Predicting Effects of Climate Change on Blue Crabs in Chesapeake Bay

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Abstract

*Callinectes sapidus* populations support fisheries extending over a broad range of latitude from the species’ tropical origins into the temperate zone. We analyzed latitudinal patterns of survival, reproduction, growth and maturation of blue crab populations in Florida, North Carolina, and Maryland/Virginia to project demographic effects of climate warming and certain other potential climate changes on the Chesapeake blue crab population. Field surveys and laboratory experiments indicate that harsh winters (<3°C, <8 ppt salinity) cause significant mortality in small (10 mm) juveniles and mature females. Brooding in populations at lower latitudes begins 3-4 months earlier than at high latitudes, allowing more broods per season. Cold winter temperature also restricts the growing season and inserts 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 spring and fall. Although there are not clear trends across latitude, size at maturity is inversely correlated with temperature within a site. While small females may molt to maturity and mate sooner, small size increases vulnerability to predation and diminishes fecundity per brood. Thus, cold winter temperatures and a short growing and reproducing season restrict the species’ northward distribution from its tropical origins. Climate change reducing the severity of winters is predicted to increase winter survival and to promote rapid growth and brood production. However, warmer temperatures may promote increased juvenile mortality and may reduce size at maturity. Demographic schedules for fishery models will need to consider complex effects of warming.

Introduction

Blue crab (*Callinectes sapidus*) populations support lucrative fisheries and blue crabs are important predators in estuaries and lagoons extending across a broad range of latitudes of the western Atlantic Ocean (Fogarty and Lipcius 2007, Hines 2007). Although blue crabs have tropical evolutionary origins, their geographic range extends into the temperate zones of both South America and North America (Williams 2007). Despite a long history of sustained high productivity, fishery stocks in Chesapeake Bay and the North Carolina sounds, as well as other locations to a lesser extent, have suffered serious declines in the past decade. These declines appear to be associated with both intensive fishing and multiple environmental stressors, ranging from poor water quality to impacts of major hurricanes.

The blue crab life cycle (Fig. 1) is complex, encompassing a larval phase of 8 zoeal stages and a post-larval megalops, followed by 16-20 juvenile instars, before molting to maturity, followed by mating and egg production (Jivoff et al. 2007, Epifanio 2007, Hines 2007). Like many estuarine species, habitat use shifts markedly as life stages disperse and migrate across the salinity gradient of the estuary to offshore. Females produce and incubate a series of egg batches in the high salinity waters near the mouth of estuaries. Larvae hatch and are advected in the plume of the estuary offshore onto the continental shelf. Post-larvae use tidal stream transport to re-enter the estuary and then settle in seagrass beds, where they metamorphose and grow for approximately seven instars to 20 mm juveniles. Juveniles then disperse into lower salinity, shallow nursery habitats throughout the estuary, where they grow to maturity and mate. Females mate only once in their lifetime, while males may mate multiple times. Following mating, inseminated females migrate back to high salinities of the estuary to produce eggs. In small estuaries, mature females may move outside the estuarine
mouth, while in large systems like Chesapeake Bay they remain in the area of the bay mouth.

The blue crab life cycle is markedly affected by the seasonal cycle of temperature (Jivoff et al. 2007, Epifanio 2007, Hines 2007). Egg production and brooding occur in the warm season, and feeding and movement cease below 10ºC, as does molting. Thus, in estuaries where winter water temperatures drop below 10ºC, blue crabs undergo a period of suspended activity, which can markedly increase the blue crab generation time. Conversely, longer warm seasons may affect demographic variables with rapid growth, development, and reproduction. Crustaceans, including brachyuran crabs, exhibit geographic variation in reproductive traits (Lonsdale and Levinton 1985, Reaka 1986, Hines 1989, Dugan et al. 1991, Lardies and Castilla 2001, Brante et al. 2003, Castilho et al. 2007, Rodgers 2010). Because seasonal cycles vary predictably with latitude, we may reasonably infer effects of climate change on seasonal features of reproduction, settlement, and growth.

In this paper we consider how climate change may affect the important economic and ecological roles of blue crabs in these systems. We use latitudinal variation in demography of blue crab populations to project the probable effects of climate change on the blue crab population in Chesapeake Bay. We also review potential effects of climate change
on community and ecosystem ecology for blue crabs, incorporating observed impacts of seasonal and annual variation in weather to highlight complex, often indirect consequences for blue crabs that make the impacts of climate change uncertain.

**Approach and methods**

To examine effects of climate change on demography, we document patterns of latitudinal variation in reproduction, growth, and maturity based on published information (see recent reviews: Jivoff et al. 2007, Epifanio 2007, Lipcius et al. 2007, Hines 2007) and our own extensive unpublished observations of blue crab biology at three main locations along the east coast of North America (Fig. 2): (1) Chesapeake Bay, Maryland, and Virginia (centered at 38°5′0″N, 76°20′0″W); (2) Beaufort Inlet, North Carolina (34°41′38″N, 76°39′59″W); and (3) Indian River Lagoon, Florida, particularly the Sebastian Inlet (27°51′30″N, 80°27′30″W). The decrease in latitude across these sites represents major climatic warming and associated seasonal variation. Plots of monthly mean water temperatures for the three main locations indicate that the major difference in the seasonal pattern is that lower latitudes have much
warmer winters, but not substantially hotter summers (Fig. 3A). Given that blue crab movement and foraging ceases at temperatures below approximately 10°C (Hines 2007), the duration of their winter shutdown of activity in Chesapeake Bay is more than 4 months, or twice as long as the short winter season in the Indian River Lagoon (Fig. 3B).

In addition, we consider impacts of interannual variation in winter temperature and salinity on blue crabs in Chesapeake Bay as a means of predicting effects of climate change on an important source of mortality for populations near the edge of their geographic range (Rome et al. 2005, Bauer and Miller 2010a,b). We also consider how climate changes in prevailing oceanographic conditions might affect larval recruitment dynamics (Epifanio 2007) for the three main locations.

To examine effects of climate changes in community and ecosystem interactions, we also compare ecology of blue crabs (Hines 2007) among the three main locations (Indian River Lagoon, Beaufort Inlet, Chesapeake Bay). We consider the probable or potential effects of climate warming and seasonal changes on other key species in Chesapeake ecosystems.

Figure 3. Seasonal variation in water temperature (top) and duration of winter (bottom) at three locations shown in Fig. 2. Sea temperatures from NOAA monitoring stations at each site.
Results

Latitudinal variation in demography

Season
Seasonal durations of blue crab life history phases increased markedly with decreasing latitude (Fig. 4). The brooding season increased from 4 months in Chesapeake Bay (late May through September) to about 9 months in Florida (February through October). Mating season increased twofold from 3.5 months in mid Chesapeake Bay (late May to early September) to about 8 months in the Indian River Lagoon (April to October/November). Duration of the post-larval settlement season also increased about twofold from about 3.5 months (mid-August through October) in Chesapeake Bay to 7 months in Florida (May through November).

Growth rates and time to maturity
Growth of juvenile blue crabs was markedly affected by seasonal variation in temperature, with seasonal growth rates increasing in warm summer temperatures and dropping to zero in winter (Fig. 5). Time to reach critical juvenile size, maturity, and generation time were much shorter at lower latitudes with longer warm seasons (Fig. 6). Depending on seasonal timing of settlement and thus whether they ceased

Figure 4. Variation in seasonal duration of settlement, mating, and brooding for blue crabs sampled at three locations shown in Fig. 2. Arrows indicate direction of effect of climate warming on the variable.
Figure 5. Seasonal variation in growth rate of juvenile blue crabs and in water temperature in the Rhode River in upper Chesapeake Bay. Mean and standard errors are indicated for growth rates. E.G. Johnson et al. (unpubl.)

Figure 6. Schedule for growth and maturity for blue crabs sampled at three locations indicated in Fig. 2. Axes show estimated times to grow to 50 mm (carapace width) juveniles, age at maturity, and generation time. Shaded bars indicate ranges in lower and upper time durations (months) for each variable. Arrows indicate direction of effect of climate warming on the variable.
Figure 7. Correlation of female blue crab size at maturity versus water temperature. Females molting to maturity were measured in locations that varied naturally in water temperature in the vicinity of Beaufort Inlet, North Carolina.

Figure 8. Seasonal variation in female blue crab size at maturity and water temperature at Beaufort Inlet, North Carolina. Solid symbols show mean and standard error of carapace width. Triangles show mean water temperature.
growing over winter, juveniles reached 50 mm size in 4-9 months in Chesapeake Bay but 2-3 months in Florida. Age at maturity ranged from 12-16 months in Chesapeake Bay but 5-12 months in Florida. Similarly, generation time decreased from 16-30 months in Chesapeake Bay to 10-16 months in Florida.

**Temperature and female size at maturity**
Female size at maturity was negatively correlated with temperature at the habitat site of molting, when salinity was constant (Fig. 7). Female size at maturity was also inversely related to seasonal variation in water temperature when salinity was constant (Fig. 8). However, mean size of mature females did not appear to exhibit latitudinal variation (Fig. 9), because other factors, such as salinity, also affected size at maturity and confounded latitudinal comparison.

**Egg size, brood production, and fecundity**
Egg diameter appeared to decrease from Chesapeake Bay to Florida, and fecundity per brood appeared to increase concomitantly (Fig. 10) (Rodgers 2010). However, these patterns may have been confounded by seasonal effects, because broods at lower latitudes were collected later in series of broods produced over a longer brooding season that started at an earlier month than broods collected in the same month in Chesapeake Bay. Broods produced later in the season may have had smaller, less yolky eggs, resulting in more eggs per brood, even if late season broods are smaller than early season broods (Prager et al. 1990, Dickinson et al. 2006). Because the brooding season increased in duration (Fig. 4), the number of broods produced per year by a female increased from 3-4 broods in Chesapeake Bay to 6-8 broods in Florida (Fig. 11); and annual fecundity also increases from 9-12 million eggs in
Figure 10. Average egg size and fecundity per brood at three sampling locations shown in Fig. 2. Arrow and ? indicate uncertainty in direction of effect of climate warming on the variable because of differences in seasonal timing of sampling among locations (see text).

Figure 11. Reproductive output per female blue crab at three sampling locations shown in Fig. 2. Range in number of broods and in number of eggs produced per season are indicated. Bar shading indicate lower and upper levels of the variables. Arrows indicate direction of effect of climate warming on the variable.
Chesapeake Bay to 21-28 million eggs in Florida. Although we have recorded females that lived to age 5 years, longevity of most females in the intensively fished Chesapeake Bay population was about 1-3 years (Fogarty and Lipcius 2007), resulting in a lifetime fecundity of 9-24 million eggs in that system. Longevity in Florida was uncertain. If it were the same as Chesapeake Bay, lifetime fecundity would be 42-56 million eggs. However, if longevity were shorter at warmer, lower latitudes (averaging, say, 1 year in Florida), then lifetime fecundity would approach the annual values.

**Mortality related to climatic conditions**

Blue crab survival at higher latitudes in the temperate zone was limited by winter severity, with harsh winters determined as combinations of cold water temperatures (<3°C) and low salinity (<8 ppt) causing markedly increased mortality, especially for small juveniles and mature females (Rome et al. 2005; Bauer and Miller 2010a,b) (Fig. 12). Winter mortality also varied with the duration of the exposure to the harsh conditions of low temperature-salinity combinations (Rome et al. 2005, Bauer and Miller 2010a,b). In Chesapeake Bay mature females migrate in the fall from low salinity nursery and mating areas to higher salinities of the lower bay in preparation for brood production. Tagging studies (Aguilar et al. 2005) and winter dredge surveys (Jensen et al. 2005) indicate that some females may stop partway down the salinity gradient as cold temperatures interrupt their migration, resulting in females being distributed along the estuarine range of salinities and winter temperatures (Fig. 13). In Chesapeake Bay, interannual fluctuations in
winter severity affected both the level of mortality (ranging from 0 to 70% in certain harsh winters) and the spatial extent of mortality in the bay, with harsh conditions extending well down below mid bay in cold, low-salinity winters, and lasting more than 5 months in the upper half of the bay (Figs. 14-15) (Bauer and Miller 2010 a,b). Thus, climate change is predicted to result in warmer, shorter winters, reducing winter mortality (Najjar et al. 2010). However, if climate change also imposes wetter winters (Najjar et al. 2010), then lower salinities may increase mortality during cold periods.

Changes in coastal currents and weather patterns along the east coast may have marked effects on larval survival and blue crab recruitment due to shifts in current systems (Epifanio 2007). However, it is
Figure 14. Average winter water temperature distribution for November 1 through April 30 for Chesapeake Bay for contrasting years 2003 and 2002. From Bauer and Miller (2010).

Figure 15. Winter duration of cold water temperatures below 10ºC during November 1 through April 30 in Chesapeake Bay for contrasting years 1996 and 2002. From Bauer and Miller (2010).
difficult to predict the effects of potential climate changes in nearshore southward flowing currents and gyres that seem to supply larvae to estuaries in the regions of the mid-Atlantic and south-Atlantic bights of North America (Epifanio 2007).

Climate change is predicted to increase the frequency and intensity of tropical storms (Karl et al. 2009). Much of blue crab larval settlement occurs in late summer and fall for northern estuaries, which coincides with hurricane season (Epifanio 2007). These storms may affect larval recruitment in systems like Chesapeake Bay, if these storms cause major disturbance of offshore surface currents and tidal surge, but storms can also cause huge runoff and flushing problems within the estuaries (Najjar et al. 2010) (see also “Dead zones” below).

**Habitat impacts of climate change in Chesapeake Bay**

Climate change is likely to affect the geographic distribution of key habitat-forming species and trophic interactions that are critical for various blue crab life stages, especially near their latitudinal limits, such as Chesapeake Bay (Pyke et al. 2008, Najjar et al. 2010).

**Seagrasses and submerged vegetation**

Eelgrass (*Zostera marina*) exhibited a major die off in 2005 in the lower Chesapeake Bay, which was attributed to high summer temperatures (Orth and Moore 2008). Eelgrass was critical habitat for juvenile blue crab abundance, survival, distribution, and foraging biology (Lipcius et al. 2007). Changes in rainfall that alters estuarine salinities also may have affected other species of submerged vegetation.

**Emergent vegetation**

Salt marshes provided crucial resources for juvenile blue crabs in adjacent unvegetated bottom (King et al. 2005). Marshes provided detritus that fuels infaunal prey resources for juvenile crab nursery habitat. With sea-level rise by the year 2100, at least 161,000 acres of salt marsh are predicted to be lost in Chesapeake Bay (Pyke et al. 2008). Mangroves have been important structural habitat along tropical shorelines, and juvenile blue crabs derived nursery habitat value from mangroves in Florida. Cold winter temperatures (freezing) limit the northern distribution of mangroves along the east coast of North America, and warming appeared to allow the northward spread of this habitat, now extending beyond Cape Canaveral. However, it is not likely that climate change will allow mangroves to spread to Chesapeake Bay in the coming century.

**Oyster reefs**

Oysters were often considered to create valuable habitat for blue crabs. However, there was very little empirical or experimental evidence that
the oyster reefs per se were utilized extensively by blue crabs (Hines 2007). Rather, epifaunal and infaunal organisms associated with oyster reefs seemed to provide food resources, especially for larger crabs. Oysters were at record low levels in Chesapeake Bay, with almost no viable oyster reefs remaining. They have been decimated by overfishing and by disease, which is especially intense at higher salinities of Chesapeake Bay. In lower latitude estuaries, oysters in the intertidal zone often have had less disease due to warm temperatures and sustained air exposure. However, in much of Chesapeake Bay, intertidal oysters were killed by low winter temperatures. With warming, intertidal oysters may persist and provide a spawning stock that may help restore reefs as a habitat.

“Dead zones”
Low dissolved oxygen develops in deeper waters of eutrophic estuaries that are stratified by warmer temperatures and freshwater runoff. Thus, if climate change results in warming and higher rainfall in estuaries like Chesapeake Bay (Pyke et al. 2008), then stratification and low dissolved oxygen will increase in extent and duration, potentially killing blue crabs. Not only can low oxygen affect survival of crabs, but such dead zones will also reduce foraging resources and distribution of blue crabs (Hines 2007). Low oxygen also may regulate their movement as juvenile crabs dispersing up-estuary and mature females migrating down-estuary encounter deeper, low oxygen waters (Aguilar et al. 2005, Johnson and Hines unpubl. data). Even if the timing of the female migration occurs after the fall turnover of the water column, low oxygen would reduce the availability of benthic prey that fuels the crabs’ movement.

Trophic interactions
Populations in the Gulf of Mexico and Florida encounter a high diversity of predatory fish and crustaceans feeding on post-larval and juvenile blue crabs, resulting in intense predation rates and low survival (Hines 2007). Climate warming is likely to allow more predator species to extend into Chesapeake Bay in greater abundance and for longer periods of time (Najjar et al. 2010). Certain key prey species for blue crabs are near their biogeographic limit in Chesapeake Bay. For example, the southern limit of the tellinid bivalve *Macoma balthica* is in Chesapeake Bay, and this species is a major component in the diet of blue crabs. If climate warming pushes *M. balthica* farther north, blue crabs will have to shift to other prey species, perhaps those spreading from the south. The effects of such species substitutions may or may not balance out in the food web.
Discussion

As a species of tropical origin, the geographic range of blue crabs is limited in higher latitudes by cold winter temperatures, especially at low salinities in estuaries. Severe winters can cause as much as 70% mortality of blue crabs in key areas of Chesapeake Bay, especially for the most sensitive life stages/sizes (Rome et al. 2005; Bauer and Miller 2010a,b). Warming winter temperatures are expected to result in reduced winter mortality of blue crabs at higher latitudes and to allow northward range expansion of fishable blue crab stocks.

Effects of climate change on blue crab demography are also expected to promote increased fishery production. Our latitudinal comparisons predict that warming climate will extend the length of the seasons for reproduction, settlement, and growth. Growth rates and maturation/generation times should also shorten the life cycle. Reproductive output should increase for the population.

Due to an array of environmental stresses, many habitat-forming species have undergone serious declines in Chesapeake Bay, including submerged vegetation due to eutrophication and increased water turbidity and epiphytes; oysters due to overfishing and disease; and salt marshes due to habitat destruction and increasingly inundation. Further stresses of climate change may push these habitats past a threshold of sustainability, and losses of such species are already occurring in some particularly warm years. If these species are not replaced by functionally similar species the consequences may be large and complex. However, because these habitat functions are generally intact at lower latitudes, “replacement species” may extend their range and sustain the ecosystem functions. Range extensions have been documented for invasive species into Chesapeake Bay, including for some habitat-forming species like the red alga *Gracilaria vermiculophylla* (Falls 2008). However, it remains to be seen if similar range extensions will occur for native species, or whether the effects of climate change with multiple environmental stressors will result in major losses of habitats. These uncertainties are further complicated by management’s restoration efforts. For example, oyster reef habitats in Chesapeake Bay are at unprecedented low levels due to fishing, shell removal and disturbance, and invasive diseases. Climate warming may promote improved winter survival of intertidal oysters, helping to restore a larger spawning stock that persists in more southern parts of the species range.

In light of the recent major decline and overfishing in the Chesapeake Bay stock of blue crabs (CBSAC 2009), especially the sharp decline in mature females in the summer spawning stock (Lipcius and Stockhausen 2002), management decisions for the fishery are ever more precarious. The complex, often interactive effects of climate change add uncertainty to these decisions. Effects of climate change are
already evident in systems like Chesapeake Bay (Pyke et al. 2008), but it remains difficult to partition population fluctuations among intense fishing, a myriad of human impacts on the nearshore environment, and climate change. While variations in weather have always been a factor of uncertainty in fishery management, the projected acceleration of climate change impacts for systems like Chesapeake Bay is certain to make these effects a focus for the future.

Acknowledgments
Thanks to David Armstrong and Gordon Kruse for encouragement to participate in this Lowell Wakefield Symposium. We also thank Sherri Pristash for organizing the symposium; Gordon Kruse and two thoughtful reviewers who made helpful comments and editorial suggestions to improve the manuscript; and Sue Keller for patient editorial assistance in preparing the manuscript. This work was funded by Maryland Sea Grant, North Carolina Sea Grant, NOAA funding to the Blue Crab Advanced Research Consortium, the Chesapeake Bay Stock Assessment Committee, NOAA Saltonstall-Kennedy fund, the Smithsonian Marine Science Network, and the Smithsonian Environmental Studies Program.

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