortality at low prey densities, thereby implying greater survival potential for crabs settling in SAV. Thus, intra-cohort cannibalism by larger juveniles upon recent settlers (megalopae and smaller juveniles) may be a major source of mortality among newly settled crabs during recruitment, especially in sandy habitats (Moksnes et al.1997), though field evidence is not available to confirm these effects.

As juveniles grow, cannibalism remains a significant source of mortality in the field (Hines et al. 1990; Mansour 1992; Hines and Ruiz 1995; see Cannibalism issue brief, this section) because large crabs of the 1+ age class can consume most sizes of the 0+ age class (Peery 1989). For example, cannibalism by large adult crabs accounted for 75-97% of mortality of juvenile crabs in the oligohaline Rhode River subestuary in upper Chesapeake Bay (Hines and Ruiz 1995). However, the relative importance of inter-cohort cannibalism is likely to vary spatially within Chesapeake Bay and may be reduced in the higher salinity regions of the lower Bay, which harbor a greater diversity of blue crab predators.

Fishes also consume smaller blue crabs, particularly during the fall recruitment season and in spring after crabs have overwintered while they are still small in size. Overton (2000) found blue crabs more commonly in the diet of striped bass, *Morone saxatilis*, < 425 mm total length (TL), although they accounted for < 5% of the total diet by weight. For larger striped bass (> 425 mm TL), blue crabs comprised < 1% of the diet, whereas menhaden accounted for 90% of the diet, suggesting a greater dependence on fish prey. Striped bass are cold-tolerant and in contrast to other predatory fish, some enter the shallows (including SAV nursery habitats) during fall and spring to feed. A two-year (2004 – 2005) field study that

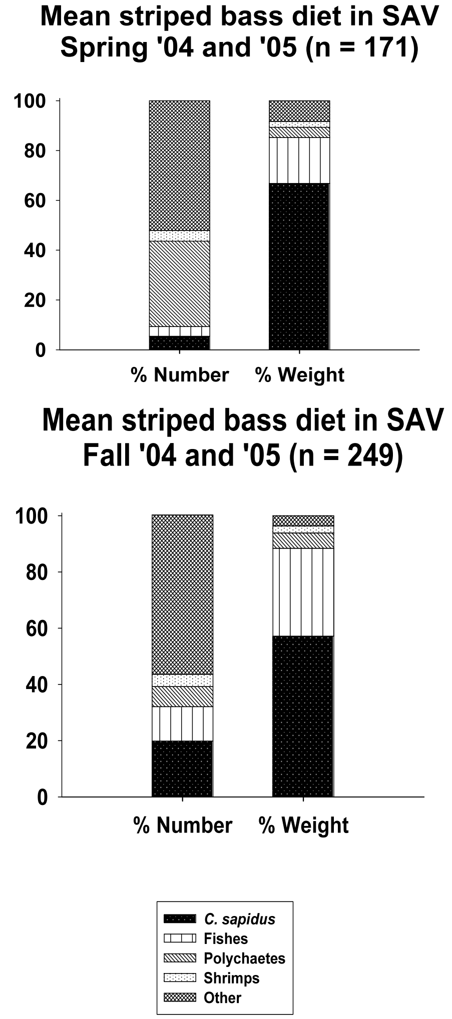

Figure 2. Seasonal diets of striped bass foraging in seagrass beds, lower Chesapeake Bay.

quantified fish predation impacts on three recruitment cohorts of blue crabs in Chesapeake Bay SAV habitats during fall and spring implicated striped bass averaging ~ 400 mm TL as the top seasonal fish predators (Figure 2; van Montfrans et al. 2005, unpublished data).

Juvenile intermolt blue crabs < 25 mm in carapace width (CW) comprised 60–70% of striped bass diet by weight (Figure 2). Consumption estimates varied between 20, 000,000-110,000,000 crabs seasonally, with consumption in spring less than in fall during the period of peak recruitment for blue crab juveniles. Although these estimates seem high initially, striped bass predation impact on newly recruited crabs was minimal. Only 2–5% of crabs available in SAV habitats were consumed seasonally, suggesting that their overall impact on juvenile blue crabs is not substantial (van Montfrans et al. 2005, unpublished data).

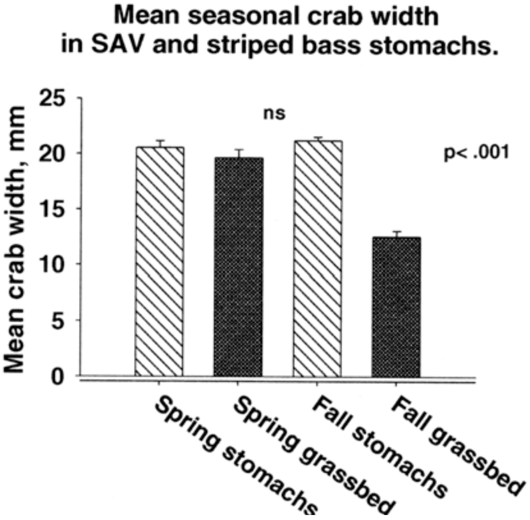

Figure 3. The size of crabs consumed by striped bass in spring was similar to that of crabs in SAV beds but significantly larger than the ambient mean size of crabs in fall.

Furthermore, striped bass consumed crabs that averaged 20–25 mm in CW during both seasons. Prey sizes were statistically similar to the mean size of crabs inhabiting SAV during spring, but significantly larger (about 2X) than the average size of crabs in SAV during the fall (van Montfrans et al. 2005, unpublished data; Figure 3). These data support the conceptual model (Lipcius et al. 2007) that larger juveniles outgrow the size-specific protection of seagrass structure after attaining a size of 20-25 mm CW and are no longer safe from predation in primary SAV nurseries. Consequently, they depart these habitats to exploit the refuge value and abundant prey of secondary nurseries (Lipcius et al. 2007). During such dispersal periods, predation by finfish could affect natural mortality on crabs once they reach a size of 20 mm CW and before they attain a refuge in size from gape-limited predators.

Atlantic croaker, *Micropogonias undulatus*, also consumed blue crabs but impacts were minimal (< 0.6% of crabs available; van Montfrans et al., unpublished data). Red drum, *Sciaenops ocellatus*, a recognized predator of blue crabs, is limited in its northern distribution along the Atlantic coast to New Jersey. Red drum are common in the Gulf of Mexico (Murdy et al. 1997) where they have a substantial predation impact on blue crabs (Guillory and Prejean 2001; Guillory and Elliot 2001). However, few red drum were collected seasonally in the Chesapeake Bay, lessening their influence (van Montfrans et al., unpublished data). This species may, however, increase in abundance in the future with increasing water temperatures accompanying global warming.

Field experiments employing tethered hard crabs (Moody 2001; Johnson et al. 2008, in review) demonstrate a strong seasonal component to blue crab mortality via predation (spring < summer > fall) and a decrease in relative mortality with increasing crab size from 10-70 mm CW (Hines et al. 2008; Johnson et al. 2008, in review). Moody (2001) postulated that intermolt (hardshelled) blue crabs attain a 95% size refuge from natural predators, excluding humans, by the time they reach 90 mm CW.

Only sea turtles (Kemp's ridley *Lepidochelys kempi*, Marquez-M. 1994; loggerhead *Caretta caretta*, Seney and Musick 2007), cobia (*Rachycentron canadum*, Arendt et al. 2001), and some sharks and rays (Bigelow and Schroeder 1953) can consume large intermolt blue crabs in the Bay. The impact of turtles and cobia is unknown, but may not be substantial because of their relatively low seasonal abundance. Cownose ray (*Rhinoptera bonasus*) abundance in Chesapeake Bay is estimated to have increased from 11 million in 1990 (Blaylock 1993) to more than 44 million in 2007, most likely because shark populations have declined (Myers et al. 2007). Blue crabs make up a small fraction of the cownose ray diet (Bigelow and Schroeder 1953), but with such dramatic increases in abundance, these rays could be having more of an influence than previously thought. Overall, humans undoubtedly have the greatest impact on crabs once they attain a size of 90 mm in CW through fishery harvest, due to the relative size refuge from predation for crabs < 90 mm CW.

When crabs are soft-shelled after molting, individuals of all sizes are extremely vulnerable to predators. Predation impacts (cannibalism and interspecific predation) on early post-molt crabs (i.e., in the soft-shelled state) are substantially higher than for intermolt (hard) individuals (Ryer et al. 1997); this may be especially true for larger individuals. Tidal state in shallow areas can influence predation rates on soft crabs with higher predation occurring during low than high tides (Ryer et al. 1997).

Indicators

Cannibalism rates by large blue crabs on smaller individuals are determined in part by density-dependent processes within habitats. Thus, the relative abundance of adult and sub-adult crabs > 90 mm CW and new recruits are key indicators. These metrics are available from various fishery-independent trawl surveys (VIMS and MDNR) and the Winter Dredge Survey. Finfish predation impacts on blue crab prey are determined by the density of gape-limited predators, their opportunistic feeding behavior and the size and density of blue crab and other prey in specific Chesapeake Bay habitats.

Both fishery-independent measures of predatory fish abundance by the Chesapeake Bay Multi-species Monitoring and Assessment Program (ChesMMAP) trawl survey and fishery-dependent landings data could serve as indicators of predatory fish abundance in the Bay for multi-species modeling efforts to assess predation impacts on blue crabs.

Summary

Predation lowers the survival of eggs, larvae, recruiting megalopae and juvenile and adult crabs in various Chesapeake Bay habitats, and is an important determinant of overall stock size. Blue crab mortality due to predation is contingent upon density-dependent cannibalism and predation by numerous finfish. Cannibalism is a major factor affecting juvenile blue crab mortality in nature (see Heck and Coen 1995; Heck et al. 2001; Heck and Spitzer 2001; Hines 2007). Once intermolt crabs attain a size of 20–25 mm CW, they become highly vulnerable to striped bass foraging in SAV. Few natural predators consume large blue crabs (> 90 mm CW); human exploitation likely has the greatest impact on these large subadults and adults. Factors that alter the balance in predator populations at the ecosystem level, such as reduction in shark populations by overfishing, can ultimately impact trophic dynamics and cause cascading effects such that the blue crab population is adversely affected. Global warming may have unforeseen consequences by altering the suite of predators (e.g., increasing red drum populations and other temperate and subtropical predators) common to Chesapeake Bay.

Cannibalism

Anson H. Hines, Desmond M. Kahn, and Eric G. Johnson

Cannibalism by large crabs attacking small crabs, and by hard, intermolt crabs attacking soft molting crabs is a major source of mortality for blue crabs. Analysis of stomach contents shows that crabs comprise significant portions of the diet of large blue crabs (Laughlin 1982; Hines et al.1990; Mansour 1992). Laboratory experiments provide detailed information on the interactive effects of size, density, and habitat on cannibalism (e.g., Peery 1989; Mansour and Lipcius 1991; Moksnes et al. 1997). The majority of the quantitative evidence for cannibalism comes from use of various tethering techniques designed to measure relative survival rates in the field (Heck and Thoman 1981; Wilson et al. 1987, 1990a, 1990b; Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; Pile et al.1996; Lipcius et al. 2005; Johnson et al. 2008, in review). Tethered crabs are free to move within the radius of their tether, and they are checked periodically for injury and survival. Although tethering can cause artifacts and biases regarding sources of mortality and altered behaviors which may serve to reduce escape success and increase overall mortality (Barshaw and Able 1990; Peterson and Black 1994; Zimmer-Faust et al. 1994; Smith 1995), these problems do not appear to be serious for blue crabs as a relative measure of predation rate in unvegetated habitats, particularly where cannibalism is the major single source of mortality (Hines and Ruiz 1995).

Analysis of the damaged remains of tethered intermolt crabs and of predators caught on tethered crabs indicates that cannibalism rates are high and account for 92% of mortality in juvenile blue crabs in estuarine habitats of upper Chesapeake Bay (Ruiz et al. 1993; Hines and Ruiz 1995). Further, no instances of fish predation have been confirmed during a 20 year tethering study in the Rhode River (Hines et al., unpublished data). This long-term study indicates that juvenile mortality has declined from 1990-present, concurrent with declines in overall crab abundance in the Bay (Hines et al., unpublished data), and that mortality peaks seasonally in summer when the abundance of large crabs is the highest (Hines et al., unpublished data). While these data do not imply causation, the patterns are robust over time (20 years) and are consistent with the important role of cannibalism as a key source of juvenile mortality. The importance of cannibalism likely varies spatially along the gradient of the Chesapeake Bay with changes in predator abundance and diversity, such that the impact of cannibalism in the lower Bay is reduced (Moody 2001, 2003). Finfish predation appears to be more important in the higher salinity waters of the lower Bay where predator diversity and abundance is higher than in the upper Bay. For example, the abundance of Atlantic Croaker, Black Sea Bass, bluefish, red drum, cobia, blue catfish, northern puffer, summer flounder, spotted sea trout, tautog, weakfish, cownose rays, all of which have been reported to prey on blue crabs to varying extents, are more common in the lower Chesapeake (Blaylock 1993; CBFEAP 2006; Bonzek et al. 2007).

Juvenile intermolt blue crabs tethered in nonvegetated habitats suffered high mortality rates. Rates include 40 to 90% of 30 to 70 mm crabs being eaten per day mostly by cannibalism in water >70 cm deep in a central Chesapeake subestuary during summer (Hines and Ruiz 1995). This study also found that mortality was lowest in shallow water (<20 cm) and increased with depth, demonstrating the importance of nearshore shallows as a refuge for small juvenile crabs (Hines and Ruiz 1995). The use of shallow water by juveniles appears to be an adaptive behavior for predator avoidance; juvenile blue crabs in tank mesocosms with depth gradients shifted their distribution to shallower areas in response to the addition of a large predatory crab (Dittel et al. 1995). However, the importance of shallow water, structured habitats is not limited to small juveniles. Molting blue crabs of all sizes also suffer high mortality rates, often attributable to cannibalism; however, the results must be interpreted with caution since experimental artifacts of tethering may be more pronounced in these cases, because molting crabs must be held in mesh bags to secure them (Shirley et al. 1990; Ryer et al. 1997). To limit the impact of cannibalism, large molting crabs often seek refuge in shallow water structured habitats, similar to the strategy utilized by small juveniles (Hines et al. 1987; Shirley et al. 1990; Wolcott and Hines 1990). Thus, shallow, water structured habitats are not only key juvenile nurseries, but are also important molting refuges for larger juveniles and adults (Ryer et al. 1997). As a result, anthropogenic modification of nearshore depth profiles (e.g., bulkheads, dredging) and removal of structured refuge along natural shoreline may severely reduce or eliminate the role of these areas as refuges for blue crabs of all sizes from predation. Further, episodic hypoxia as a result of diel cycling or wind-induced seicheing can induce movement of large predatory crabs from deeper waters into shallow areas increasing the potential for cannibalistic interactions and reducing the value shallow water provides as refuge for juveniles (Eggleston et al. 2005).

The scale of studies on predator effects has yet to be expanded. Cannibalism by large blue crabs upon smaller crabs and molting crabs appears to be a major source of mortality that is common throughout most estuarine habitats, which often shapes the distribution of blue crabs among microhabitats by size, sex, and molt stage.

Indicators

The relative abundance and distribution of adult and juvenile blue crab cannibals are key indicators. These indices can be estimated from fishery-independent surveys currently conducted in Chesapeake Bay. Spatially explicit measures of large blue crab abundance are available from the winter dredge survey. However, the winter dredge survey does not provide an accurate index of relative abundance for small juvenile crabs (CW < 30mm); because sampling is not conducted in shallow nurseries and gear efficiency for small crabs in not known. A coordinated survey in Maryland and Virginia targeting juvenile blue crabs would be helpful and provide an important Baywide index of recruitment.

Summary

- Cannibalism is a major source of mortality for juvenile blue crabs in Chesapeake Bay.
- Shallow nearshore waters and structurally complex habitats such as seagrass, salt marsh, coarse woody debris, and some species of macroalgae provide refuge from cannibalism and are key nursery habitats for juveniles and important molting areas for adults.

- The relative importance of cannibalism versus interspecific predation to blue crab mortality varies substantially both spatially and temporally within Chesapeake Bay.

Prey

Gina M. Ralph, Romuald N. Lipcius, Rochelle D. Seitz,
and Jacques van Montfrans

Introduction

While blue crabs are opportunistic, generalist predators that forage on a diversity of organisms, bivalve molluscs compose the largest dietary volume and weight (up to 60 %) in most habitats (Hines et al. 1990; Hines 2007). Research on blue crab feeding ecology in the James, York and Rappahannock Rivers demonstrated that diets are similar between tributaries with thin-shelled clams (*Macoma* spp.) dominating the diet but varying with crab size and age (Mansour 1992). Small juveniles (< 60 mm carapace width) consume amphipods and polychaetes, whereas larger juveniles (> 60 mm carapace width) and adults predominantly prey on bivalves and crabs (i.e. blue crabs and mud crabs). Cannibalism is most common in large adults, with conspecific prey comprising the second highest component of gut contents (Mansour 1992). The frequency of cannibalism varies seasonally. Highest rates occur during fall when juvenile blue crabs recruit to lower Bay tributaries, and in areas with low clam densities. Other important prey include small crustaceans, fishes, and polychaetes, though plant material and detritus is also common (Figure 4). Blue crab distribution is positively correlated with clam densities in sandy habitats at both the local (1 km) and regional (10-50 km) scales (Seitz et al. 2003a), suggesting that processes that impact prey availability may be important in regulating the population dynamics of blue crabs. Eutrophication, the increase in nutrient and dissolved organic matter concentrations, leads to hypoxia and organic enrichment, both of which can impact the abundance and composition of the benthic community (Gray et al. 2002). Alteration of benthic habitat and shorelines can replace highly productive, heterogeneous benthic communities with less productive communities (Sherk 1990; Lawless 2008). In addition, competitors such as cownose rays and various finfish species, can reduce the abundance of prey for blue crabs (Martin et al. 1989; Blaylock 1993).

Hypoxia

The spatial and temporal extent of hypoxia has been increasing within Chesapeake Bay and has had significant impacts on benthic communities (Diaz and Rosenberg 2008; Long and Seitz 2008). In general, two major types of hypoxic events occur in the Chesapeake Bay. Seasonal hypoxia occurs in the summer following the spring bloom, generally lasting until autumn, when there is significant stratification and a large quantity of phytoplankton biomass that is decomposed, as typically occurs in deeper mainstem waters. Periodic oxygen depletion can occur more often than seasonal hypoxia, but is usually less severe, and is caused by intermittent changes in weather events or the spring-neap tidal cycle, as occurs in some smaller systems such as the York River (Diaz and Rosenberg 2008). The duration, severity, and areal extent of hypoxic events likely determine community responses to the event (Seitz et al. 2003b; Diaz and

Rosenberg 2008). Many infaunal organisms move to the surface of the sediments during periodic hypoxia (Jorgensen 1980; Long and Seitz 2008). In addition, burial rates can be slowed, as occurs in *M. balthica* when exposed to hypoxic as compared to normoxic conditions (Tallqvist 2001). Brief, less severe events can increase predation as mobile predators can more successfully exploit weakened prey, particularly if the prey have migrated to the surface of the sediment (Nestlerode and Diaz 1998; Long and Seitz 2008), whereas longer, more severe events can reduce predation by quickly killing the prey as well as weakening the predators (Holland et al. 1987). A quantitative mesocosm experiment (Seitz et al. 2003b) demonstrated that *M. balthica* is more tolerant of hypoxia than blue crabs, but, in the mesocosms, the crabs were forced to remain within the hypoxic mesocosm. In the field, mobile predators such as blue crabs likely move out of the area during hypoxic events and then return to exploit stressed prey (Pihl et al. 1992; Long and Seitz 2008).

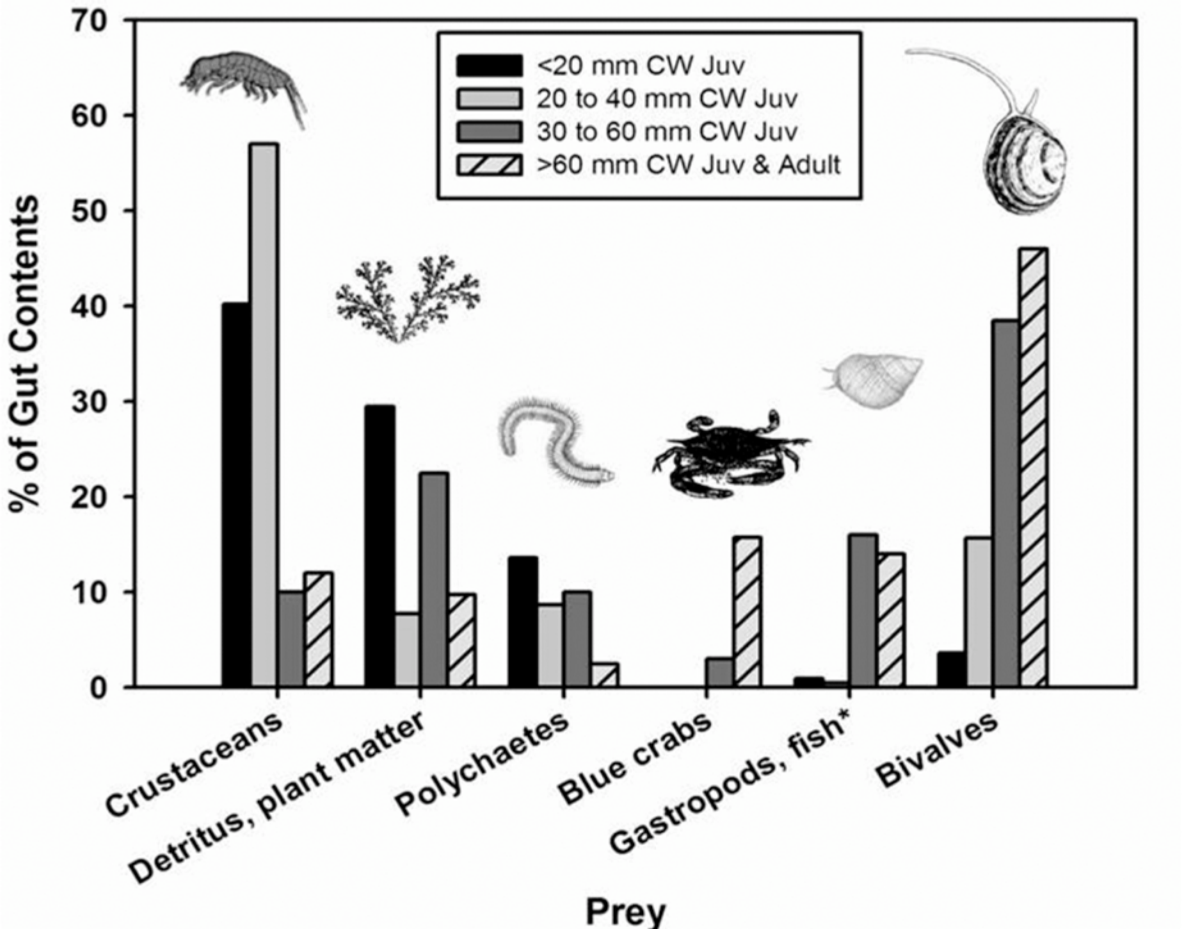

Figure 4. Gut contents of blue crabs < 20 mm to > 60 mm carapace width. From Lipcius et al. 2007.

Organic Enrichment

Under eutrophic conditions, excess organic matter is produced in the water column and exported to the sediments (Gray et al. 2002). There appears to be a gradient in the response of benthic communities to changes in organic enrichment, based on species composition, with four major stages (Pearson and Rosenberg 1978), though Gray et al. (2002) suggest that this may be a response to a gradient of hypoxia rather than of organic enrichment. Benthic community composition under normal conditions consists, in general, of large, deep-burrowing, k-selected species, whereas organically enriched areas support smaller, surface-dwelling, r-selected species. Under grossly polluted conditions, no macrofauna can survive. Sedimentation and excess organic matter can also smother benthic organisms that are unable to respond to increased sedimentation rates (Pearson and Rosenberg 1978; Gray et al. 2002).

Benthic Habitat Alteration

Various human actions in the marine environment lead directly to benthic habitat alteration, including dredging, dredge spoil disposal, and oyster reef construction. In upper Chesapeake Bay, there was a 71% reduction in the average number of individuals in a spoil disposal area, and benthic diversity decreased in both the dredged and dredge spoil disposal areas, when compared to a site that was not impacted by the dredging. A year and a half later, the dredged area had still not recovered, while the dredge spoil deposition area had recovered. A different response occurred in lower Chesapeake Bay, with rapid resettlement by infaunal species of both dredged and disposal areas (Sherk 1990). In an attempt to revive the oyster fishery, shell and artificial oyster reefs are being placed over benthic communities in muddy substrates. These reefs support completely different faunal communities, and the impact of oyster reef creation on the nearby benthic communities has not been well studied.

Shoreline Alteration

In an attempt to protect coastal property from erosion, the shoreline is often ‘hardened’ by the owners, by replacing natural marsh with either rip-rap (large rocks) or bulkhead (vertical seawalls). Natural marshes provide ecosystem functions essential to the health of the Bay, including nutrient trapping and assimilation, sediment stabilization, and buffering against erosion. In addition, marsh detritus can be an important food source for deposit-feeding infauna and the marsh itself is nursery habitat for many juvenile fishes and crustaceans (Lawless 2008), including blue crab (Lipcius et al. 2007). Few studies have examined the impact of shoreline development on shallow, subtidal ecosystems in which blue crabs are prevalent. In Linkhorn Bay, impoverished benthic communities were associated with extensive bulkhead stabilization (Tourtellotte and Dauer 1983). Shallow habitats near marshes had higher biomass of the clams *M. balthica* and *M. mitchelli* than regions without marshes, particularly at salinities greater than 8 ppt (King et al. 2005). At small spatial scales, the type of shoreline, including natural marsh, rip-rap, and bulkhead, impacted the biomass and diversity of the benthic community in nearby shallow habitats (Seitz et al. 2006; Lawless 2008). Benthic abundance and diversity was higher in subtidal habitats adjacent to natural marsh than in those associated with bulkheads, and was intermediate adjacent to rip-rap shorelines. The lower abundance and diversity of deposit-feeding species like *M. balthica* could be caused by decreased flow of marsh carbon via marsh detritus to the shallow water habitats near ‘hardened’ shorelines (Seitz et al. 2006).

Competition

The indirect effects of predation by other predators through prey depletion can influence community dynamics and the structure of natural communities. In addition, the type of predator interaction will determine the response of the prey assemblage. Exploitation competition would likely lead to the depletion of shared resources or higher utilization of unshared resources, whereas interference would likely lead to an increase in the prey assemblage (Martin et al. 1989). Cownose rays are voracious predators, particularly of bivalve molluscs, and are currently abundant in Chesapeake Bay. There is the potential for negative impacts on stocks of comercially and ecologically important shellfish, including the eastern oyster, hard clam, and soft-shell clam (Blaylock 1993), which are also important prey for the blue crab.

Indicators

Benthic biomass and abundance are affected by eutrophication, benthic habitat and shoreline alteration, and the abundance of competitor species. Moreover benthic abundance may exert bottom-up control of blue crab populations. Benthic secondary production of k-selected species, including *M. balthica* and large polychaetes, is likely to be the most effective indicator of the health of benthic systems. However, it may be necessary to use indirect indicators when direct estimation of benthic secondary production is not feasible. The two primary parameters of hypoxic events that determine the impact of the events on the benthic community are the areal extent and duration. These two metrics may also be useful indicators of habitat degradation affecting blue crab prey. Further, the linear extent of natural and ‘hardened’ shoreline and the areas of dredging and dredge spoil disposal are indicators of the health of the nearby benthic communities. Finally, changes in the abundance and identity of competitor species, such as cownose rays and certain finfish species, may be used to quantify effects on blue crab prey.

Impacts of Fishery Exploitation on Foodweb Dynamics

Eric G. Johnson and Thomas J. Miller

Introduction

Fishing pressure can alter predator-prey relationships and trophic interactions among species linked through a complex foodweb and can have substantial implications for blue crab ecosystem-based fishery management in Chesapeake Bay (Chesapeake Bay Fisheries Ecosystem Plan Technical Advisory Panel, CBFEAP 2006; Miller et al. 2006). Such interactions may be particularly relevant for the blue crab which is important as both predator and prey in the Chesapeake Bay ecosystem (Baird and Ulanowicz 1989). Herein, we summarize the major potential direct and indirect impacts of fishery exploitation on predator-prey relationships and trophic interactions of the blue crab in Chesapeake Bay. We restrict the scope of our discussion to alterations of predator-prey dynamics resulting from fishery exploitation, and only briefly consider fishery impacts associated with habitat and water quality that are the purview of other issue briefs (see Habitat degradation issue brief, Section 2: Habitat).

Fishery Exploitation of Finfishes

Blue crab megalopae and juveniles are prey for numerous finfish predators with only a limited number of species able to consume adult crabs (Guillory and Elliot 2001; CBFEAP 2006; Hines 2007; see Predation issue brief, this section). In Chesapeake Bay, the major finfish predators on blue crabs that also support commercial or recreational fisheries are American Eel (*Anguilla anguilla*), Atlantic croaker (*Micropogonias undulatus*), black sea bass (*Centropristis striata*), red drum (*Sciaenops ocellatus*), spot (*Leiostomus xanthurus*), spotted sea trout (*Cynoscion nebulosus*), striped bass (*Morone saxatilis*), summer flounder (*Paralicthys dentatus*), weakfish (*Cynoscion regalis*) and white perch (*Morone americana*). Thus, changes in the abundance of these predator species resulting from fishery exploitation could potentially impact blue crab population dynamics through linkages in the Bay food web. However, evidence from gut contents analyses indicates that blue crabs typically comprise a small percentage of the diets of most of these fishes (van Montfrans et al. 2005; Bonzek et al. 2007). For example, predation by Atlantic croaker had a minimal impact on natural mortality in lower Bay seagrass beds despite their relatively high abundance in these habitats (van Montfrans et al. 2005). Alternatively, while blue crabs are an important component of the diet of red drum which prey heavily on blue crabs, drum are not abundant in Chesapeake Bay potentially limiting their overall population level impacts (van Montfrans et al. 2005). The overall importance of finfish predation is likely to be greater in higher salinity waters of the lower Bay where the abundance of most of these species is higher (Bonzek et al. 2007).

Among the finfish that prey on blue crabs, striped bass in particular has been postulated to negatively impact blue crab populations through predation. Striped bass are an apex predator within Chesapeake Bay that feed predominantly on forage fish species (Atlantic Menhaden, bay anchovy, herring), but also on other fish species, polychaetes and benthic invertebrates including blue crabs. Unlike many finfish predators, striped bass are cold-tolerant and can remain in shallow water blue crab nursery areas during fall when juvenile blue crabs are recruiting to Chesapeake Bay, and in spring following overwintering. In Chesapeake Bay, the abundance of striped bass has increased following a fishery moratorium and interstate management plan developed by the Atlantic States Marine Fisheries Commission (ASMFC). Increases in striped bass populations, coupled with concurrent declines in key forage species (e.g., Atlantic menhaden; Uphoff 2003; Wood et al. 2000) and anecdotal reports by commercial watermen and recreational anglers of heavy crab predation by striped bass, have fueled controversy about the potential role of the striped bass predation in recent blue crab population declines.

An evaluation of available evidence indicates that predation on blue crabs by striped bass is not likely to have caused substantial population declines of blue crab in Chesapeake Bay. First, if striped bass predation was an important mechanism regulating blue crab populations, population abundances of these species would be expected to show an inverse relationship, yet analyses of historical trends from fishery-independent surveys demonstrate that this is not the case (Mosca et al. 1995). Additionally, blue crabs have historically comprised only a small fraction of the striped bass diet (Austin and Walter 1988). However, more recent studies do provide some indications that the importance of blue crabs as prey for striped bass may have increased. Two independent assessments of striped bass predation on juvenile blue crabs in lower Bay seagrass beds reported that blue crabs are commonly found in the stomachs of striped bass foraging in this habitat (Orth et al. 1999; van Montfrans et al. 2005). However, the authors conclude that striped bass predation is probably not sufficient (2-5%) to significantly influence juvenile blue crab population dynamics in seagrass habitats (van Montfrans et al. 2005). Additional studies indicate that striped bass predation on juvenile blue crabs is habitat-specific and restricted largely to seagrass beds; stomachs of striped bass captured in the open waters of the Bay mainstem rarely contain blue crabs (Bonzek et al. 2007). The importance of predation by striped bass also varies spatially with significantly higher predation in the lower Bay relative to the upper Bay (Booth and Gary 1993). To date, collective evidence suggests that the recovery of striped bass in Chesapeake Bay has not substantially increased mortality of blue crabs. However, striped bass are clearly predators on blue crabs, and further declines of alternative prey (e.g., Atlantic menhaden) or alterations in habitat abundance or quality (e.g., loss of seagrass) may have the potential to alter the strength of trophic interactions between these species in the future.

The abundance of large predatory sharks in coastal ecosystems has declined dramatically as a result of overfishing (Myers et al. 2007). Predatory release of smaller elasmobranch prey species such as the cownose ray, *Rhinoptera bonasus*, has allowed populations to explode with cascading effects on an array of bivalve prey species on which the rays feed. The dramatic increase in ray populations could have both direct predatory and indirect competitive effects on blue crab foodweb dynamics. Cownose rays are known to prey on blue crabs, although crabs comprise only a small portion of their diet. However, given the magnitude of the increase in ray populations in Chesapeake Bay, these impacts could be significant. Cownose rays are also voracious predators of bay scallops, hard clams, soft-shell clams and oysters capable of extirpating bivalve populations at local scales (Smith and Merriner 1985; Blaylock 1993;

Petersen et al. 2001). Bivalves are also the dominant prey for adult blue crabs (Laughlin 1982; Hines et al. 1990; Mansour 1992; see Prey issue brief, this section). The considerable overlap in diet indicates a high potential for negative trophic interactions through competition between these species where they co-occur. Competitive interactions with blue crabs are likely to be higher in the mesohaline regions of Chesapeake Bay where cownose rays are more abundant (Blaylock 1993). In addition to direct competition for prey resources, foraging by cownose rays for infaunal bivalves within submerged aquatic vegetation can uproot and destroy important seagrass nurseries for juvenile crabs (Orth 1975).

There is ongoing controversy regarding the relative importance of finfish predation in regulating Chesapeake blue crab populations (Hines 2007). Thus, the importance of fishery exploitation on foodweb interactions is also uncertain. However, it should be noted that the impacts of finfish exploitation and predation are complex and not well understood, and are likely to vary substantially both spatially and temporally in Chesapeake Bay.

Oysters

Similar to coral reefs in tropical waters, oyster reefs serve as important structured habitat for fish and crustaceans in temperate estuaries. Further, oyster reefs are an important component of the foodweb in coastal ecosystems. The combined effects of harvest, pollution and disease have reduced the once plentiful oyster populations in Chesapeake Bay to only 1% of historic levels with potential consequences on foodweb dynamics for blue crabs. Blue crabs are known predators on oyster juveniles (Laughlin 1982; Eggleston 1990a, 1990b, 1990c; Micheli and Petersen 1999). Despite strong evidence that blue crabs forage on juvenile oysters, the strength of prey-predator interactions between these species is uncertain. Nevertheless, the major decline in the abundance of oysters in the Bay may have a direct impact on crab populations by reducing the availability of oyster prey.

Facilitation by Epibenthic Predators

Blue crab foraging efficiency on infaunal bivalve prey in soft-bottom communities is affected indirectly by the presence of other epibenthic predators. Siphon nipping by fishes and decapod crustaceans facilitates enhanced blue crab foraging by forcing clams to reduce burial depths where they then become vulnerable to predatory blue crabs (Hines et al. 1990; Hines and Lipcius, unpublished data). Of the numerous finfish that actively consume clam siphons, summer flounder, spot and Atlantic croaker support commercial and recreational fisheries in Chesapeake Bay (CBFEAP 2006). Thus, the abundance of these species may directly enhance prey acquisition, and potentially growth, for blue crabs. While facilitation of blue crab foraging as a result of siphon nipping has been documented at local scales, whether or not this relationship is important to overall population dynamics in Chesapeake Bay is not known.

Cannibalism

Cannibalism is a major source of mortality for blue crabs in Chesapeake Bay (Hines 2007; see Cannibalism issue brief, this section), and thus fishery removals of large predatory adult crabs has direct implications for population dynamics. The important role of cannibalism in blue crab population dynamics is supported by direct evidence from the analysis of stomach contents

(Laughlin 1982; Hines et al. 1990; Mansour 1992), empirical experimental studies (Hines and Ruiz 1995; Pile et al. 1996; Moksnes et al. 1997; Moody 2001, 2003; Lipcius et al. 2005) and indirect inference from the analysis of long-term fishery-independent survey data (Tang 1985; Lipcius and Van Engel 1990; Hines et al., unpublished data). The overall impact of cannibalism on population dynamics is complex and varies by habitat, life-stage, and is both spatially and temporally variable within the Bay.

Although inter-cohort cannibalism by large crabs on juveniles and both inter- and intra-cohort cannibalism following molting appears to be common in all life stages (Ryer et al. 1997), the density-dependent effects of cannibalism appear to be restricted principally to megalopae and early juvenile instars (Pile et al. 1996; Moksnes et al. 1997). Analysis of stock-recruit dynamics in Chesapeake Bay indicates a non-linear relationship (e.g., Ricker stock-recruitment model; Ricker 1954) between spawning stock abundance and subsequent recruitment (Tang 1985; Uphoff 1998; Lipcius and Van Engel 1990; Lipcius and Stockhausen 2002) indicating a strong density-dependent mechanism operating during early life history. While other density-dependent processes are likely co-occuring, compensatory mortality due to cannibalism has been identified as the most likely mechanism to explain the observed pattern (Lipcius and Van Engel 1990; Kahn et al. 1998; Eggleston et al. 2004). Losses due to cannibalism during early life stages may be partially mitigated by density-dependent secondary dispersal from initial settlement habitats at high densities (Etherington and Eggleston 2003; Reyns and Eggleston 2004, 2006), and may serve to reduce intra-cohort competition and mortality. Evidence for density-dependent emigration comes from studies conducted in seagrass beds in North Carolina, thus, the importance of this process in Chesapeake Bay is not known. Seagrass defoliation in the lower Bay may serve to exacerbate density-dependent cannibalism effects for early instars both by increasing absolute mortality as crabs shift to alternative nursery habitats, and through alterations of the cannibal-prey functional response (Moksnes et al. 1997).

The likely effect of intense fishing pressure on the blue crab stock in Chesapeake Bay is decreased per capita natural mortality as a result of compensatory mechanisms. At the current low levels of juvenile and adult abundance (CBSAC 2008), the impact of density-dependent growth and mortality due to competition and cannibalism is probably reduced. However, density-dependent mechanisms will become increasingly important to population dynamics as the population increases, and potentially as key primary settlement habitats (e.g., seagrass) decline in abundance. Although a detailed understanding of the strength of compensatory processes in this species remains largely unknown; cannibalism is likely to play an important role in population regulation.

Indicators

Blue crabs are a central component of the complex Chesapeake foodweb serving as both predators and prey. The relative abundance of key finfish predators and both adult and juvenile blue crab cannibals are key indicators. These metrics are available from fishery-independent surveys currently conducted in Chesapeake Bay. Spatially explicit measures of large blue crab abundance (CW > 60) are available from the winter dredge survey. The winter dredge survey does not provide an accurate index of relative abundance for small juvenile crabs (CW < 30mm); because sampling is not conducted in shallow nurseries and gear efficiency for small crabs in not known. A coordinated survey in Maryland and Virginia targeting juvenile blue crabs would be helpful and provide an important Baywide index of recruitment. The Chesapeake Bay Multi-species Monitoring and Assessment Program (ChesMMAP) trawl survey provides relative abundance of finfish predators and was designed to support multispecies management efforts.

Summary

- Fishery exploitation is likely to result in significant impacts for blue crab trophic dynamics due to this species' central role in the foodweb and importance as a key predator and prey in Chesapeake Bay.

- Fishery removals directly impact rates of cannibalism and are likely to play an important role in population regulation.

- The relative impacts of fishery removals on finfish predation and cannibalism are not well understood and are likely to vary substantially both spatially and temporally in Chesapeake Bay.

Invasive Species

Anson H. Hines and Jacques van Montfrans

Introduction

Many invasive species pose a threat to endemic fauna and flora throughout the world. Only rarely do invasive species provide a benefit for native species. The blue crab is affected by numerous non-native introductions in the Chesapeake Bay. Some have a direct influence while others indirectly affect the blue crab population.

Fish Predators

Blue catfish are endemic to the Mississippi River drainage system. They were introduced into the tidal waters of the James and Rappahannock Rivers in the early 1970's. In 1985 several blue catfish were also introduced into the Mattaponi River. Those fish eventually also colonized the Pamunkey River. The Piankatank River and Potomac River have also been colonized so that now, blue catfish occur in all of Virginia's major tributaries of the Chesapeake Bay (Greenlee 2009). In many regions of tributaries, they dominate the total fish biomass.

Reproductive maturity occurs at ~ 6 years when fish attain a size of ~ 17 inches and weigh less than 5 lbs. By the time individuals are 11 – 14 years of age, they can weigh 50 lbs or more. Blue catfish from the Rappahannock River grow more slowly and do not generally reach 20 lbs until age 14. Blue catfish populations in the James River have exploded to the extent that they currently constitute up to 75 percent of all fish biomass in certain sections of the river according to Virginia Commonwealth University scientist, Greg Garman.

A primary reason for these introductions was to develop a recreational trophy fishery for blue catfish. The current (05-20-2009) state record blue catfish in Virginia weighed in at 102 pounds, 4 ounces, and measured 52-3/4 inches in length with a girth of 41-1/2 inches and was caught in the James River. This world class fishery attracts numerous recreational anglers form the Commonwealth and neighboring states. The Virginia Department of Game and Inland Fisheries has strongly promoted the recreationally fishery, partially because it receives revenues generated from the sale of freshwater fishing licenses.

There is also a small commercial fishery for blue catfish in Virginia that exploits approximately 1.5 million pounds annually. The commercial fishery has a maximum size restriction of 32 inches in an attempt to protect the trophy recreational fishery and to comply with the consumption advisory on this species (no consumption of fish over 32 " from the James River; 1 meal per month of blue catfish caught from other tributaries).

Little is known about the impact of this species on local fauna but the potential for significant impacts are likely great. Blue catfish are voracious predators and consume long-established endemic species such as white catfish and channel catfish. They also prey upon other fishes and will eat almost anything including muskrats, crabs, herons and other blue catfish. Since blue catfish tolerate salinities down to ~ 15 ppt, they also may impact blue crab where the two populations overlap.

Overall, there is little published information regarding catfish predation impacts on blue crabs. VIMS trawl survey data indicate that few blue crabs are consumed in deeper waters where trawl sampling occurs. Impacts on crabs in shallow water are poorly understood. Shallow water typically harbors high densities of small crabs and, crabs seek shallow water shelters for molting. Furthermore, commercial hard and soft crabbers constantly complain that blue catfish enter their pots in large numbers and consume a portion of their blue crab catch. There is a strong need to scientifically investigate the impact of blue catfish on blue crabs in the wild and on the economic impact of predation that occurs within crab pots.

Habitat

Pragmites australis is an invasive species of emergent marsh vegetation that has displaced native marsh grass across vast areas of the Chesapeake Bay watershed. It continues to spread at alarming rates and is exceedingly dense and highly productive. Variably high densities of juvenile blue crabs (up to 13 crabs m^{-2}) are sustained by salt marshes and marsh creeks in Chesapeake Bay (Orth and van Montfrans 1987; Lipcius et al. 2005; Seitz et al. 2005).

Consequences of *P. australis* invasions for blue crabs in Chesapeake Bay are poorly understood. In New Jersey, blue crab use of emergent vegetation was affected by vegetation type with native *Spartina alterniflora* preferred by crabs over the invasive *P. australis* (Jivoff and Able 2003). Densities of juvenile (5-10 mm CW) blue crabs in the Hudson River estuary salt marshes dominated by this invasive reed averaged 0.06 to 0.39 crabs m^{-2} in summer (Hanson et al. 2002). Up-estuary habitats associated with, and adjacent to, salt marshes may be as important as seagrasses for blue crab nursery habitat because of high food availability and lower predation levels (Seitz et al. 2003a; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Thus, the disruption or alteration of marsh shoreline by invasive *P. australis* may well be detrimental to the overall abundance of blue crabs in Chesapeake Bay.

Gracilaria vermiculophylla is a non-indigenous macroalga native to eastern Asia (Ohmi 1956, Bellorin et al. 2004). This species has been introduced into Chesapeake Bay and now occurs widely in lower Bay tributaries. Preliminary studies indicate *Gracilaria* may serve as alternative nursery habitat for juvenile blue crabs (Mahalak 2008, Johnston and Lipcius, unpublished). Further studies of the nursery value of this species for juvenile blue crabs indicate that survival is enhanced in *Gracilaria* habitats, but the survival benefit was a function of both crab and algal patch size (Falls 2008). Currently, the overall importance of *Gracilaria* is unknown because the spatial and temporal variation in the abundance this species in Chesapeake Bay has not been quantitatively evaluated.

Competitor Crab Species

The eastern mid-Atlantic coast is the site of multiple invasions from three predatory crab species: European green crab (*Carcinus maenas*), Japanese shore crab (*Hemigrapsus sanguineus*), and Chinese mitten crab (*Eriocheir sinensis*). All of these invasive crabs are highly effective predators in nearshore coastal habitats and can have substantial negative impacts for important bivalve and crustacean fisheries. Invasive crabs impact native blue crab populations as predators (Grosholz et al. 2000) or through competition for prey resources and refuge habitat (McDonald et al. 2001, MacDonald et al. 2007).

The invasive European green crab, introduced into Chesapeake Bay not long ago, might be limited in geographic distribution by blue crabs because of their larger size and aggressiveness (de Rivera et al. 2005). Although green crabs extend to lower, warmer latitudes within their native range in the eastern Atlantic, the southern limit of the invasive green crab population along the northwestern Atlantic occurs between Delaware and Chesapeake Bays, where blue crab abundance increases markedly. Moreover, the abundance of green crabs is inversely related to blue crab abundance within bays in the region of overlap of the two species between Cape Cod and Chesapeake Bay (de Rivera et al. 2005). At sites spanning the geographic overlap, mortality of green crabs tethered increased in correlation with abundance of blue crabs, and carapace remains of tethered crabs were indicative of blue crab predation. Tidal amplitude drops dramatically in the vicinity of Chesapeake Bay, which greatly diminishes the intertidal zone that appears to afford green crabs refuge from subtidal blue crab predation.

The Asian shore crab has invaded the coastal bays and spread along the mid-Atlantic region over the past 15+ years. This species inhabits the intertidal zone and may serve as prey for blue crabs on high tides.

The Chinese mitten crab has been introduced into Chesapeake Bay and other mid-Atlantic estuaries during the past ~4-5 years, although recorded numbers are low. Mitten crabs were reported in Chesapeake Bay for the first time in 2005, reproductive females in 2007, and new records indicate their presence in Delaware Bay and the Hudson River estuary (Ruiz et al. 2006). Most reports come from adult mitten crabs caught in blue crab pots by commercial fishermen. In 2008, 100+ juveniles were reported in the Hudson River, and in 2009 approximately 50 mitten crabs were reported in Ruratan Bay, New Jersey. Sexually mature males and ovigerous females have been documented in Chesapeake Bay as well as New Jersey. Most of the mitten crab life cycle occurs in freshwater, well beyond the range of blue crabs. However, adults migrate to brackish salinities of the mid-estuary to mate, spawn and hatch eggs. Larval development occurs in the estuary, and juveniles migrate up into freshwater tributaries to grow to maturity. Mitten crabs are omnivores and may compete for food with blue crabs. Depending on size, blue crabs may be able to prey upon mitten crabs.

Prey Species

Blue crabs appear to limit abundances of certain invasive species. Experiments indicate that predation by large blue crabs may limit abundances of young rapa whelks *Rapana venosa*, a species which has been recently introduced in lower Chesapeake Bay (Harding 2003), although the rapa whelk appears to be well-established as an invasive species within areas of abundant crabs (Mann and Harding 2000).

Blue crab predation is predicted to limit the down-stream spread of invasive zebra mussels, *Dreissena polymorpha*, in the Hudson River estuary (Boles and Lipcius 1997). Interactions within Chesapeake Bay tributaries may similarly limit the spread of zebra mussles should this species invade the Chesapeake Bay watershed.

Disease

Currently, there are no known introduced diseases that infect blue crabs in the Chesapeake region (see Disease issue brief, this section). Although White Spot Syndrome Virus has been reported from the blue crabs (Chang et al. 2001), the validity of the primer set has been questioned (Chapman et al. 2004) Research on the Yellow Head Virus (YHV) has shown that the blue crab would be a poor host, and this virus is unlikely to have significant impacts.

Disease Impacts on Predators and Prey

Gretchen A. Messick, Eric Schott, and Jeffrey D. Shields

Disease in Predators

Numerous animals prey upon blue crabs with their impacts varying greatly by species (Guillory and Elliot 2001; Hines 2007; see Predation issue brief, this section). Thus, the impacts of disease on these predator species have the potential to impact predator-prey dynamics in Chesapeake Bay.

Striped Bass (Morone saxatilis)

Striped bass are currently experiencing an epizootic of mycobacteriosis in Chesapeake Bay (Kane et al. 2007), with prevalence of 25% to 80%. There is insufficient data to determine whether mycobacteriosis has increased natural mortality on the striped bass stock in the Chesapeake Bay. Striped bass are also prone to external lesions called Ulcerative Dermatitis Syndrome (UDS). Under most circumstances, the fish's immune system wards off infection, but stressors such as poor water quality, excessive handling, or poor nutritional health may reduce the fish's ability to counteract invading pathogens. A comprehensive review of infectious and noninfectious diseases and parasites of striped bass is provided by Mitchell (Mitchell 1984; Paperna and Zwerner 1976; Gauthier et al. 2009**)**

Atlantic Croaker (Micropogonias undulatus)

Although there is no documentation of the susceptibility of croaker to various disease-causing organisms, several related species, in particular red drum, are known to suffer heavy mortalities due to pathogens during larval and juvenile stages. The most common pathogen impacting red drum culture is the parasitic dinoflagellate *Amyloodinium ocellatus.* This organism attacks the gills of red drum resulting in reduced oxygen uptake by the fish. Fish are generally less susceptible to *Amyloodinium ocellatus* at salinities below 6 ppt (Gatlin 2000). To date, over 90 parasites and/or diseases have been identified from the croaker (Etzold and Christmas 1979). The effects of these parasites and diseases on the survival and growth of croakers are not yet known.

Weakfish (Cynoscion regalis)

Weakfish are susceptible to pollution-induced disease such as fin rot. While pollution can affect weakfish populations, the fish are able to recover quickly when the pollution source is removed (Mercer 1989). Linten (1905) described 14 parasites of weakfish from North Carolina, including the cestodes *Scolex polymorphous, Rhinobothrium* sp., *Rhynchobothrium spedosum, Otobothrium crenacolle, Tetrarhynchus bisulcatus,* and *Symbothrium* sp.; trematodes *Distomum* *vitellosum, Distomum polyorchis,* and *Microcotyle* sp.; acanthocephalan *Echinorhynchus pristis;* and nematodes, *Ascaris* sp.

Spot (Leiostomus xanthurus)

Parasites of spot include copepods of the genera *Lernaeenicus* and *Ergasilus*, as well as a marine leech, *Myzobdella lugubris* (Sawyer et al. 1975). Internal parasites include trematodes, microsporideans, and acanthocephalans (Govoni 1983; Sprague and Hussey 1980).

Northern Puffer (Sphoeroides maculatus)

Heavy infections of *Trichodina spheroidesi* and *Trichodina halli* were associated with large areas of denuded gill filaments, which caused deaths of northern puffers on the New Jersey coast of the USA in the early 1940s (Padnos and Nigrelli 1942).

American Eel (Anguilla anguilla)

An Asian parasite likely introduced in aquaculture has spread rapidly in American eels in the past few years. This worm infests the eel's swim bladder. While it may not be a problem in shallow water, once the eels mature and begin their long return swim to the Sargasso, a non-functioning or even somewhat impaired swim bladder could doom eels to dying in the open ocean. Biologists simply do not know the extent of this parasite's damage to the American eel population.(http://www.fws.gov/northeast/AmEel/facts.html; Barse et al. 2001).

Disease in Prey

Blue crabs feed on at least 99 species from various phyla (see Prey issue brief, this section). Zooplankton in the size range of 45-80 microns is probably among the chief sources of food organisms for blue crab larvae, especially in the early stages (Costlow and Bookhout 1959; Sulkin and Epifanio 1975). In larger crabs, molluscs typically take up 20-40% of stomach content, arthropods 10-26%, chordates, (fishes) 5-12% and annelids (polychaetes) 1-7% (Hines 2007). In Chesapeake Bay the diet of blue crabs was described as consisting of about 60% bivalve mollusks, with the remainder comprised of polychaetes, amphipods, dead fish, and juvenile blue crabs (Baird and Ulanowicz 1989; Darnell 1958; Nelson 1981; Paul 1981; Tagatz 1968a). Since mollusks are the dominant prey of juvenile and adult blue crab (Eggleston et al. 1992; Hines et al. 1990; Laughlin 1982; Mansour 1992; Meise and Stehlik 2003) we focus the discussion of diseases on them. An excellent resource for diseases in mollusks is the extensive worldwide synopsis of shellfish diseases of commercially important molluscs, echinoderms and crustaceans provided by Bower & McGladdery (Bower 2007; Bower and McGladdery 1997). Additional volumes include Kinne (1983-1990) and Sparks (1985).

Eastern Oyster (Crassostrea virginica)

Two single-celled oyster parasites, *Haplosporidium nelsoni*, which causes MSX, and *Perkinsus marinus*, which causes Dermo, are currently major sources of oyster mortality in the Bay. While MSX and Dermo are not harmful to humans, they can kill more than 90 percent of exposed oysters within two to three years.

MSX can affect oysters of all ages. Once an oyster is infected, MSX develops rapidly and kills the oyster within several weeks. *H. nelsoni* thrives in warm, high-salinity waters, which is why MSX is restricted to the middle and lower Chesapeake Bay. MSX-resistant populations have begun to evolve in oysters in both Chesapeake and Delaware bays, raising hope for the long-term oyster restoration potential.

Discovered in the Bay in 1949, Dermo is a parasitic disease that, like *H. nelsoni*, spreads quickly in warm, high-salinity waters. Since the mid-1980s, drought, above average winter temperatures, and poor management practices have caused *P. marinus* to spread to the upper Bay and tributaries. Because of its increased range and tolerance of lower salinities, Dermo is more damaging than MSX to oyster populations throughout the Bay. (http://www.chesapeakebay.net/oysterdiseases.aspx?menuitem=19507; Galstoff 1964; Mackin et al. 1950).

Additional diseases of oysters include *Haplosporidian costale* (seaside organism) in high salinity waters (Andrews et al. 1962; Wood and Andrews 1962), and a trematode *Bucephalus haimaenus* found oysters from brackish waters. Gonads and digestive diverticula can be almost completely replaced by trematode cercariae, affecting reproduction but [not] causing mortality (Galstoff 1964).

Softshell Clam (*Mya arenaria*)

The soft shell clam, *Mya arenaria* can be infected with at least two species of *Perkinsus* (*P. marinus* and *P. chesapeaki*) (Kotob et al. 1999; McLaughlin et al. 2000; McLaughlin and Faisal 2000; McLaughlin et al. 2000). The sometimes massive aggregation of *Perkinsus* sp. and hemocytes form lesions that may interfere with respiration, reproduction, growth and/or survival thus having an impact on fishery productivity.

A disseminated neoplasia affects soft shell clams, causing proliferative cells to fill vascular spaces, blocking hemolymph flow, compressing adjacent organs, and killing the clam. The cause is unknown, but is possibly of viral etiology. In Chesapeake Bay, highest prevalence occurs over fall and winter and individuals with severe disease tend to die during winter and in early spring (Farley 1976; Farley et al. 1986; Farley et al. 1991; Sunila 2003).

Additional parasites that infect *Mya arenaria* include a virus that causes proliferative disorder (Bower 2002; Harshbarger et al. 1979), a microsporidian (Bower et al. 1994; Farley 1977), *Rickettsia*-like and *Chlamydia*-like organisms (Bower 2004; Harshbarger et al. 1977) and a gonadal neoplasia (Bower 2006). The effect of these conditions on *Mya arenaria* populations is not known.

Miscellaneous Clams

Macoma balthica, the Baltic or macoma clam, is reported to be infected by *Perkinsus chesapeaki* in Chesapeake Bay (Reece et al. 2008), as well as by epizootic neoplasm (Christensen et al. 1974). *Mercenaria mercenaria,* Atlantic hardshell clam or quahog, is affected by QPX. Although QPX has not had a significant impact on Virginia's hard clam fishery and aquaculture industry, the pathogen has been detected in three of the state's most productive hard clam grow out areas (Ragone-Calvo et al. 1998). Additionally, using histology and/or PCR, evidence of *Perkinsus chesapeaki* has been found in quahog clams, as well as in *Mulinia lateralis* dwarf surf clam, *Tagelus plebeius* stout razor clam, *Rangia cuneata*, and *Cyrtopleura costata* Angel wings: *Perkinsus chesapeaki* found in with PCR in Chesapeake Bay (Reece et al. 2008).

Issues

- There is little to no data on actual or hypothetical reduction or increase in numbers of blue crabs in Chesapeake Bay due to parasitism in either predators or prey.

- The extremely varied diet of blue crab makes it difficult to predict what the effects of a disease in a specific prey species will be. A dramatic reduction in a major prey abundance, such as the oyster or soft clam, may lead to a major shift in the blue crab diet.

- Virtually nothing is known about disease in other major prey categories such as polycheate worms.

- The fact that large blue crabs are the dominant predator of juvenile blue crabs (Hines and Ruiz 1995) may have significant effects on blue crab disease transmission.

Summary

- There are numerous pathogens and parasites found in both blue crab predators and prey. Some are known to cause significant mortalities whereas others pose no known threat.

- Parasitism in blue crab predators and prey likely impacts blue crab populations in Chesapeake Bay but very little information is available on effects.

- Assays for disease or parasitism in blue crab populations have traditionally been through histological investigation. Molecular assays are being developed but these assays indicate the presence of a parasite, not the parasite's effect on host or population. Cannibalism is a major source of mortality for blue crabs in Chesapeake Bay.

- The relative impacts of pathology and parasitism in predators and prey of blue crabs in are not well understood and are likely to vary substantially both spatially and temporally in Chesapeake Bay.

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STOCK ASSESSMENT

Blue Crab Stock Assessment

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Population Dynamics

The blue crab exhibits highly variable population dynamics. If we use commercial landings as a surrogate for population abundance, landings data for Atlantic coastal states for 1950-2008 (Figure 1) yield coefficients of variation that average 54.0% (range 27.7-120.3%). Such complex population dynamics are common in crustaceans (e.g., Higgins et al. 1997). A range of factors likely contribute to the level of variability exhibited by the blue crab and by other crustaceans. The life history of many crabs is complex (Wilbur 1980) in that different life stages occupy different habitats. This can introduce complex patterns of connectivity among these different spatial regions that can alone introduce complexity into the population dynamics of such populations (Gilpin and Hanski 1991). Like many other marine invertebrates, crabs are highly fecund, to compensate for highly variable survival during early life history. Stochasticity in early survival introduces a high degree of variability into annual recruitments. Once a cohort has recruited to the adult population, it is exposed to a range of sources of mortality, including disease, cannibalism, predation and harvest. Variability in each of these factors introduces variability into the overall dynamics of the population. Finally, like many coastal taxa, the blue crab population is likely influenced by environmental factors such as temperature (Bauer and Miller in press-a).

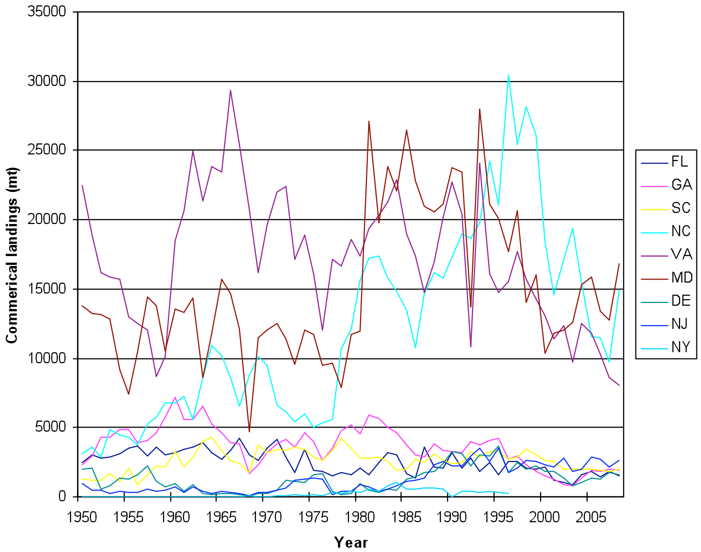

Figure. 1. Time series of commercial landings of blue crab in Atlantic states as a surrogate for abundance. Note that although landings in individual states exhibit different trends (likely related to market forces), each time series is highly variable reflecting the complex nature of crab dynamics.

Here, we review factors that influence the dynamics of blue crab in Chesapeake Bay. We focus on factors that would be of high relevance to development of ecosystem-based approaches to fisheries management in the Chesapeake Bay. All the authors listed on page B/4-1 contributed to the papers in the Blue Crab Stock Assessment section of this report.

Patterns and Processes

Population Connectivity

The traditional approach to population dynamics emphasized single, closed populations in which the vital rates within the population may be age-, size-, stage- or time-dependent (Miller 2001b). However, the complex life history of blue crab (Figure 2), in which different life stages occupy different habitats that may be spatially separated, means that a simple aggregate representation of blue crab population dynamics is likely to be insufficient (Miller 2003). Levins (1970) first utilized the term 'meta-population' to account for this patchiness. A metapopulation consists of many local populations ("subpopulations"). In Levins' original concept, the subpopulations may or may not be connected to each other. Each subpopulation had a finite risk of going extinct, but could be recolonized by immigrants from other viable subpopulations. In this formulation, subpopulations could remain extant over long periods of time because of the pattern of connectivity they shared with other subpopulations. Levins' original concept has been extended beyond a simple presence / absence categorization to consider population dynamics, population genetics and evolutionary processes (Gilpin and Hanski 1991; Hanski and Gilpin 1997). Within marine ecosystems, connectivity between populations can occur either via migration or larval dispersal.

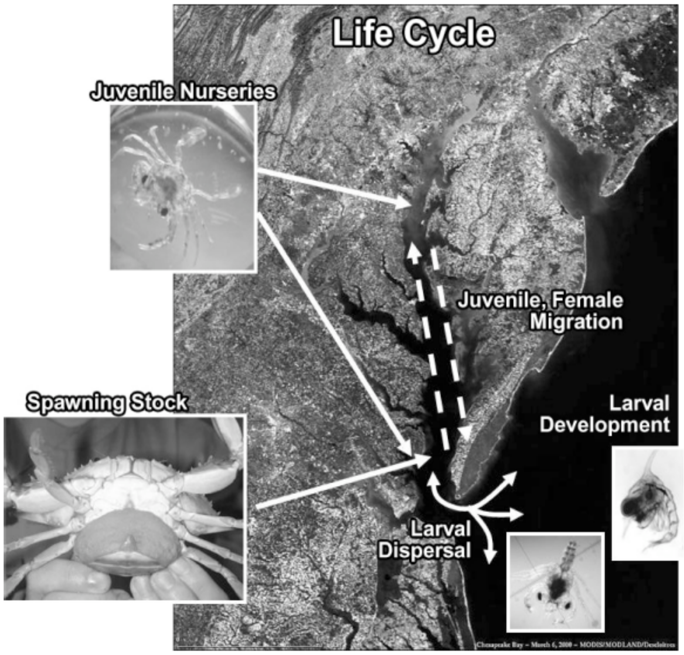

Figure 2. Complex migratory life cycle for the blue crab (Callinectes sapidus) in Chesapeake Bay, showing the distribution of key life stages among ecosystems distributed along the salinity and offshore gradients. (Reprinted from Hines et al. 2008b.)

As habitat patches vary in type, quality, and spatial arrangement, individuals may reside in individual habitats that may be categorized as either 'source' or 'sink' habitats (Lipcius et al. 2005; Lipcius et al. 1997). It is important to distinguish between the classical definition of sources and sinks that relate to the origins and destinations of dispersal (Cowen et al. 2000; Cowen et al. 2006) and a population dynamic definition of source-sink dynamics, which emphasizes habitat quality and its effects on demographic rates (Pulliam 1988).

Adult and juvenile blue crabs are estuarine dependent, but the zoea (larvae) require warmer, saltier water in which to develop (Costlow and Bookhout 1959; Epifanio 2007). It is the megalopa (last larval stage) that reinvades the estuaries to connect these two habitats and population stages (Epifanio 2007). Once in the estuary, post-larval dispersal ensures that a wide range of habitats within the estuary are utilized (Lipcius et al. 2007). Here we identify two scales of population connectivity: regional - which considers the potential for connectivity among the estuaries along the Atlantic coast of North America; and local – which considers the potential for connectivity among habitats within the Chesapeake Bay.

Regional Connectivity

Large populations of blue crab occur in Delaware Bay, Chesapeake Bay, and Pamlico Sound, N.C., with smaller populations from New York to Texas. Connectivity between coastal and estuarine populations appears to be strong, as suggested by two episodes of relatively quick recolonizations of coastal habitats after population collapses due to disease in Georgia and seaside Virginia habitats. However, connectivity between estuaries is believed to be relatively weak. McMillen-Jackson and colleagues (McMillen-Jackson and Bert 2004; McMillen-Jackson et al. 1994) found clinal variation along the Atlantic coast, suggesting that local gene flow may be low or restricted. More recently, scientists at the Center for Marine Biotechnology have succeeded in developing genetic techniques to distinguish crabs from the Chesapeake from those from North Carolina (A. Place, COMB, pers. comm.). Thus, while there is no definitive evidence of genetic structuring indicative of separate populations, there is clear evidence of localized populations that experience limited gene flow between them. Supporting this genetic evidence, oceanographic sampling of zoea, and coupled physical-biological models suggest that larvae are retained near natal estuaries by northward flowing water during the late summer when zoea larvae are most common (Epifanio et al. 1989; Johnson and Hess 1990; Johnson 1995). Tagging studies suggest that there is little adult migration between estuaries (Fischler 1965; Judy and Dudley 1970; Schwartz 1997). Collectively, the genetic and inter-population connectivity data indicate that populations in each of the major estuaries along the Atlantic coast can be treated as distinct populations with minor larval exchange. The current precautionary management approach that considers the blue crab stock in Chesapeake Bay as a distinct population is therefore warranted (Fogarty and Lipcius 2007; Miller et al. 2005).

Local Connectivity

Traditionally, the population of blue crabs within the Chesapeake Bay is considered well-mixed. The mixing of larvae that occurs during the oceanic phase of the life history likely ensures that the Chesapeake Bay population does not exhibit within-Bay genetic structure. However the pattern of dispersal of post larvae within the bay (Lipcius et al. 2007) may lay the foundation for spatial population structure within the Bay (Miller 2003). Juveniles usually remain within the primary nursery habitat until they are about 20–30 mm in carapace width, though there is some evidence of density-dependent dispersal from primary nursery habitats. Secondary dispersal occurs around the 7th to 9th instar, at which time the juveniles have reached a relative size refuge from predation (Lipcius et al. 2007). By late fall and early the following spring, juveniles disperse from higher salinity settlement habitats to lower salinity habitats (Hines et al. 1990; Hines et al. 1987). Once this secondary dispersal has occurred, tagging studies indicate that there is relatively little movement until the reproductive migration in the late fall and winter. The importance of this local connectivity to the overall population dynamics has received little attention. However, it will be extremely pertinent if spatial approaches to management are adopted within an ecosystem-based framework.

Recruitment Variability

Initial recruitment of blue crab in Chesapeake Bay occurs, primarily in late summer and fall (August-November) as megalopae reinvade the estuary. Recruitment in Chesapeake Bay has most commonly been evaluated using data collected during standardized trawl and seine surveys that quantify the relative abundance of juveniles. Historically, blue crab recruitment in these surveys has exhibited a large degree of inter-annual variability with the magnitude of recruitment varying between 5- and 40- fold (Figure 3A-C) among years depending on the recruitment index. However, of particular concern is that juvenile recruitments in recent years have remained consistently low, potentially resulting from severe declines in the reproductive spawning stock size during this same period (Lipcius and Stockhausen 2002).

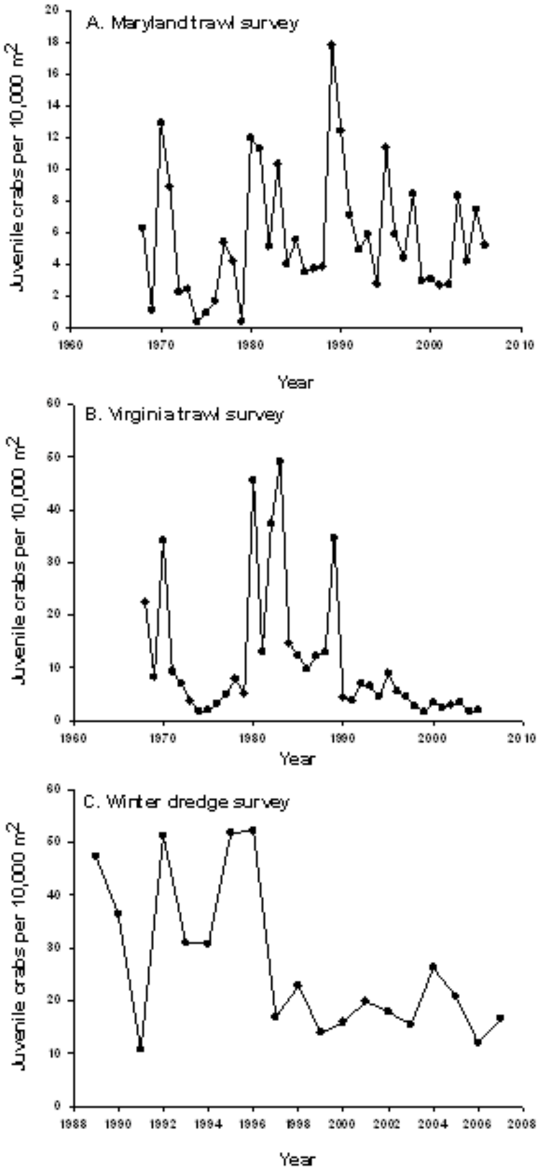

Figure 3. Annual indices of juvenile blue crab recruitment from three fishery-independent surveys in Chesapeake Bay.

Stock and Recruitment

Recruitment connects one generation to the next. Thus, the relationship between spawning stock abundance and subsequent recruitment is a fundamental issue in fisheries management. In Chesapeake Bay, the relationship between the abundance of mature spawning females and recruitment at various life history stages has been a focus of considerable research (Fogarty and Lipcius 2007; Lipcius and Stockhausen 2002; Lipcius and Van Engel 1990; Miller and Houde 1999; Tang 1985; Uphoff 1998). Collective evidence from studies in Chesapeake Bay and other estuarine systems (Eggleston et al. 2004; Kahn 2003; Wong 2008) reveals several consistent trends related to blue crab stock-recruit relation ships in estuaries of the Atlantic Coast: (i) a generally positive relationship between stock and recruitment when stock size is low, (ii) density-dependent compensatory mortality at high stock sizes (e.g., a Ricker 1954 type stock recruitment relationship), and (iii) high variability consistent with the importance of density-independent environmental processes. Although stock-recruit functions are characterized by high variability limiting their predictive capability, the probability of experiencing above average recruitment is increased when spawning stock abundance is also above average, and conversely, low spawner abundance increases the probability of poor recruitment in a given year (Miller and Houde 1999).

Density-dependent regulation appears to be most important for blue crab populations in Chesapeake Bay during the early post-settlement juvenile stages. Compensatory mortality in these early juvenile stages may be primarily driven by cannibalism (Hines and Ruiz 1995; Pile et al. 1996). Although cannibalism continues to be a major source of mortality for larger juveniles and adults, density-dependent impacts of cannibalism appear to be less important for these life stages (Lipcius et al. 2007).

At high levels of spawner abundance, the blue crab population in Chesapeake Bay may be regulated by a combination of density-independent environmental forces which determine initial settlement magnitude and density-dependent compensatory mortality during the early juvenile stages which regulate survival to the adult phase. However, at current low levels of spawner abundance, the Chesapeake Bay blue crab population is likely recruitment-limited. It is therefore of critical importance to maintain a sufficient abundance of adult spawning females to increase the probability of high recruitment.

Environmental Drivers of Recruitment

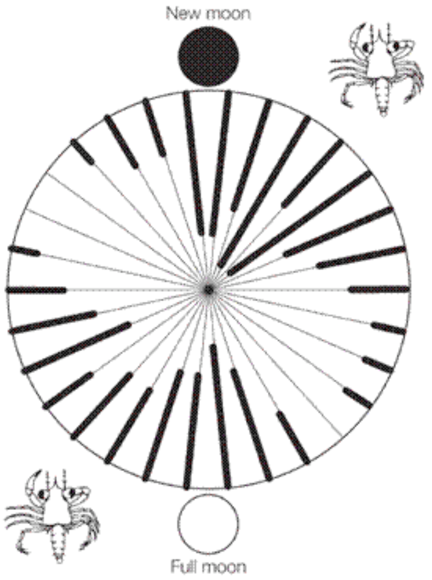

Figure 4. Semi-lunar periodicity in settlement of blue crab megalopae in Atlantic coast estuaries. The length of the solid bars indicated the cumulative number of settlement peaks at each stage of the lunar cycle from data for the Delaware Bay, Tangier Sound, York River, North Carolina and Charleston, SC. (Reprinted from Lipcius et al. 2007.)

Larval retention in coastal waters and postlarval settlement in Chesapeake Bay are facilitated by a complex interplay of seasonal physical oceanography and crab behavior. In the mid-Atlantic Bight, larvae are retained near the natal estuary by northward flowing surface currents induced by the prevailing south winds during summer (Epifanio 1995; Garvine et al. 1997; Johnson and Hess 1990; Johnson 1995; McConaugha 1988). Across-shelf transport of megalopae back to nearshore coastal waters likely results from the passage of frontal systems through the region. These systems induce southward (wind-driven) and westward (Ekman transport) flows that deliver megalopae from the shelf to coastal estuaries. Indeed, several authors have noted a correlation between episodic peak settlement events of megalopae in the Chesapeake Bay and southward blowing winds along the adjacent continental shelf (Epifanio et al. 1989; Garvine et al. 1997; Goodrich et al. 1989). Other studies have also found a semi-lunar periodicity in settlement, suggesting a tidal influence (Figure 4, Metcalf et al. 1995; Olmi et al. 1990; van Montfrans et al. 1995). Once in the vicinity of coastal estuaries, a suite of behavioral responses to salinity and other chemical cues promote estuarine ingress, up-estuary transport, and finally, settlement and metamorphosis of megalopae into appropriate primary nursery habitats (Brumbaugh and McConaugha 1995; Devries et al. 1994; Forward et al. 1995; Forward et al. 2003a; Forward et al. 2003b; Tankersley and Forward 1994; van Montfrans et al. 2003). The observed patterns of daily recruitment in Chesapeake Bay, characterized by consistent low levels, intermittent peaks of extremely high settlement (Figure 5, van Montfrans et al. 1995) and high inter-annual variability, are consistent with a strong dependence on stochastic environmental forcing.

Other environmental factors and stochastic events may also impact recruitment of blue crabs in Chesapeake Bay. Storm surges resulting from tropical cyclones can transport massive volumes of oceanic water into the Bay thereby enhancing recruitment directly through increased delivery of megalopae to primary settlement nurseries. Similarly, slow moving storms bringing heavy rainfall to the coastal watershed increase freshwater discharge from the Bay and can enhance two-layer circulation at the Bay mouth (Johnson and Hess 1990), potentially influencing postlarval transport into the estuary (Roman and Boicourt 1999). Minimum winter temperatures in the Bay are significantly correlated with low recruitment (Uphoff 1998); a finding consistent with studies of winter mortality demonstrating that small juveniles are particularly vulnerable to low water temperatures (Bauer and Miller in press-b; Rome et al. 2005).

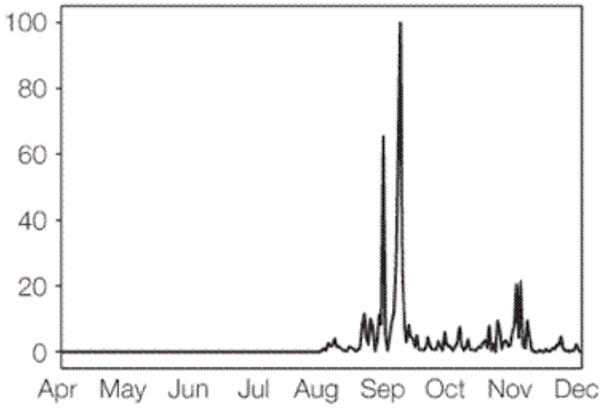

Figure 5. Representative settlement pattern of blue crab megalopae in the York River. (Modified with permission from Lipcius et al. 2007.)

Overall, stochastic environmental processes are major factors influencing inter-annual variation in the magnitude of recruitment to Chesapeake Bay and play a key role in overall population dynamics. The extent to which recruitment processes may be altered by global climate change, and the potential impacts on blue crab recruitment into Chesapeake Bay, are unknown.

Juvenile and Adult Mortality

As with other species, estimating the natural mortality rate (M) of blue crab has proved both difficult and controversial. Initial efforts to estimate M have focused on the whole life cycle. In particular, whole-life cycle Ms have been estimated for use in stock assessments. Rugolo et al. (1997) estimated M= 0.35 year^{-1} from its assumed relationship with the expected maximum age in the population. This approach has been criticized on both empirical grounds over the assumed maximum age and on theoretical grounds (Hewitt and Hoenig 2005). Since then several estimates of M have been published. Hewitt et al. (2007) used a meta-analysis of life history based and direct estimates of M, who considered M to range between 0.7 and 1.1. For the Delaware Bay stock, Helser and Kahn (1999) estimated M from an extrapolation of the regression of total mortality on fishing effort back to zero effort. However, the reliability of the estimates of length-based total mortality used in this study is unknown, because they assume constant growth, an assumption that is violated by the terminal molt of adult females (D. M. Kahn, pers. obs.). Kahn and Helser (2005) estimated M from the application of a catch-survey model and a catch equation, with annual estimates ranging between 0.2 and 2.00. The resulting annual estimates of M were significantly correlated with recruitment, substantiating findings in Kahn et al. (1998) that density-dependent mortality is a prominent feature of the Delaware Bay stock.

Whole life cycle estimates of M may not apply to all life stages and indeed may not apply to any single life stage. Life stage specific estimates of M have been published. Miller (2001b) used size-spectrum theory to estimate M for early life stage blue crabs for a matrix projection model of blue crabs in Chesapeake Bay. For finfish, size-based approaches have been developed to estimate the pattern of M over the life cycle (Lorenzen 1996), although this approach has not been applied to crustaceans. Empirical estimates of M are available for specific stages. Lambert et al. (2006) used a mark-recapture approach involving adult female crabs, which were believed not to molt following tagging, to estimate survival. Many researchers have used tethering experiments to estimate mortality in juvenile crabs (e.g., Hines and Ruiz 1995). These studies have consistently shown an important role for cannibalism in juvenile and small adult blue crab (Hovel and Lipcius 2002; Mansour and Lipcius 1991; Moksnes et al. 1997; Ryer et al. 1997).

Environmental Drivers of Mortality

Research indicates a strong role of habitat type in mediating mortality rates in blue crab. For example, it has been suggested that an early reliance on structured habitat by post-larval and early juvenile crabs is an anti-predator behavior (Hovel and Lipcius 2002; Orth and Montfrans 1987; Pile et al. 1996). Loss and fragmentation of these habitats will likely alter patterns of post-larval and early juvenile survival (Hovel and Lipcius 2002; Orth and Montfrans 1987). Subsequently, early juveniles disperse from these habitats in a density-dependent fashion, suggesting a role for food limitation or cannibalism (Etherington and Eggleston 2003; Etherington et al. 2003). At these life history stages, habitats still provide protection during vulnerable intermolt periods. However, as late juveniles and adults body size confers a predation refuge (Hines et al. 1987; Hines and Ruiz 1995), habitat use becomes dominated by foraging demands rather than avoidance of predation.

It is unlikely that temperature and salinity conditions induce mortality in blue crabs during summer months. However, as noted previously, temperature-induced winter mortality is not uncommon (Bauer and Miller in press-a; Bauer and Miller in press-b; Rome et al. 2005). Estimates from a bay wide winter dredge survey suggest mortality levels as high as 56.5%, although averaged ~11% (Sharov et al. 2003).

Hypoxia can also be an important source of mortality. Anecdotal evidence suggests that crab jubilees, mass strandings of blue crab on shore, are a behavioral response to avoid poor water quality (Eggleston et al. 2005). Blue crabs have been shown to alter their behavior in response to oxygen depletion (Bell et al. 2003a; Bell et al. 2003b). More recently, modeling studies have implicated a role for hypoxia in determining the dynamics of crab populations (Aumann et al. 2006).

Disease

A variety of infectious diseases have been determined to cause mortalities of blue crabs in Chesapeake Bay. There are numerous reviews and synopses, describing viruses, bacteria, fungi, protozoans, and metazoans that infect blue crab. Shields and Overstreet (2007) provide the most recent review. Several infectious agents, under certain environmental circumstances, may have the potential to limit blue crab fisheries, and to severely affect crabs held in captivity. However, very little is known about the quantitative effects of diseases, either individually or in aggregate, on blue crab populations.

Diverse viruses are reported to infect blue crabs, although not all are pathogenic or cause mortalities. Three are considered lethal: Reo-like virus (RLV), Bi-faces virus (BFV), and Picorna-like Chesapeake Bay virus (CBV) (Shields and Overstreet 2007). Studies on the prevalence of known viruses are few, in part owing to the laborious process of identifying them by electron microscopy. Molecular (PCR) techniques can allow faster and broader screening of crabs for known disease agents (Chang et al. 2001). For example, genome-level detection of the reo-like virus BCRV1 has permitted screening of over 400 crabs in a relatively short time, providing evidence that wild hard crabs have a prevalence of under 2%, while pre-molt and captive crabs have a ~50% prevalence (Bowers et al. 2009).

Several bacteria are known pathogens in blue crab. The disease syndrome known variously as shell disease, rust disease, black spot, or burnt spot is caused by chitinoclastic bacteria and other chitin destroying microorganisms ubiquitously found in estuarine waters (Johnson 1983). Shell disease is therefore common and widespread among crustaceans, especially those that molt infrequently, or in the case of mature female crabs, have stopped molting. The syndrome includes necrotic, blackened lesions on the crab's exoskeleton, thus decreasing its market value, making it unmarketable, or allowing secondary infections to invade tissues and kill crabs. Most chitinoclastic bacteria isolated from lesions in blue crabs belong to several genera including *Vibrio* and *Pseudomonas*.

Many blue crab mortalities are attributed to systemic bacterial infections, especially in animals subjected to crowded, confined conditions. Paradoxically, it is widely accepted that various species of bacteria can be isolated from the hemolymph of apparently healthy crabs. Species reported include *Vibrio cholerae. V. vulnificus, and V. parahaemolyticus, Pseudomonas, Acinetobacter, Bacillus, Flavobacterium*, and a heterogeneous group of coliforms including *Escherichia coli* . *V. cholerae, V. parahaemolyticus and V. vulnificus* can cause human disease through ingestion of improperly cooked or handled crabs. The role of bacterial infections in mortality of wild blue crabs is not known, but it is reasonable to expect that under stressful conditions, bacterial sepsis may occur.

A parasitic phycomycetous fungus *Lagenidium callinectes* Couch infects egg masses of many blue crabs from spawning grounds in the lower Chesapeake Bay. This fungus could limit the production of crab larvae and contribute to yearly fluctuations in crab populations. Ovigerous blue crabs have been known to experience high prevalence of fungus infections throughout the summer in Chesapeake Bay (Shields and Overstreet 2007). *L. callinectes* has a wide salinity tolerance, but is primarily restricted to lower regions of Chesapeake Bay where salinity is relatively high.

Multiple species of microsporidia infect blue crabs. Crabs heavily infected with a microsporidian are occasionally termed "cotton crabs" due to the cotton like opaqueness of infected muscle observed through the carapace. One species that is widespread and causes considerable harm to the host is *Ameson michaelis*. Infected animals die rapidly if stressed. This parasite is considered highly host specific since only *Callinectes sapidus* is infected. Another microsporidian, *Nosema sapidi*, can induce extensive destruction of muscle tissue, leading to white, opaque muscles. Little is known about a third species, *Pleistophora cargoi*, on either crab health or populations. Although microsporidian infections are relatively rare in Chesapeake Bay, prevalence reached 10% during a survey of dredged crabs in Maryland portions of Chesapeake Bay during winter. In this survey, prevalence averaged 4% for the three years of survey (Messick 1998).

A well documented disease of blue crabs is the "grey crab disease" caused by *Paramoeba perniciosa*. Heavily infected animals often have a darkly discolored or grey sternum and ventral surfaces. Heavily infected crabs are sluggish, have reduced clotting abilities, and often die especially after being stressed by handling. The parasite is generally limited to infect crabs in salinities over 25. Infected peelers or late pre molt crabs die soon after molting. The parasite caused an estimated 30% loss to the population of crabs in Chincoteague Bay in June 1971 (Newman & Ward 1973).

A widely-studied protozoan parasite of blue crabs is the dinoflagellate *Hematodinium sp*. First reported in portunid crabs from France , it was later reported in blue crabs sampled for *Paramoeba perniciosa*. Heavily infected crabs appear lethargic whereas lightly to moderate infected crabs have no gross signs of infection. Experimentally inoculated crabs reach mortality rates of 87 to 95% (Messick pers. comm.). *Hematodinium sp*. is endemic in high salinity waters of the mid-Atlantic States and has not been reported in waters of salinity < 11 (Newman and Johnson 1975). Since the parasite is limited to high salinity waters, few infections are reported within Chesapeake Bay, with prevalences of 4.6% at the mouth and 4.0% along the lower eastern shore tributaries (Messick & Shields 2000). The parasite has been detected in crabs in all seasons except late winter and early spring and has a definite seasonal pattern in Maryland coastal bays (Messick & Shields 2000).

The blue crab hosts a variety of ciliates. *Mesanophrys chesapeakenis* is an opportunistic, facultative scuticociliate parasite initially reported in 0.3% of over wintering dredged blue crabs (Messick & Small 1996). However, hemolymph-borne ciliate prevalence over 5% was detected in overwintering broodstock from Chesapeake Bay (Schott, unpublished). Infected crabs are lethargic with heavy infections associated with mortalities in Mississippi (Shields and Overstreet 2007). Infections occur more frequently in captive or injured hosts than in healthy, unstressed hosts.

Fishery Impacts

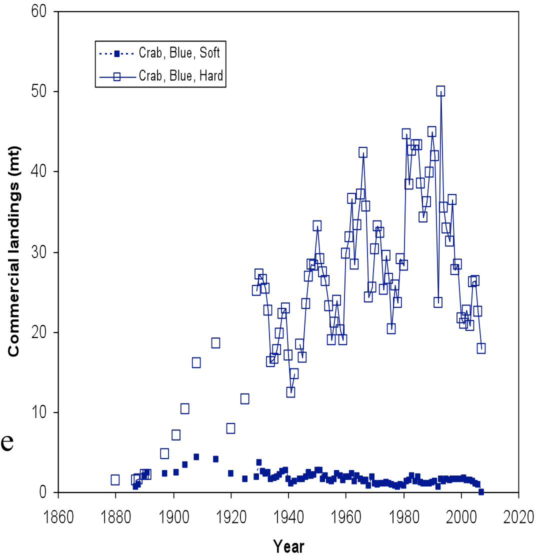

Fig. 6. Time series of blue crab landings reported to the National Marine Fisheries Service for Maryland and Virginia. Note these landings estimates include values for the coastal ecosystem in addition to the Chesapeake Bay. Additionally, the data have not been corrected for potential reporting changes – see text for explanation.

The blue crab has been subject to commercial exploitation for centuries. Estimates of landings in the commercial sector are available sporadically from 1880 and consistently since 1950. Despite some concerns over changes in reporting practices (Fogarty and Miller 2004; Miller et al. 2005), several patterns can be usefully identified in landings data (Figure 6). In the earliest years of the fishery, the weight of soft crabs reported in the landings is equivalent to that of hard shell crabs – and given their differing body weight, numerical landings of soft crabs must have substantially exceeded those of hard crabs during this period. Kennedy et al. (2007) attribute this pattern to the higher price of soft crabs in the market place. Soft crab landings have remained at broadly similar levels since 1880. In contrast, landings of hard crabs increased rapidly after 1880 as a result of improved refrigeration and transportation. Total crab landings increased steadily in the century following 1880, peaking in the 1980s at approximately 40 x10^3 metric tones (mt), although they demonstrate a striking oscillatory behavior that has been attributed to climatic factors (Figure 6, Hurt et al. 1979). Between 1960s-1980s landings varied by a factor of 2 from 20-40 x 10^3 mt (Figure 6). After the mid-1990s, landings decreased by a factor of 2 from approximately 40 -20 10^3 mt. Explanations for the recent decline include overfishing (Miller et al. 2005), and changes in ecosystem production following hurricane passage.

The exploitation fraction, U, in a fishery can be estimated as,

$$U = \frac{C}{N} \qquad \textit{Eq. 1},$$

where C is the catch, and N is a measure of abundance. Thus exploitation rates can only be calculated in the blue crab fisheries since the 1950s when fishery-independent estimates of crab abundance became available. When a fishery-independent index of abundance is used for N in equation 1, the rates so calculated are termed relative exploitation rates. The indices of abundance are typically scaled by a multiple so that the calculated Us range from 0<u<100.

However, because survey catchabilities are not known, relative exploitation rates cannot be directly compared in a single year. However, trends in relative exploitation rates are still of utility.

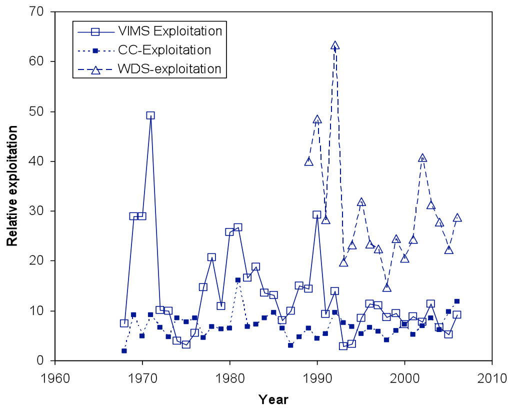

Figure 7. Relative exploitation rates for the Chesapeake Bay blue crab population for 1968-2006 based on the VIMS juvenile trawl survey, the Calvert Cliffs pot survey and the WDS (winter dredge survey). Exploitation rates were not calculated prior to 1968 because of concerns over gear changes in the VIMS trawl survey. No adjustments were made to landings in estimating relative exploitation rates.

The first estimates of relative exploitation were published by Rugolo et al. (1997). These authors calculated exploitation rates using fishery-independent indices of abundance from both the Calvert Cliffs pot survey and the Virginia Institute of Marine Science's juvenile trawl survey to estimate trends in population abundance. We updated these authors' calculations to include a third fishery-independent survey, the bay wide winter dredge survey (WDS) which was not available when the authors conducted their analyses. The results are presented in Figure 7. All three indices are variable. The coefficients of variation (cv's) for the Calvert Cliffs-based relative exploitation rate and the WDS-based relative exploitation rate are 35.9 and 39.6% respectively. In contrast the cv's for the VIMS trawl based estimates is higher at 70.2%. In each case there is a clear trend in the exploitation rates such that Us for the most recent periods (~ after 1992) are low.

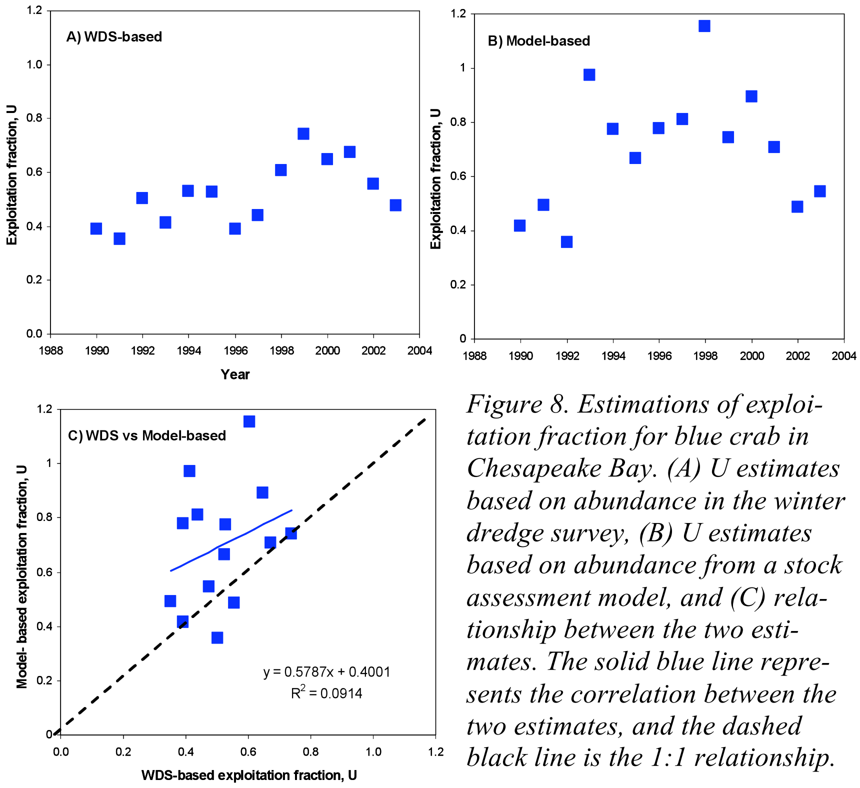

Figure 8. Estimations of exploitation fraction for blue crab in Chesapeake Bay. (A) U estimates based on abundance in the winter dredge survey, (B) U estimates based on abundance from a stock assessment model, and (C) relationship between the two estimates. The solid blue line represents the correlation between the two estimates, and the dashed black line is the 1:1 relationship.

More recently, estimates of absolute exploitation rates have been calculated. In one approach, N is estimated from the WDS conducted the previous winter which provides an estimate of the abundance of crabs > 25 mm carapace width (cw) (Sharov et al. 2003), Thus, the approach assumes that all crabs > 25 mm cw become vulnerable to the fishery in the following year, and that crabs < 25 mm cw do not become vulnerable to the fishery in the following year. Abundance estimates from the survey are corrected for overwinter mortality. This approach is currently used as the principal management tool for blue crab in Chesapeake Bay. A time series of U estimated in this way is shown in Figure 8A. Estimates calculated using this approach rose from about 40% in 1990 up to a peak of almost 80% in 1999, and then declined to about 45% in 2003. The higher values in this time series are of concern as exploitation rates of 50% or more may not be sustainable. A second approach uses estimates of absolute population abundances from a catch-survey model, modified to incorporate multiple surveys (Miller et al. 2005). The model uses inverse variance weightings to combine WDS, VIMS trawl and a MDNR summer trawl survey. The approach does not differentiate based on crab size; rather it uses a total population estimate at the beginning of the season for N. The model relies on an estimate of natural mortality to calculate exploitation. The time series of U estimates from this approach, based on a natural mortality rate M= 0.9 yr^{-1}, are shown in Figure 8B. It should be noted that two of these values are U>1 which implies more crabs were harvested than were available. This indicates concerns over recruitment estimates in the model.   For 1993 through 2001, these estimates ranged between 0.65 and 1.15, which are of concern and seem to be above sustainable levels. Estimates from the two models are compared in Figure 8C. Use of the model-based approach generally produces higher estimates of U than does the Sharov et al. approach that uses the winter dredge survey (Figure 8C).

Status of the Stock

The blue crab stock in Chesapeake Bay has been assessed twice in the past fifteen years (Miller et al. 2005; Rugolo et al. 1997). The Miller et al. (2005) assessment examined fishery-independent and fishery dependent data up to 2003. These authors re-examined evidence for natural mortality in blue crab (Hewitt et al. 2007), reconsidered the impacts of reporting changes in harvests (Fogarty and Miller 2004), and employed an empirically-based approach using winter dredge survey data (Sharov et al. 2003) and a second model-based approach to estimating exploitation by the fishery. Miller et al. also updated biological reference points. Using the empirical approach to estimating exploitation and abundance, Miller et al. concluded that in 2003 the blue crab stock in Chesapeake Bay was not overfished and overfishing was not occurring although exploitation rates were above the target. The assessment presented evidence that the stock had been experiencing overfishing from 1998-2002 (Figure 9A). In a companion analysis that used a modified Collie-Sissenwine (1983) model thereby allowing inference to be drawn about stock status for years prior to the winter dredge survey, Miller et al. concluded that the stock had experienced overfishing from 1972-

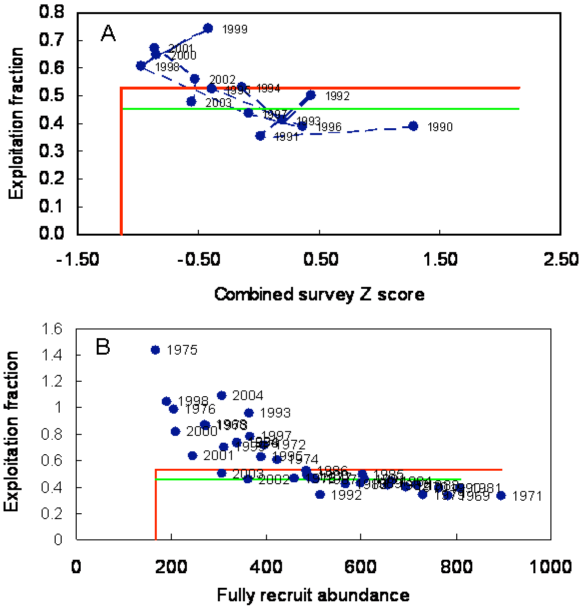

Figure 9. Status of the Chesapeake Bay blue crab stock for 1998-2003 based on (A) empirical estimates from the winter dredge survey and (B) s modified Collie Sissenwine model. Shown are estimations of the exploitation fraction (catch/ available abundance) and standardized abundance from fishery-independent indices (A) or from the model (B). Also indicated on the plot at the overfished threshold (vertical red line), the overfishing threshold (horizontal solid red line) and the target exploitation fraction (horizontal solid green line). The model-based approach assumes a natural mortality rate, M=0.9 yr^-1.

1976 and from 1995-2001 (Figure 9B). Paralleling the recent periods of overfishing, Miller et al. reported that abundances in the principal fishery-independent surveys had been below average since the early 1990s and that landings had declined over the same period (Figure 10).

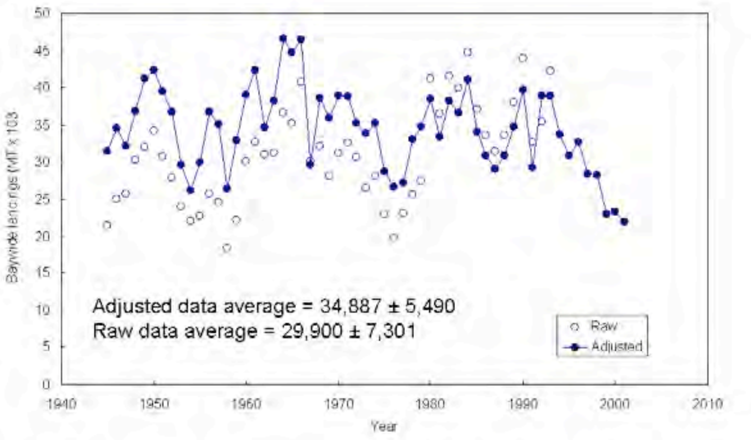

Figure 10. Baywide commercial landings of blue crab in Chesapeake Bay. Reporting changes in all jurisdictions have impacted estimates of landings. Shown in the plot are estimates of both the raw landings (open symbols) and the adjusted landings (solid symbols).

Numerous other analyses, in support of assessment activities in Chesapeake Bay, have been conducted. These analyses have indicated substantial declines in crab abundance, in recruitment (Lipcius and Stockhausen 2002), and in the distribution of crabs during winter months (Jensen and Miller 2005).

Indicators and Issues

Indicators

Population Structure

1. *The Center of Mass of the Crab Distribution.* Jensen and Miller (2005) calculated the center of mass of the crab population in Chesapeake Bay and showed it was related to population abundance. Calculation of the center of mass may help identify primary habitat, as has been shown in other systems (MacCall 1990). Currently, this analysis can only be conducted on the bay wide winter dredge data

Population Abundance

2. *Time Series of Each Fishery-independent Survey.* The importance of fishery-independent surveys of abundance cannot be over-emphasized. Continued analyses of fishery-independent surveys will be the foundation of future assessments of population status and trends. Each individual survey contains important information. However, we have yet to develop a single integrated, statistically optimal, index of abundance for blue crab. Development of an integrated index of abundance should be a priority.

3. *Index of Recruitment.* All of the indices currently in existence focus on juvenile crabs > 30 mm cw. This does not provide an adequate index of recruitment. Design and implementation of a new survey that focuses on the abundance of small crabs would be of high utility.

Mortality

4. *Disease.* The overall influence of disease on blue crab stocks, and the effect of stock size on disease processes, are largely unexplored. Most of the blue crab population is recruited annually, and prediction of harvests or population sizes are assessed by winter trawl surveys. Spatial or annual variability in crab abundance could be a sign of diseases. It is logical to expect that large disease effects may be manifest as incongruities between juvenile numbers and later adult populations. For a more effective estimate of disease effects, trawl surveys could incorporate health assessments. Boatside visual metrics of crab health are currently inadequate, however, and health assessments must rely on histology of a relatively small number of animals. Molecular methods may permit larger numbers of crabs to be assessed, but the one-by-one nature of molecular detection is not suitable for looking at more than a few known disease agents.

5. *Exploitation.* Indices of relative exploitation in each of the principal fisheries should be developed and monitored for status and trend.

Fishery Status and Trends

6. Status and trends relative to biological reference points: Work to assess the current status of the Chesapeake Bay blue crab population relative to accepted biological reference points should be continued. However, the reference points should be carefully evaluated and where necessary updated.

Issues

Population Structure

1. Research findings have shown regional variation in several vital rates. Moreover, spatial approaches to management of blue crab in Chesapeake Bay have been adopted and additional ones have been considered. However, a thorough, detailed exploration of the consequences of the spatial processes on the resultant dynamics of blue crab remains lacking. The only comparative analyses conducted to date do indicate that spatial considerations may change important inferences regarding population dynamic processes (Miller 2003). A more complete evaluation of the role of spatial structure in blue crab populations, and in models of blue crab populations is warranted.

Population Abundance

2. *Population Indices.* The abundance of blue crab in Chesapeake Bay is believed to be accurately and precisely estimated in the annual winter dredge survey (WDS) (Sharov et al. 2003). This has provided a valuable tool for management. There is uncertainty, however, in the conversion of dredge catch-per-tow into absolute abundances, caused by the uncertainty in the estimation of the catchability coefficient.

   However, this survey provides an annual snapshot of abundance only. In winter, the young-of-year crabs have not attained exploitable size. Analysis of data from Delaware Bay found that the survival into exploitable size was variable among years and influenced by density of primarily the young-of-year crabs (Kahn et al. 1998; Kahn and Helser 2005). Therefore, while very valuable, the winter dredge survey does not provide a complete picture of the exploitable stock size later during the fishing season. Yet, crab population dynamics and exploitation patterns demonstrate considerable intra-annual dynamics that may not be reflected in the winter dredge survey. This suggests the need for other fishery-independent surveys to provide information on intra-seasonal patterns.

   Additionally, more intensive analysis of available survey data would make better use of existing survey efforts. For example, post-hoc resampling of the surveys to develop spatially-explicit patterns may assist with explorations of the importance of spatial processes in the dynamics of blue crab (Jensen and Miller 2005). Analyses to track survey indices of various life-stages and analyzing year to year survival of these life stages would inform about variation in survival in relation to density (Kahn et al. 1998). If analyzed correctly, trawl survey data can provide information on stock recruitment functions (Kahn et al. 1998; Kahn and Helser 2005).

3. *Recruitment Indices.* We currently lack a bay wide index of recruitment that is relevant to stock- recruitment modeling. The application of the winter dredge survey, or individual state surveys (Fogarty and Lipcius 2007) are not ideal as these survey indices incorporate varying amounts of post-settlement periods which may mask the recruitment signal. Thus, the extent to which density-dependent processes regulate recruitment in blue crab remains poorly quantified.

Sources of Mortality

4. *Natural Mortality Estimation.* There remains considerable uncertainty in our knowledge of the scale, variability and pattern of natural mortality. Most efforts at quantifying natural mortality have been conducted either at the whole life cycle level (Hewitt et al. 2007), or on very local levels focusing on individual life stages (Hines and Ruiz 1995). An integrated effort to quantify natural mortality for cohorts as they develop (longitudinal) or for a single life stage across space and time (cross-sectional) would be beneficial.

5. *Disease.* The spatially and annually variable nature of crab populations (related to recruitment and environmental variability) make it difficult to detect the effects disease on crab populations. Understanding the effects of disease by relying on incidental observation of diseased animals is problematic. Moribund animals will become prey to other crabs before they can be observed, and animals in poor health may not enter pots or hold a trot line. In a system as large as Chesapeake Bay, a disease-related mass mortality of blue crabs could easily be overlooked. In coastal bays, mortalities might be detected as a result of visual observation of dead crabs, or the absence of harvest in pots, but the recreational fishing effort there, as in the Chesapeake Bay, is so variable that it may confound efforts to monitor populations over a season.

Fishery Concerns

6. *Reliability of Landing Estimates.* Landings estimates have been collected by both states for many years. However, the reliability of these estimates remains poorly quantified. The approaches used to estimate landings have changed over time from an informal survey of dealers, to a statistical survey of a sample of harvesters to mandatory reporting. The impacts of these reporting changes have only recently been evaluated (Fogarty and Miller 2004; Miller et al. 2005). Systems by which reported landings are checked against fishery-dependent sampling or dealer reported are not fully implemented.

   Landings in individual sectors are less certain than for the overall landings. Recreational catch has only been estimated for a few years (Ashford and Jones 2001; Ashford and Jones 2002). It is not known whether there are trends in recreational harvest. The reliability of catches in the soft and peeler sector of the fishery is of unknown reliability (Miller 2001d). Uncertainties over sector specific landings impact the ability to generate sector specific exploitation rates (see #8 below).

7. *Uncertainty in Exploitation Rates, U.* The uncertainty associated with estimates of U relates primarily to which fraction of the stock to use in calculations. Exploitation rate is defined as the fraction of the exploitable stock that is harvested (Ricker 1975). Thus, determining the pattern of recruitment to the fishery is critical. Sharov et al. (2003) based calculations on WDS estimates of either crabs > 60mm cw (assumed to be age-1+) or all crabs. U estimates based on the abundance of crabs > 60 mm were greater than 1, indicating that this component is not a suitable foundation for exploitation estimates (Sharov et al. 2003). However, whether the abundance of crabs > 15mm cw during winter is a completely reliable basis for calculating U remains uncertain. Kahn and Helser (2005) calculated exploitation for blue crab in Delaware Bay. These authors indicated that because of variable and density-dependent juvenile survival, the proportion of the total stock at the beginning of the year that grew to exploitable size varied among years. As a result of these concerns, these authors produced bounded estimates of exploitation, feeling that this was a more appropriate presentation given underyling uncertainties in N. In summary, specification of the appropriate estimate of abundance introduces potentially substantial uncertainty into estimates of exploitation.

   Currently estimates of U are assumed to be point estimates and no variance is provided. It is possible to estimate variance for both approaches. The catch estimate is considered a census and thus is not directly associated with a variance estimate. Variances for N are available either directly from the survey, or from model output. Accordingly, minimum variance estimates can be calculated based on the variance of the inverse of a normal random variable. Alternatively, if it is believed that C is not a true census, then bootstrapping could be used to develop variance estimates of U.

8. *Sector-, Stage- and Spatially-Specific Exploitation Fractions.* To date exploitation estimates have been calculated for the commercial fisheries in aggregate. However, it is possible to partition the exploitation estimates into component fisheries including the hard crab pot fishery (hcp), a soft and peeler fishery (s&p), a trotline fishery (tf), the winter dredge fishery (wdf) and a recreational fishery. In principal

$$U = \sum_{sector} U_i \qquad \text{Eq. 2}$$

   However, attention needs to be paid to determining the appropriate N for each component – particularly for the calculation of $U_{s\&p}$ as the whole population N may not be appropriate for this sector given the presence of an effective terminal molt. No work has been done to explore how the winter dredge survey data may be segregated to estimate a more appropriate $U_{s\&p}$. However, it should be noted that this adjusted $U_{s\&p}$ will not be appropriate for Eq. 2 because of differences in the underlying Ns used to calculate the respective exploitation fractions. To date, detailed calculations of U_i's have not been completed. A sample of possible time series is shown in Figure 11.

   Stage-specific and spatially-explicit exploitation fractions are more difficult to generate for reasons similar to the difficult of estimating $U_{s\&p}$. Stage-specific exploitation fractions require estimation of appropriate N_0s. Given the seasonal growth dynamics of blue crabs (Bunnell and Miller 2005; Puckett et al. 2008), calculating the appropriate N is not trivial. Thus it is unlikely that stage-specific Us will be forth coming though they would be of use to management. However, sex specific exploitation fractions may be of extreme utility.

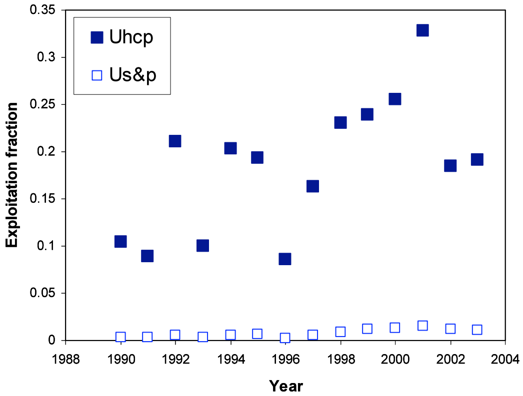

Figure 11. Time series of sector specific exploitation for the hard crab pot fishery (hcp) and the soft peeler fishery (s&p). Note the $U_{s\&p}$ *is calculated based on the overall abundance at the beginning of the season.*

9. Uncertainty in biological reference points: Estimates of U are compared to an overfishing reference point to determine stock status. The current overfishing reference points is based on a spawning potential ratio calculation designed to maintain at least 10% of the virgin spawning stock potential (Miller 2001c). Rugolo et al. (1997) and Miller (2001a) explored the sensitivity of overfishing reference points to uncertainty in life history parameters. However, except for Helser et al. (2001) there has been no systematic investigation of the uncertainty associated with the calculated reference point. In particular, the reference points are sensitive to uncertainty in the estimate of natural mortality, which Kahn and Helser (2005) and Kahn et al. (1998) found to be variable and density-dependent.

   While there was substantial improvement between the first (Rugolo et al. 1997) and second bay wide stock assessment (Miller et al. 2005), a substantial weakness in both assessment frameworks remains related to the management control rule and biological reference points. The management control rule for blue crab in Chesapeake Bay was developed in 2001 (Miller 2001c). It establishes biomass and exploitation thresholds which should not be exceeded and recommends a target exploitation rate that is both sustainable and statistically differentiable from the threshold. The biomass threshold was defined empirically as the lowest observed biomass in recent history that has supported a fishery. This standard was selected in the absence of a theoretical standard that could be applied, such as the biomass at maximum sustainable yield. The exploitation threshold was based on the retention of at least 10% of the virgin spawning potential based on analogies with other crustacean fisheries which have been successfully managed with this standard. However, as with the biomass threshold there was no theoretical foundation on which to base the selection of the exploitation threshold. Similarly, the target was chosen somewhat arbitrarily as simply double the exploitation threshold.

   The spawning-potential ratio (SPR) method which was employed to estimate the exploitation threshold is a simple approach which is basically an extension of yield-per-recruit modeling, with spawning biomass accumulation as the relevant parameter as opposed to yield. While it may be acceptable as a rough first cut at the issue, the problem with this approach is that it makes the unscientific assumption that basic population rates, such as growth, survival, maturity and fecundity are unaffected by population density. That assumption has been rejected conclusively by the findings of population biology. Several writers, including Beverton and Holt (1957) and Goodyear (1980) have proven that fisheries require the existence of compensation in order to remain in existence. Therefore, the SPR approach ignores the ability of populations to compensate for reduced abundance, in many cases, by increasing survival, growth and reproduction rates. Conversely, it ignores the strong possibility that these rates may decline at high densities.

Future analyses should focus more on quantifying patterns of density-dependence. Kahn et al. (1998) and Kahn and Helser (2005) have demonstrated that a high level of density-dependence and compensatory ability is exhibited by the Delaware Bay stock. Examinations of one important aspect of potential compensatory response, the stock-recruitment relation in the Chesapeake, have been presented by Tang (1985), Lipcius and Van Engel (1990) and Uphoff (1998). This work has recently been summarized by Fogarty and Lipcius (2007). However, some of these early studies did not adequately delineate the actual spawning stock or the recruits with respect to time. Recent studies have indicated that blue crab growth can be much faster and is likely more variable than has been appreciated previously (Puckett et al. 2008). A failure to incorporate the appropriate lags between spawners and recruits has introduced uncertainty into stock and recruitment relations – see Kahn et al. (1998) for discussion. Lipcius and Stockhausen (2002) presented stock-recruit models, but recruits were measured at the larval stage, prior to the juvenile stage, the stage at which Kahn et al. (1998) reported compensation in the Delaware Bay. Consequently, the full effect of compensation in the stock-recruit relationship in the Chesapeake has yet to be explored, although the data is readily available from various surveys. Results of stock-recruitment modeling can be combined with yield-per-recruit modeling to estimate maximum sustainable yield reference points that incorporate a limited amount of compensation.

The lack of a theoretical framework from which to develop reference points for blue crab reflects a general lack of understanding of the compensatory potential in this species. Until more research is conducted that provides a detailed understanding of the compensatory ability of this species, specification of biological reference points will continue to be problematical.

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SOCIOECONOMICS

Insert Socioeconomics sections here