Migratory behavior of adult female blue crabs, *Callinectes sapidus*, in Pamlico Sound: implications for assessment and protection of the spawning stock

by
Margaret Goldman
August 2007

Date: 8/25/07

Approved:

Dr. Dan Rittschof, Advisor

Masters project submitted in partial fulfillment of the requirements for the Master of Environmental Management degree in the Nicholas School of the Environment and Earth Sciences of Duke University

2007

Migratory behavior of adult female blue crabs, *Callinectes sapidus*, in Pamlico Sound: implications for assessment and protection of the spawning stock

by
Margaret Goldman
August 2007

Masters project submitted in partial fulfillment of the
requirements for the Master of Environmental Management degree in
the Nicholas School of the Environment and Earth Sciences of
Duke University

2007

North Carolina statistical data were provided at the author's request by the North Carolina Division of Marine fisheries. Analyses of these data and conclusions drawn therefrom are those of the author and do not necessarily represent the views from the North Carolina Division of Marine Fisheries.

Abstract

The blue crab, *Callinectes sapidus*, supports North Carolina's largest and most valuable commercial fishery, but according to the 2004 stock assessment, recent fishery-dependent and -independent data suggest the population is in decline. Of particular concern is the status of the spawning stock. Annual recruitment is largely dependent on the size of the spawning stock. A decline in spawning stock abundance and biomass predicts future decline in the population. In order to develop effective management strategies to protect the spawning stock, it is first necessary to (1) understand the migratory behavior of adult female crabs within the Croatan Albemarle Pamlico Estuary System (CAPES) and (2) acquire data that can be used to accurately assess the status of the spawning stock.

Assessment of the spawning stock in the CAPES is currently based on the assumptions that crabs remain in the estuary to spawn and that mature female abundance peaks in the estuary in late summer/early fall. However, recent studies on blue crab reproduction and migration indicate that blue crabs have multiple clutches, migrating seaward with each successive clutch. Upon reaching coastal waters, crabs do not reenter the estuary. Instead, they continue to spawn in the ocean. Based on this new model, peak spawning occurs in the ocean in the fall.

In this study, I examine trawl and gill net survey data collected by the NCDMF to evaluate the use of these surveys in assessing the spawning stock. The demographics of female crabs caught in each survey indicate that gill net survey data collected year-round in east Pamlico Sound may provide a better estimate of spawning stock abundance than trawl survey data collected in June and September in central and west Pamlico Sound. A comparison of the east gill net survey data with post-larval settlement in the estuary suggests that a cumulative index, which would provide us with an estimate of the total number of crabs migrating to the ocean each year, would be a more accurate reflection of the spawning population than a monthly index.

Introduction

The blue crab (*Callinectes sapidus*) supports North Carolina's largest and most valuable commercial fishery, but in recent years commercial landings and value have declined, raising concern over the health of the stock. The 2006 fishery yielded the second lowest landings and the lowest value in the ten year period from 1997-2006 (NCDMF, 2007). Possible factors contributing to this decline include overfishing, unfavorable environmental conditions (loss of habitat, hypoxia, hurricanes, drought), disease, predation and cannibalism (NCDMF, 2004). Blue crabs are harvested in North Carolina as hard crabs, peeler crabs (just before molting), and soft shell crabs (just after molting). While uncertainty over the impact of the peeler fishery on the blue crab population (Eggleston *et al*., 2004) and increasing numbers of immature females taken for the soft-crab industry (Chaves & Eggleston, 2003) have raised concern, hard crabs account for 97% of the total blue crab harvest (NCDMF, 2004). The harvesting of mature females before reproduction for the picking houses in the fall can be particularly stressful on the spawning stock (Uphoff, 1998, Rittschof, pers. comm.). Increasing concerns over fluctuations in blue crab landings and increasing fishing effort have led the North Carolina Division of Marine Fisheries (NCDMF) to identify protection of the spawning stock as a primary concern in its 2004 Fishery Management Plan.

Currently, spawning sanctuaries are the main strategy employed by the NCDMF to protect the spawning stock. Five spawning sanctuaries were established in 1965 at Oregon, Hatteras, Ocracoke, Bardens, and Drum inlets. These areas are closed to commercial crabbing from March 1 to August 31. Recent studies have demonstrated that the sanctuaries provide minimal protection for the spawning population (Medici *et al*. 2006, Eggleston *et al*., unpubl., Ballance & Ballance, 2004). The sanctuaries are small (covering only 12,039 ha) and provide only temporary protection to mature females, which move over spatial scales larger than the sanctuary boundaries (Eggleston *et al*., 2004). Furthermore, the boundaries of the sanctuaries are not strictly enforced (Ballance & Ballance 2004, Medici *et al*., 2006). Medici *et al*. (2006) identified as many as 124 illegal pots on six different days in the Ocracoke inlet sanctuary while conducting a tracking study in 2003.

Outside the spawning sanctuaries, mature females are not protected. A maximum size limit for females was enacted in January 2006 to protect females larger than 6 ¾ inches (5 ¼ for female peeler crabs), but only 1% of female crabs in Pamlico Sound are above this limit (Medici *et al*., 2006) and the rule permits a 5% tolerance. Furthermore, the rule is only in place from September 1 through April 30, so large females may be protected from the peeler fishery in the spring only to be harvested in the hard crab fishery in the summer (D. Rittschof, pers. comm.).

In order to protect the spawning stock, an understanding of the migratory behavior of female blue crabs within the Croatan Albemarle Pamlico Estuary System (CAPES) is necessary. It is well established that after mating in low-salinity areas of the estuary, female crabs migrate seaward to high salinity spawning grounds to release larvae (Van Engel, 1958, Milikin and Williams, 1984). The details of this migration, however, are largely unknown in the CAPES. In North Carolina, the mating season begins in early spring and continues well into the fall (Millikin & Williams, 1984). After mating, blue crabs may (1) remain on the mating grounds until they extrude their first clutch of eggs (oviposition) and then migrate seaward to release larvae, or they may (2) begin migrating before they extrude their first clutch of eggs (Z. Darnell, pers. comm.). In a tidal system, the migration of female crabs to spawning grounds is facilitated by selective tidal-stream transport (STST) (Tankersley *et al.,* 1998). Crabs can move approximately 5 km d^{-1} (Carr *et al*., 2004) using ebb-tide transport (ETT), allowing them to travel over 60 km in the two week period it takes their eggs to develop (Z. Darnell, pers. comm.). At this rate, female crabs could extrude their first clutch of eggs on the mating grounds in west Pamlico Sound and reach the spawning grounds in east Pamlico Sound in time to release larvae. However, much of the western CAPES is non-tidal, and little is known about how crabs migrate in a non-tidal system. Since salinities can fall below 10 ppt in the western areas of the CAPES where crabs mate, it is unlikely that crabs extrude their first clutch before migrating. The eggs would be unable to tolerate salinities this low (Z. Darnell, pers. comm.) It is therefore likely that the second hypothesis is correct, and crabs migrate to higher salinity before they extrude their first clutch.

Tankersley *et al*. (1998) proposed a two stage model for this migration. During Phase I, newly mated non-ovigerous crabs use ETT to travel seaward toward the lower reaches of the estuary. The timing and duration of this phase are uncertain. Crabs may migrate immediately after mating, or they may remain in low salinity waters for some time to build up energy stores before migrating (Medici *et al*., 2006). In a large-scale mark-recapture study, Medici *et al*., (2006) found that crabs tagged and released in the western tributaries of Pamlico Sound in the summer and fall began migrating seaward in late September-early October. It is unlikely though that crabs that mate in the spring would delay migration until the fall (Z. Darnell, pers. comm.). In high salinity water

(~35 ppt), oviposition typically occurs 4-7 weeks after mating, depending on carapace width. Time to oviposition may be longer in low salinity water, but if the 4-7 weeks is correct, crabs that mate in April/May could produce their first clutch of eggs as early as late May/June (Z. Darnell, pers. comm.). Crabs reaching the lower estuary in the fall probably will not spawn until the following spring, since food supply for larvae would be low during cold months (Medici *et al*., 2006).

According to Tankersley *et al*.'s (1998) model, once crabs reach high salinity, they cease ETT while their ovaries and eggs complete development. The first clutch of eggs is extruded, and over a period of 14 days, the egg mass, or 'sponge', develops from yellow/orange to brown to black. During Phase II, females with late-stage sponges migrate vertically toward the surface during nocturnal ebb tides and are transported seaward toward the entrance of the estuary where they release larvae. After releasing larvae, spawning crabs reenter the estuary using flood-tide transport (FTT). Crabs may undergo multiple spawning migrations in a season.

Tankersley *et al*.'s model has recently been revised based on work by Carr *et al*. 2004, Hench *et al.,* 2004 and Forward *et al*., 2005. The new research indicates that females undergo ETT throughout embryo development and after larval release. In addition, recent work by Dickinson *et al.* (2006) in Beaufort, NC indicates that female blue crabs may produce as many as eight clutches over a 25-week spawning period. Thus, according to the new model developed by Forward *et al*. (2005), when female crabs begin to spawn, they continually migrate seaward with each successive clutch. Upon reaching coastal waters, crabs do not reenter the estuary. Instead, they continue to reproduce in the ocean, where there is a greater probability that their larvae will be transported to offshore developmental areas (Forward *et al*., 2005).

Based on a small peak in post-larval settlement in the estuaries in the spring and a larger peak in the fall, peak spawning is thought to occur in April/May and August/September (Dudley & Judy, 1971, Eggleston *et al*., 2004). Ballance & Ballance (2004) observed peak numbers of ovigerous females at Ocracoke and Hatteras inlets during April/May and especially August. Currently, the spawning stock in Pamlico Sound is assessed based on these seasonal peaks in abundance of mature females in the estuary (Eggleston *et al*., 2004). However, according to Forward *et al.*'s (2005) model, mature females are continually leaving the estuary to spawn in the ocean. As the spawning season progresses, an increasing proportion of the spawning population will be found in the ocean. Larval release will continue after the observed peaks in the number of ovigerous females in the estuary (Forward *et al*., 2005). Therefore, in assessing the spawning stock, we should not be concerned with seasonal peaks in abundance in the estuary, but rather with the total number of crabs migrating to coastal waters to spawn over the course of the entire spawning season. Assessing the spawning stock in this way requires spatially and temporally comprehensive data on adult female blue crab abundance on the spawning grounds.

In North Carolina, two fisheries independent research surveys, (NCDMF Programs 120 and 195) are used to develop indices of abundance in the Pamlico Sound estuary system, but a lack of coherence in trends among these indices points to considerable uncertainty regarding stock status (Eggleston *et al*., 2004). The adult survey, Program 195, is used to estimate spawning stock abundance and biomass. The

2004 stock assessment found no statistically significant decline in spawning stock biomass from 1987-2003, although the mean index of SSB from 2000-2002 declined 72% from the previous 10-year average (Eggleston *et al*., 2004). The ability of Program 195 to accurately assess the spawning stock is likely impeded by its limited spatial and temporal coverage. The survey area is comprehensive for western and central Pamlico Sound, but omits much of the Outer Banks and the inlet areas. Albemarle Sound, which contributes a significant percentage of annual landings in NC (25% of hard crab landings from 1994-2001 (Eggleston *et al*., 2004)), has not been surveyed since 1989. Furthermore, the survey is conducted only in June and September, with only the September data used to estimate spawning stock biomass (SSB). Spawning occurs from late spring to fall (Eggleston *et al*., 2004), and since the survey is capturing females that have not yet made it to the spawning grounds, it is highly unlikely that crabs caught in September will spawn that same year. A more representative sampling program would include the spawning grounds and sample more frequently throughout the spawning season. For example, in the Chesapeake Bay, researchers have been able to accurately assess spawning stock abundance and fit stock-recruitment relationships with trawl survey data collected in the lower bay spawning grounds from July through September (Lipcius & Stockhausen, 2002).

In North Carolina, the Pamlico Sound Independent Gill Net Survey has been in place since 2001, and samples monthly from February to December, in west and east Pamlico Sound. The objective of this program is to calculate annual indices of abundance of economically important finfish, but blue crabs are among the top six species caught (K. West, pers. comm.). Detailed data on sex and maturity stage and on environmental variables are collected. These data have not previously been examined, but due to their spatial and temporal coverage, they have great potential to shed light on the migratory behavior of mature female crabs, as well as potential for use in assessing the spawning stock.

The purpose of this research is to analyze the trawl and gill net survey data in ways that may improve our understanding of the migration of adult female blue crabs to spawning grounds, and, in turn, provide insight into how we might better assess and protect the spawning stock in Pamlico Sound. Throughout my analysis, I continually revisit Forward *et al.*'s (2005) model of continuous seaward migration. If most spawning occurs in the ocean, how do we use data collected in the estuary to assess the spawning population?

First, I compare the use of the gill net survey to assess spawning crabs with that of the trawl survey by examining the demographics of female crabs caught in each survey. Since mature females migrate to high salinity to spawn, it is expected that the east Pamlico Sound gill net survey will capture a higher percentage of mature and ovigerous females than the west gill net and trawl surveys.

Next, I analyze catch-per-unit-effort (CPUE) of mature female crabs in each survey for spatial and seasonal patterns. While the trawl survey data have already been analyzed extensively in the stock assessment to quantify the spawning stock, very little spatial analysis has been done on this data. Eggleston *et al.* (unpubl.) used the NCDMF trawl data supplemented by 21 additional sampling stations to look at the geographic distribution and abundance patterns of mature females in Croatan and Pamlico Sound in 2002. The authors were interested in determining the timing of down-estuary migration and identifying potential migration corridors. They hypothesized that there would be an eastward shift in abundance of mature females from June to September as crabs migrated across the Sound to spawn. No change in distribution was identified, perhaps because the authors' hypothesis was based on the wrong assumption: that crabs remain in high salinity areas of the estuary to spawn. Here, I apply the same analysis to the entire survey dataset, 1987-2006, but this time with the assumption that mature females are accumulating in the ocean, not in the estuary. Based on the new model of spawning migration, we should not see an eastward shift in abundance in the estuary from June to September.

The gill net survey provides an excellent opportunity to look at spatial and seasonal patterns in the spawning migration in Pamlico Sound. Since this data is collected monthly from February to November and includes both east and west Pamlico Sound, we may be able to visualize the continuous migration of crabs through the estuary to the ocean. To determine when crabs are migrating and when they are spawning in the estuary, I examine CPUE mature and ovigerous females in east and west Pamlico Sound. Trends in CPUE should give us a clue as to whether crabs are remaining in the estuary or moving out to the ocean to spawn.

The final part of this research will focus on the relationship between mature female abundance on the spawning grounds and post-larval settlement in the estuary. This relationship is critical for developing accurate models for estimating spawning stock and recruitment. Unpublished data from Eggleston *et al*. on post-larval settlement indicate that the main recruitment period of blue crabs to Pamlico Sound is late summer-early fall. Similarly, Dudley and Judy (1971) found peaks in megalopal concentrations in

Beaufort inlet in September-November. Since larval duration of the blue crab is approximately 30 days (Eggleston *et al*., 2004), peak spawning in North Carolina is predicted to occur in August/September. Alternatively, peak postlarval settlement may be a result of continual spawning from spring to fall with oceanographic conditions most favorable for inshore transport of megalopae in the fall (Eggleston *et al*., 2004). Here, CPUE mature females in east Pamlico Sound is compared with seasonal settlement of megalopae at the Duke University Marine Lab dock in the Newport River Estuary to determine which of these hypotheses is supported by the gill net data.[1]

Results of this analysis will be used to inform fisheries managers concerning assessment and protection of the spawning stock and to identify future research needs. A final report will be submitted to the NCDMF.

Methods

Trawl and gill net survey data were obtained from the NCDMF. Data on post-larval settlement in the Newport River estuary were obtained from Matt Ogburn, PhD candidate in Marine Science and Conservation, Duke University.

Program 195: Trawl Survey

The North Carolina Pamlico Sound Survey was initiated in 1987 as a deep water trawl survey (>6 ft) of economically important finfish and non-finfish species (Appendix A.1). Fifty-two grids, selected randomly based on depth and geographic location, are

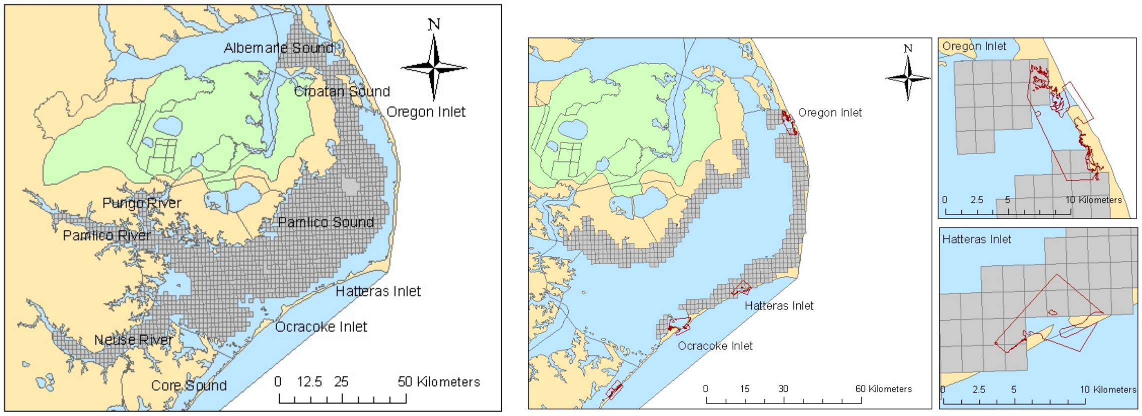
[1] This part of the analysis was done in collaboration with Matt Ogburn, PhD candidate in Marine Science and Conservation at the Duke University Marine Lab, Beaufort, NC.

sampled over a two week period. Samples consist of 20 minute tows using double rigged 30 foot mongoose-type Falcon trawls. The net design and survey methods are similar to those used by the Southeast Area Monitoring and Assessment Program – South Atlantic (SEAMAP-SA) Shallow Water Trawl Survey. The SEAMAP trawl survey was initiated in 1986, funded by the National Marine Fisheries Services (NMFS) and conducted by the South Carolina Department of Natural Resources – Marine Resources Division (SCDNR-MRD) (ASMFC, 2000). The survey is designed to provide long-term fisheries independent data that present an accurate, unbiased accounting of seasonal abundance and biomass of target finfish and non-finfish species (ASMFC, 2000, 2007).

The P195 trawl survey area covers most of Pamlico Sound, Pamlico River, and the Neuse River, and originally extended through Albemarle Sound to a line from the mouth of Alligator River to the mouth of North River. In 1990, the Albemarle Sound strata were eliminated because the NCDMF felt that these strata were not representative of the entire Albemarle Sound system. Since Albemarle Sound is difficult to trawl due to the nature of the bottom, the NCDMF decided to concentrate their resources on the Pamlico Sound system, adding more stations in the Pamlico, Neuse, and Pungo Rivers. The seven designated strata since 1990 are: Neuse River; Pamlico River; Pungo River; Pamlico Sound east of Bluff Shoal, shallow and deep; and Pamlico Sound west of Bluff Shoal, shallow and deep. Since 1991, sampling occurs in June and September. Mature female blue crabs are worked up individually with carapace width, sex and maturity recorded. A map of the sampling area is displayed in Figure 1(a).

Program 915: Gill Net Survey

The Pamlico Sound Independent Gill Net Survey (P915) was initiated in March 2001, and field sampling began in May 2001 (Appendix A.2). Four objectives are identified in this survey: (1) calculate annual indices of abundance for Pamlico Sound for Atlantic croaker, bluefish, red drum, southern flounder, spot, weakfish, spotted seatrout and striped bass, (2) supplement samples for age, growth, and reproduction studies, (3) identify bycatch problems in Pamlico Sound, and (4) characterize habitat utilization in Pamlico Sound. Sampling was originally conducted in all 12 months of the year. Due to extremely low catches and unsafe working conditions, however, the sampling season was shortened in 2002. Sampling no longer occurs from December 15 - February 14. The gill net survey employs a stratified random sampling design similar to that used in the Trawl Survey. The sampling area consists of two regions: eastern Pamlico Sound adjacent to the Outer Banks from southern Roanoke Island to the northern end of Portsmouth Island, and western Pamlico Sound from Stumpy Point Bay to Abel's Bay. The area extends into both the Oregon and Hatteras inlet spawning sanctuaries, but lies completely outside the Ocracoke inlet sanctuary. Four areas are sampled on the east and four on the west, twice a month from March to November, and once a month in February and December. For each grid selected, both shallow (≤ 6 ft) and deep (> 6 ft) strata are sampled with a separate array of nets. Each array of nets consists of 30-yard segments of 3, 3 ½, 4, 4 ½, 5, 5 ½, 6, 6 ½ inch stretched mesh webbing, totaling 240 yards of gill nets. Each month, a total of sixteen core samples are collected in each region (8 in February and December). A map of the survey area is displayed in Figure 1(b).



(a) **(b)**

Figure 1. Grid coverages for NCDMF Pamlico Sound Surveys (a) P195 trawl survey: Fifty-two randomly selected grids are surveyed over a two week period in June and September. The Albemarle Sound strata were eliminated in 1990. (b) P915 gill net survey: twice a month from March to November, four randomly selected grids are surveyed in east and west regions. For each grid selected, both shallow and deep samples are collected, for a total of 16 samples in each region each month. In February and December, only eight samples are collected. Spawning sanctuary boundaries are marked in red.

Megalopae data

Post-larval collections were conducted at the Duke University Marine Lab dock, located approximately 3 km within the Newport River Estuary, NC. Sampling was conducted daily from June 2 to November 15 in 2004 and 2005 and from June 1 to November 15 in 2006. A detailed description of the materials and methods used to collect *Callinectes sapidus* megalopae is available in Sea Grant Report No. 2004-1772-33 (Forward, 2007, Appendix A.3).

Composition of female catch in the Trawl and Gill Net Surveys

Trawl survey data on female crabs from June and September, 1987-2006, were extracted from the survey database maintained by the NCDMF, and the total number of immature, non-ovigerous, and ovigerous crabs were calculated for each year. To determine the spatial distribution of ovigerous crabs within the survey grid, their locations were mapped using ArcMap 9.2 software (fig. 2).

Gill net survey data on female crabs caught in east and west Pamlico Sound, from May 2001 to November 2006, were extracted from the survey database, and the total number of immature, non-ovigerous mature, and ovigerous crabs was calculated for each month of each year. Ovigerous crabs caught on the east were further separated by sponge color, which was recorded in the survey as yellow-orange or brown-black. Female crabs were coded by maturity stage and their locations mapped using ArcMap 9.2 (fig. 3).

Spatial and Temporal Trends in Mature Female Catch Per Unit Effort

Trawl Survey

To investigate patterns in the distribution of mature female crabs in the trawl survey sampling area, catch per unit effort (#mature females/tow) was calculated for June and September for all years, 1987-2006. Using the geographic coordinates for each sample recorded in the database, I used ArcMap 9.2 to generate figures similar to those produced by Eggleston *et al*. (unpubl.), showing the geographic distribution of mature females in the survey area. The mean CPUE at each sample location was displayed as a circle, whose diameter was proportional to CPUE. As was done in 2002, I used these figures to (1) determine if there was an eastward shift in abundance of mature females from June to September and (2) identify possible migration corridors.

If there was a shift in abundance in these years, then we should see relatively large diameter circles on the west side in June and on the east side in September. The presence of a shift would indicate that crabs remained in the estuary to spawn, as predicted by Tankersley *et al*.'s (1998) migration model. The absence of a shift, on the other hand, would indicate that spawning crabs passed through the lower estuary and moved out to coastal waters, as predicted by Forward *et al*.'s (2005) model.

If crabs used specific migration corridors to move across the sound, the CPUE figures should show relatively high abundance within certain geographic regions. In the Chesapeake Bay, migrating females are found predominantly in depths greater than 10 m, leading fisheries managers to establish a marine protected area and corridor (MPAC) in the deep channels of the bay to protect crabs either en route to or at the spawning grounds during the reproductive period (Lipcius *et al*., 2003). The 2002 study found no clear signs that mature females used specific corridors to migrate to spawning grounds. The authors attributed this to the morphology and bathymetry of Pamlico Sound, a uniformly shallow system that is primarily wind-driven and lacks a tidal signal (Eggleston *et al*., unpubl.). An examination of the survey data in all years, however, may reveal spatial trends that were not apparent in 2002.

Gill Net Survey

To investigate temporal and spatial trends in mature female crabs caught in the gill net survey, mean catch per unit effort of immature, mature, and ovigerous crabs was calculated for each month by dividing the number of crabs caught by the number of samples taken that month. Several months were short of the full sixteen samples (eight in February and December), most likely due to weather conditions (K. West, pers. comm.). Also, at the time of writing, data for 2006 was available on the west side only through

November, and on the east side only through September. To examine the spatial distribution of mature females in east Pamlico Sound, CPUE mature females was mapped for each year, similar to the trawl data.

Comparison of east gill net data with seasonal settlement of megalopae

High megalopal settlement in North Carolina estuaries in the fall has long been attributed to peak spawning of blue crabs in the estuary in late summer/early fall. An alternative hypothesis is that peak settlement in the fall is due to continual spawning of blue crabs from spring to fall, with oceanographic conditions most favorable for inshore transport only in the fall (Eggleston *et al*., 2004). To test these hypotheses, biweekly megalopal settlement in the Newport River Estuary was plotted against monthly and cumulative CPUE mature females in east Pamlico Sound for the years 2004, 2005 and 2006. If the former hypothesis is correct, we expect monthly CPUE to peak in late summer/early fall, one to two months before megalopal settlement peaks in the estuary. If the latter hypothesis is correct, we expect cumulative CPUE to peak in late summer/early fall.

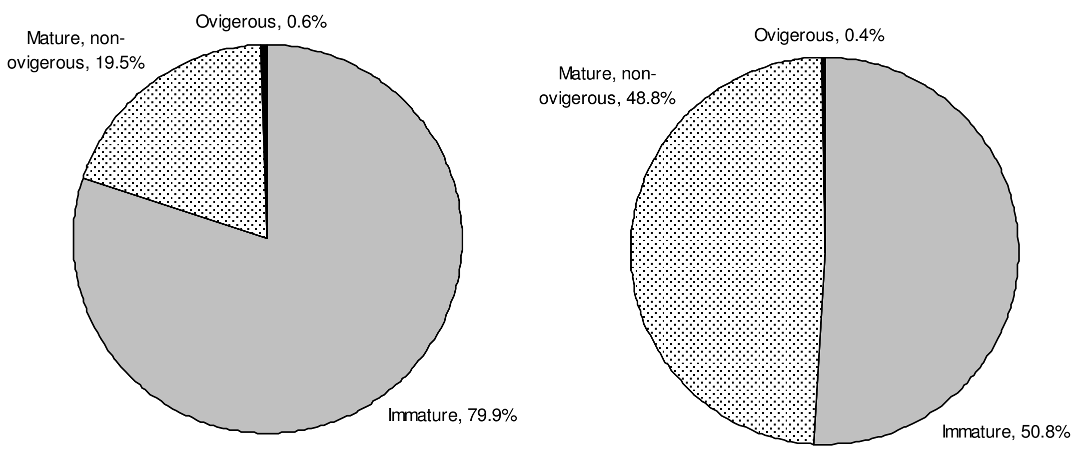
Results

Composition of Female Catch

Trawl Survey

From June to September, the percentage of female crabs that have reached maturity increases from 20 to almost 50%. This change is expected. Since the major recruitment period is in late fall, the percentage of females that have reached maturity should increase throughout the summer and peak the following fall.

On average, ovigerous crabs make up only 2% of the mature females caught in June and less than 1% of the mature females caught in September (fig. 2). When ovigerous crabs are caught in the trawl survey, they tend to be caught about halfway across Pamlico Sound, toward the easternmost reaches of the survey area (fig. 3), at average salinities of 21-22 ppt. From these results, we can infer that mature females in Pamlico Sound begin migrating before they extrude their first clutch of eggs. Salinity in west Pamlico Sound is too low for sponge development. Judging by the low numbers of mature females with eggs in this survey, it is likely that many mature females do not begin spawning until they have already left the survey area.



(a) June **(b) September**

Figure 2. P195 Trawl Survey: Average annual female catch by maturity stage, (a) June (b) September, 1987-2006.

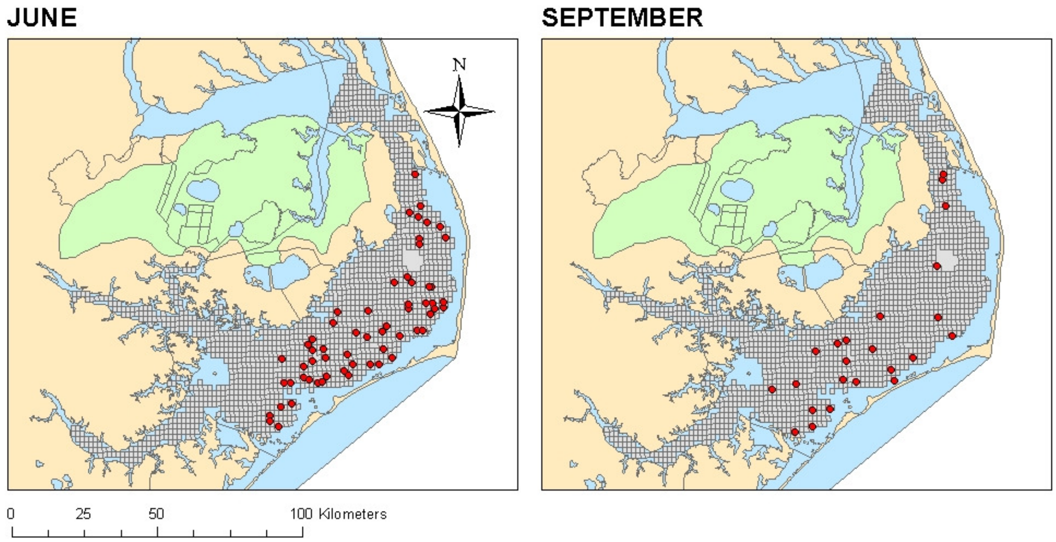


Figure 3. P195 Trawl Survey: survey locations where ovigerous crabs were caught, 1987-2006.

Gill Net Survey

The gill net survey catches predominantly immature females in west Pamlico Sound and mature females in east Pamlico Sound (fig. 4). On the east side, the percentage of mature females with eggs varies from month to month, but in the spring and summer months can be as high as 96%. On the west side, mature females rarely have eggs. The presence of sponge crabs on the west side may be explained by salinity conditions. Sponge crabs were caught on the west side in three of the six years surveyed (15 in 2001, 14 in 2002, and 3 in 2004.) Their presence in 2001 and 2002 was likely due to low freshwater runoff, providing the salinity conditions necessary for egg development, ~ 20-25 ppt (Warner, 1976, as cited by Ballance & Ballance, 2004) (fig. 5). Sponge crabs were found on average at salinities of 21 ppt.

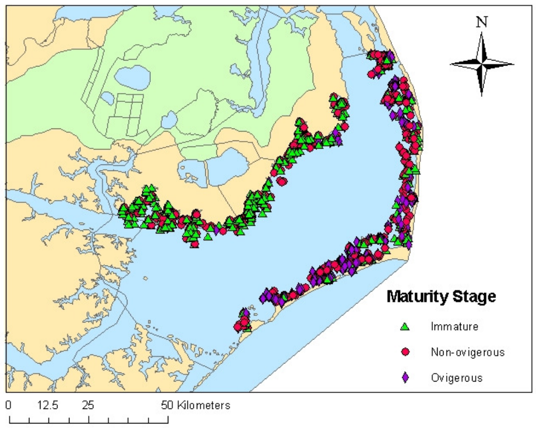


Figure 4. Gill Net Survey: female crabs by maturity stage

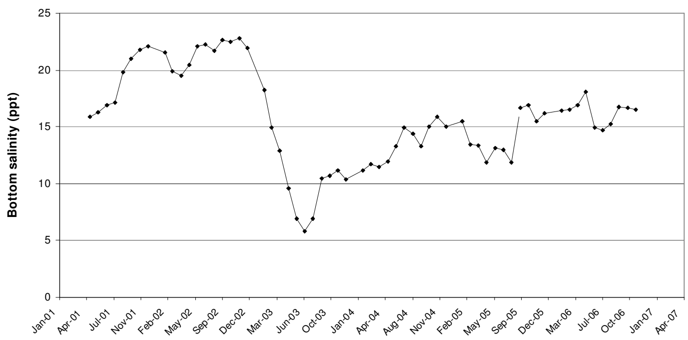
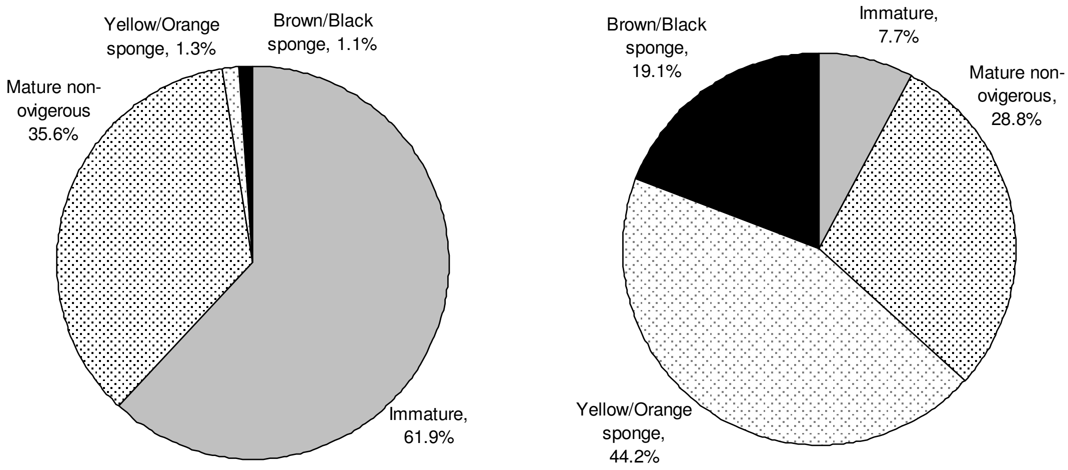


Figure 5. Bottom Salinity (ppt) of samples collected in the west Pamlico Sound Gill Net Survey

Of all females caught in the gill net survey, 2.4% of those caught on the west side were ovigerous and 65% of those caught on the east side were ovigerous (fig. 6). On the east side, yellow/orange sponge crabs occurred about twice as frequently as brown/black sponge crabs.



(a) West **(b) East**

Figure 6. P915 Gill Net Survey: females by maturity in (a) west and (b) east Pamlico Sound

As predicted, the east gill net survey catches the highest percentage of mature and ovigerous females. When we couple what we see in the survey data with Forward *et al.*'s model of crab migration, we obtain a clear picture of the movement of mature females to spawning grounds. After mating in low salinity waters of western Pamlico Sound, non-ovigerous crabs begin to migrate seaward. Upon reaching high salinity areas of the estuary (~ 21 ppt), they begin to spawn, producing multiple clutches as they continue to migrate seaward during ebb tides. High salinity areas in the estuary may shift from year to year, depending on freshwater runoff, but most spawning in the estuary occurs along the Outer Banks. Based on Forward *et al.*'s model, we can infer that mature females caught along the Outer Banks in the east gill net survey are migrating toward the inlets at all stages of egg development and in between clutches. They may cycle through one or two clutches in the estuary, but once they reach the inlets, they continue seaward and release subsequent clutches in the ocean. Since migration is in one direction, there is a continuous movement of crabs out of the estuary.

Spatial and Temporal Trends in the Trawl and Gill Net Surveys

Trawl Survey

The CPUE figures derived from the trawl survey data offer no clear evidence of an eastward shift in the distribution of mature females from June to September (Appendix B). Mature female abundance in the estuary drops dramatically from June to September, often by well over 50%. The absence of an eastward shift and a decline in mature female abundance are consistent with the model of continuous seaward migration. By September, most mature females have either been caught in the fishery or have left the estuary to spawn in the ocean.

As in the 2002 study, there is no indication that blue crabs use specific migration corridors to migrate across the Sound. This suggests that there may be few environmental cues for mature females to follow during their migration (Eggleston *et al*., unpubl.). The figures do reveal, however, that relative abundance of mature females is consistently high in the northern areas of Pamlico Sound. Crabs migrating from Albemarle and Croatan Sounds are clearly an important contribution to the spawning stock. By not sampling in Albemarle Sound, the trawl survey is likely omitting a large portion of the potential spawning stock.

Gill Net Survey

Because it samples year-round and includes the easternmost reaches of the estuary, the gill net survey allows for a more thorough investigation of blue crab migratory patterns. When CPUE mature female crabs is broken down by region and month and plotted over time, some interesting trends become apparent in the data (fig.7). Mature females are rarely caught on the west side before May, indicating that crabs likely begin migrating in late spring. In the summer, CPUE of mature females is much higher on the east side than on the west side. Relatively low CPUE mature females on the west side relative to the east side could be explained by a variety of factors. The likelihood of catching a crab that is a mature female is much lower in the west, where there are more immature females and males in the population. High harvest rates on the west side, particularly of mature crabs, could explain the difference. Also, low CPUE on the west side in the spring and summer months may be explained by mature females leaving the area soon after mating.

In the fall, the trend is reversed, with CPUE mature females generally higher on the west side than on the east side. Mature females gradually disappear from the east and ovigerous crabs are pretty much gone from the estuary by September. By early fall, most spawning females have moved out to coastal waters. Crabs continue to spawn in the ocean as long as temperatures are warm enough – as late as November (Forward *et al*., 2005, Dickinson *et al*., 2006).

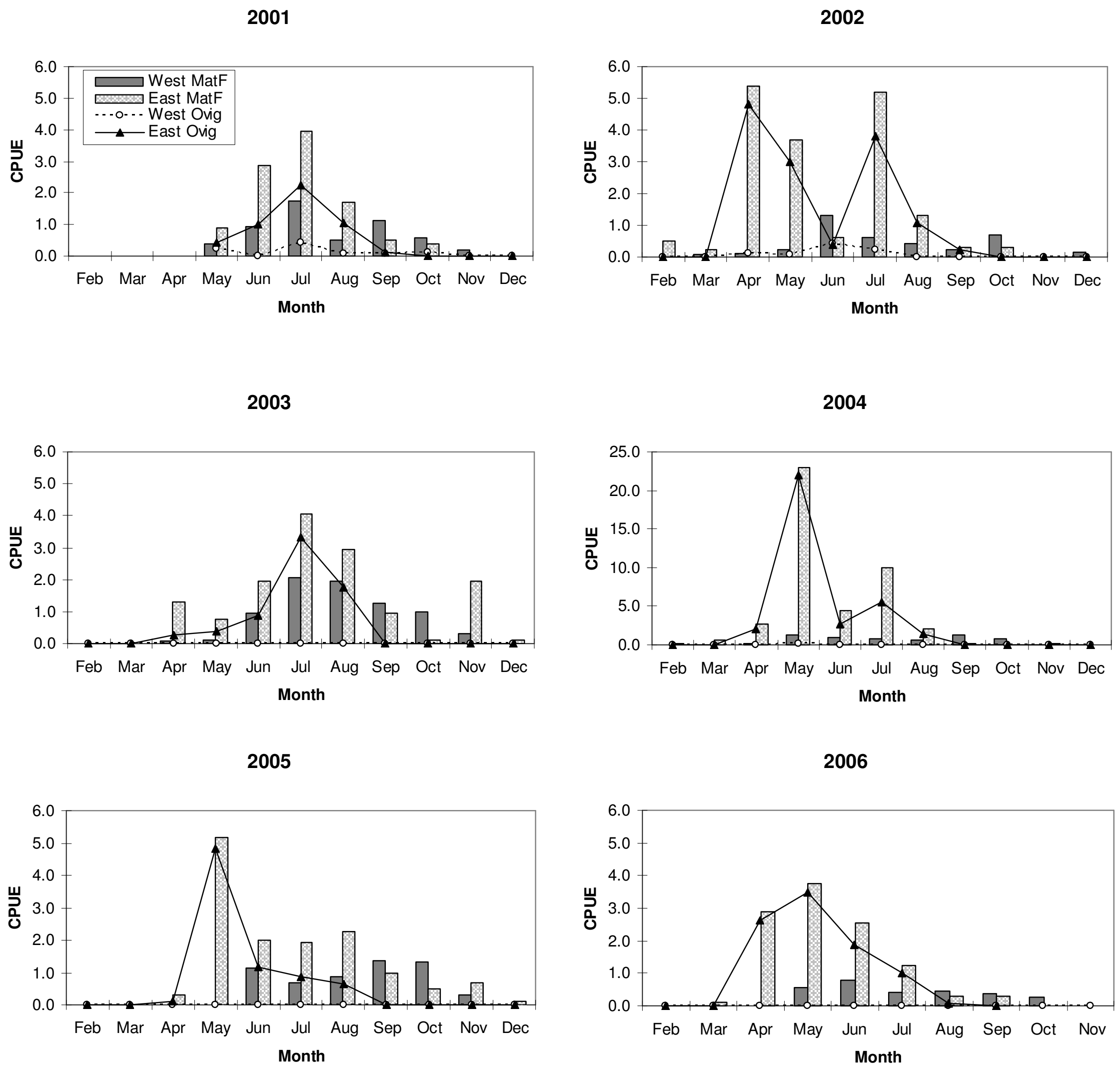


Figure 7. P915 Gillnet Survey: CPUE mature and ovigerous females, east and west Pamlico Sound. Note the scale is different for 2004, due to very high CPUE in May and July. In 2006, survey data were available only through November on the west side and September on the east side.

The absence of ovigerous females in east Pamlico Sound in the fall indicates that mature females arriving on the spawning grounds in the fall will not begin spawning until the following spring. Peaks in abundance of mature females in east Pamlico Sound in April/May can be attributed to crabs restarting spawning after over-wintering near the Outer Banks (D. Rittschof, pers. comm.). In the gill net survey, seasonal peaks in abundance of mature females on the spawning grounds have varied from year to year, generally occurring in April/May and/or July. In the past three years, CPUE mature females in east Pamlico Sound was relatively high in April/May compared to July. Since crabs are continually moving through the estuary and accumulating in the ocean, spawning crabs are underrepresented by the gill net survey in late summer/fall. Therefore, in assessing the spawning stock, we should not be thinking in terms of peak abundance of spawning crabs in the estuary. Rather, we should be considering the cumulative total of mature females passing through the estuary spawning grounds on their way to the ocean. By adding monthly CPUE over time, we should be able to get a fairly good index of the number of crabs migrating out to the ocean each year to spawn. From figure 8 below, we can see that cumulative CPUE levels off in late summer/early fall, so this is when we should expect to see the largest numbers of spawning crabs in coastal waters.

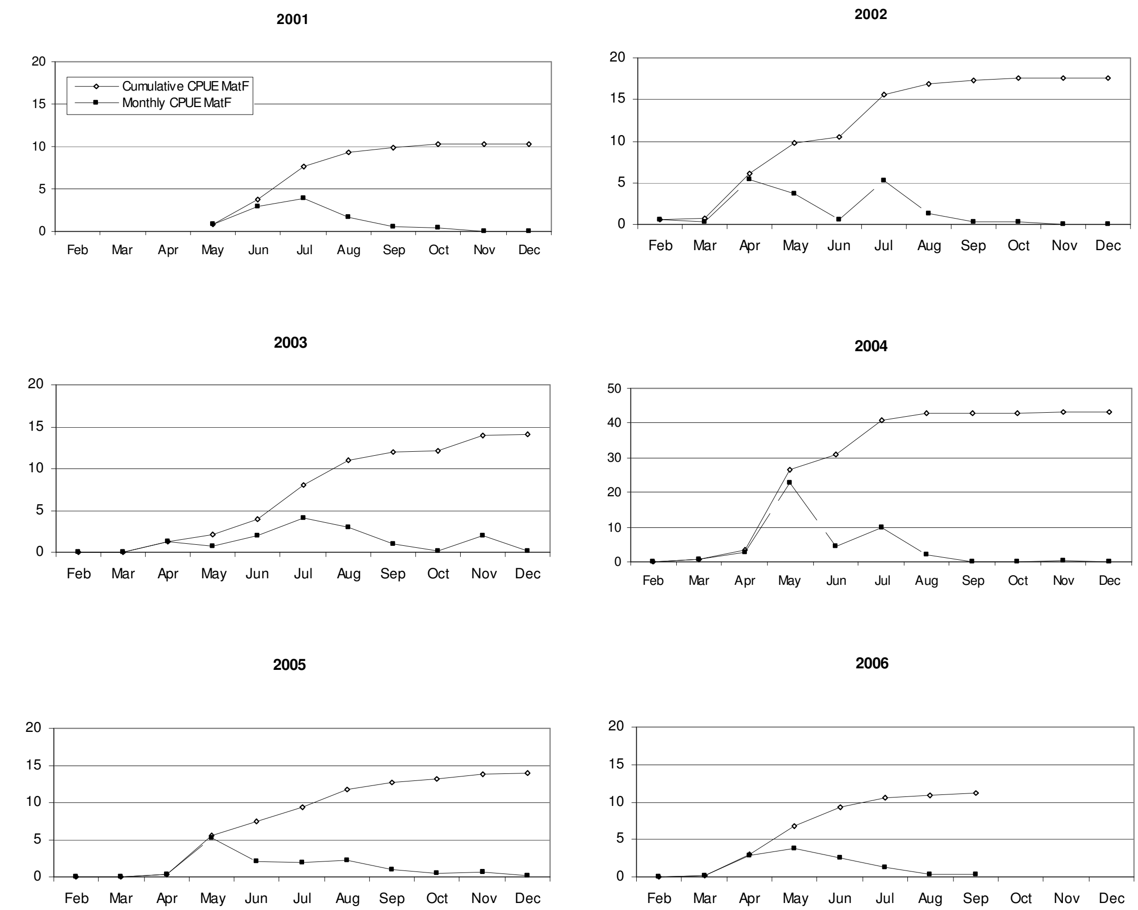


Figure 8. P915 east gill net survey: monthly and cumulative CPUE MatF. Note the scale is different in 2004.

To determine whether there were any spatial trends in the distribution of spawning crabs along the Outer Banks, I created maps of mature female abundance in the east gill net survey area. From these maps, it is clear that mature females tend to aggregate near Ocracoke, Hatteras, and Oregon inlets (fig. 9), indicating that they are heading toward coastal waters. No differences in the geographic distribution of crabs at different stages of embryonic development are evident (fig. 10). However, yellow-orange sponge crabs are about twice as abundant as brown-black sponge crabs. Most crabs with late-stage eggs have probably already reached the inlets and coastal waters, outside the reaches of the survey.

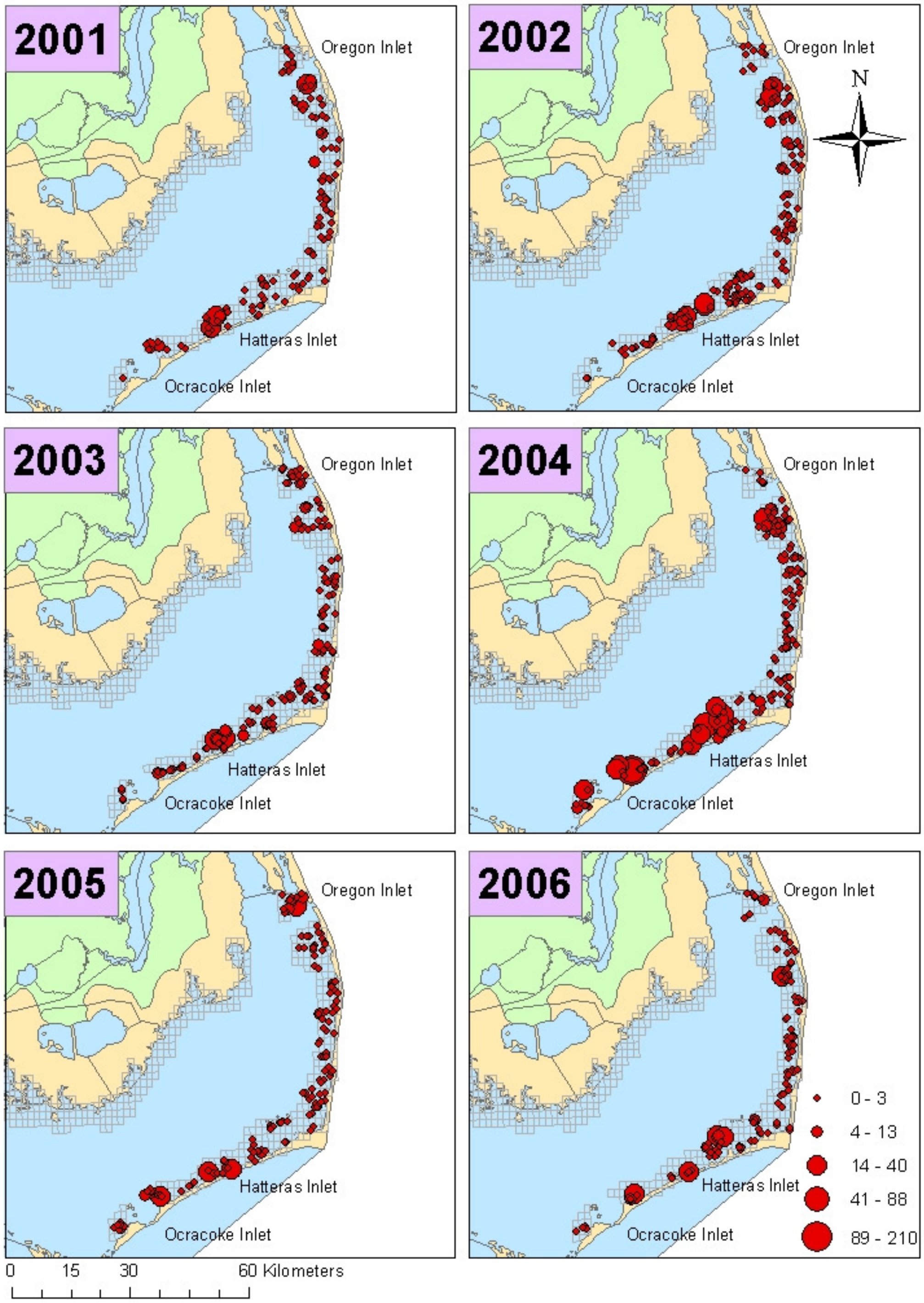
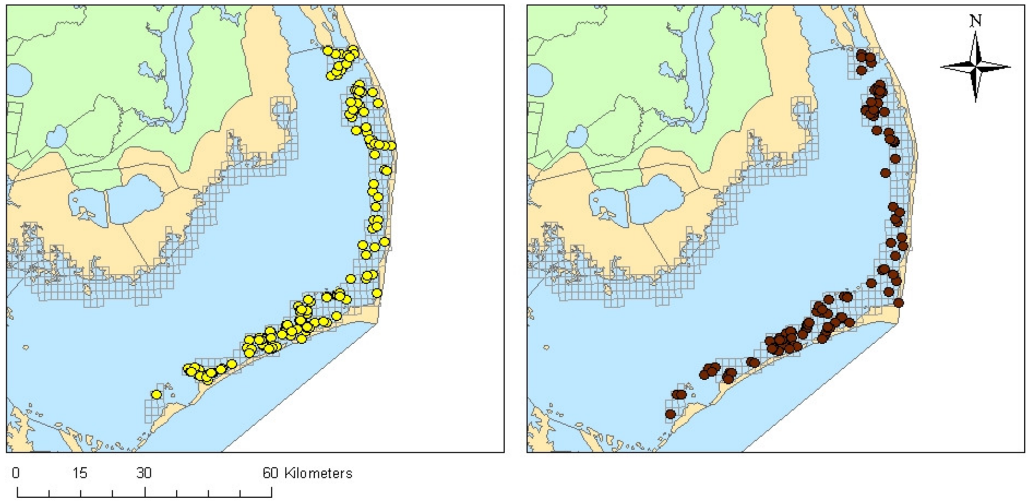


Figure 9. CPUE mature females in the east Gill Net survey. Larger diameter circles indicate higher CPUE.



(a) **(b)**

Figure 10. Ovigerous crabs caught in East Pamlico Sound, 2001-2006, by sponge color (a) yellow/orange, (b) brown/black

Comparison with seasonal settlement of megalopae

When adult female crabs release their larvae, the larvae are exported to the continental shelf where they develop through seven zoae stages in four to five weeks (Epifanio, 1995). During the post-larval stage, megalopae re-enter the estuary and settle in benthic habitats such as seagrass or shallow detrital habitats (Etherington & Eggleston, 2003). Re-entrance into the estuary is associated with southward, alongshore wind events, occurs in discrete pulses, and does not necessarily occur in parent estuaries (Epifanio, 1995). In North Carolina, post-larval settlement is highest in Pamlico Sound in the fall (Eggleston *et al*., 2004). Near Beaufort inlet, peak settlement occurs in September/October (Dudley and Judy, 1971, Forward *et al*., 2004).

In 2004, 2005, and 2006, megalopal settlement in the Newport River Estuary near Beaufort inlet remained low until mid-august, with peak settlement in September/October. Peak spawning is predicted to occur 4-5 weeks before this, in August (Eggleston *et al*., 2004). As discussed in the section above, however, CPUE mature females in the east gill net survey peaked in May of these years. Cumulative CPUE, on the other hand, consistently leveled off in late summer/early fall, indicating peak numbers of spawning females in coastal waters at this time (fig. 11). High megalopal settlement in the fall may also be attributed to retention of megalopae in coastal waters during the summer (Tilburg, 2007) and oceanographic conditions most favorable for inshore transport in the fall (Eggleston *et al*., 2004). This suggests that patterns in megalopal settlement are a function of continual spawning from spring to fall, with peak numbers of spawning females in the ocean in late summer/early fall and re-entrance of megalopae into the estuary in the fall during favorable wind and tidal conditions (Epifanio, 2005, Eggleston *et al*., 2004).

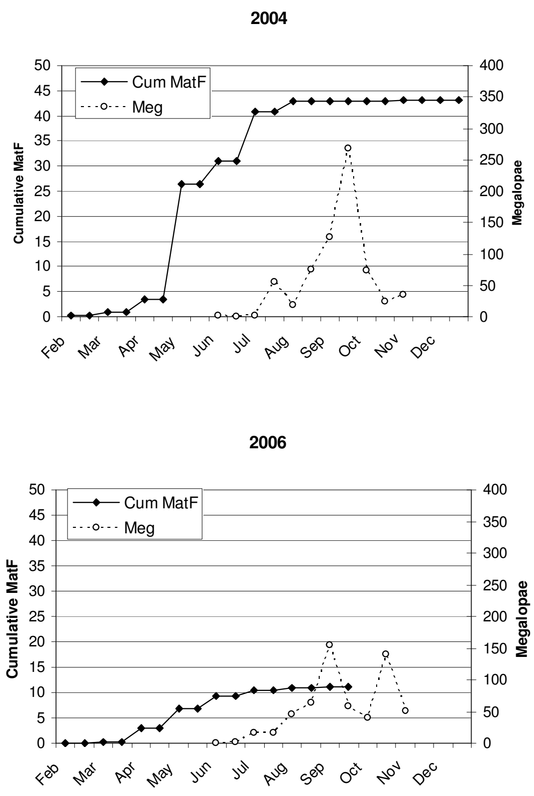


Figure 11. Biweekly megalopal settlement at the Duke University Marine Lab Dock and cumulative CPUE mature females in the east gill net survey.

Discussion

A lack of comprehensive spatial and temporal data on adult female blue crabs, and the nontidal, wind-driven nature of the CAPES have limited our understanding of the migratory behavior of adult females and our ability to assess the status of the spawning stock. The trawl survey used to calculate annual indices of spawning stock abundance stops short of the spawning grounds and therefore targets only the potential spawning population, not the actual spawning population. Only a tiny fraction of crabs caught in the trawl survey have eggs, and these crabs tend to be found in central and eastern Pamlico Sound. Currently, the September trawl data are used to calculate spawning stock abundance and biomass, but the absence of ovigerous crabs on the estuarine spawning grounds in the fall (as shown by the gill net survey) indicates that the June trawl data would be more appropriate. Mature females caught in the trawl survey in September have not yet reached the spawning grounds, and most likely will not spawn until the following spring. The June trawl data also pose a problem though. Blue crabs are under intense fishing pressure in the CAPES. Many of the crabs caught in this survey may not even make it to the spawning grounds. Another concern with using the trawl data to estimate spawning stock is that the sampling area does not include Albemarle Sound, an important habitat for blue crabs, judging by the high level of commercial landings in this region. Without accounting for adult females migrating from Albemarle Sound, the survey misses a significant portion of the potential spawning population. Finally, in assessing the spawning stock in this way, we are assuming that the spawning stock each year is represented by peak abundance of spawning females in the estuary during late summer/early fall. But recent research on the movement of blue crabs during the spawning migration indicates that mature females continue to migrate seaward after releasing their first clutch of eggs. Therefore, the true spawning population is in the ocean, and to assess this population we need to know how many crabs migrate to coastal waters over the course of the spawning season.

Unfortunately, we have no long-term data on blue crabs that covers the entire spawning season. The Pamlico Sound Independent Gill Net Survey, however, was initiated in 2001 and is conducted monthly from mid-February to mid-December. While the survey is not designed to target blue crabs, blue crabs are a significant portion of the catch. Since the survey is conducted in east and west Pamlico Sound, the gill net data offer a unique opportunity to look at female crabs at the beginning and end of their migration.

The absence of adult females in west Pamlico Sound before May indicates that crabs begin migrating to the spawning grounds in late spring. Crabs caught on the east side in April/May most likely arrived on the spawning grounds the previous fall and over-wintered near the Outer Banks. In the spring and summer, nearly 70% of the mature females caught in the gill net survey on the east side of Pamlico Sound are ovigerous, indicating that most spawning in the estuary occurs along the Outer Banks. The gill net survey data reveal a distinct spawning season for blue crabs in the estuary, from April to September. Mature females are sometimes caught in the survey outside this period, but no ovigerous crabs are caught. By September, most spawning crabs have left the estuary and moved out to coastal waters, where they continue to spawn as long as temperatures are warm enough. Viewing the migration as movement in one direction implies that the number of mature females in coastal waters is continually increasing throughout the spawning season. Thus, rather than using just one month as our index of spawning stock abundance, we should use all months of the spawning season.

The use of a cumulative abundance index rather than a monthly abundance index for estimating spawning stock is supported by trends in megalopal settlement in the estuary. Megalopal settlement peaks in late summer/fall in North Carolina estuaries, about the time when cumulative CPUE mature females in east Pamlico Sound levels off. By contrast, there is little correspondence between trends in monthly CPUE and post-larval settlement.

Since the gill net survey samples 11 months out of the year and covers the easternmost areas of the Sound, the gill net survey may provide a better index of spawning stock abundance than the trawl survey. However, whether the gill net data accurately represent mature female abundance on the spawning grounds remains to be seen. The gill net survey is not designed for this purpose, so further analysis of factors that affect catch efficiency is necessary. In addition, the gill net survey area may be omitting a large portion of the spawning population by not sampling near Bardens and Drum inlets. An accurate assessment of the spawning stock requires adequate coverage of the spawning grounds.

Recommendations and Conclusions

Just as in Medici *et al*. (2006) and Eggleston *et al*. (unpubl.), the results of this study indicate that protection of the blue crab spawning stock in the CAPES will require more comprehensive management measures than those currently employed. The spawning sanctuaries are small relative to the scale of movement of spawning crabs

(Medici *et al*., 2006, Eggleston *et al*., unpubl.). Expanding the sanctuary area to include the entire Outer Banks would protect mature females during the later phase of their seaward migration. Crabs that made it to the Outer Banks would be able to move out to coastal waters where they would continue to spawn. A ban on fishing in this region, however, would disproportionately disadvantage Outer Banks crabbers. Furthermore, such a ban would not address the issue of how to ensure that mature females make it to the spawning grounds. If they are not protected en route to the spawning areas, mature females have a very good chance of being caught in the intensive hard crab fishery. Unlike in the Chesapeake Bay, there do not appear to be any specific corridors that blue crabs use to migrate across the Sound, so establishment of a protected area corridor does not seem to be a viable option, at least based on our current knowledge of blue crab migratory behavior. Managers may therefore want to consider protection measures other than expanding closures of specific areas during designated times.

One possible alternative to spawning sanctuaries raised by Medici *et al*. (2006) is a partial or total ban on the harvest of females (with and/or without a sponge). Banning the take of females would increase the number of individuals contributing to the production of larvae. If a ban were placed on the harvest of ovigerous crabs, it would essentially have the same (although slightly weaker) effect as establishing a protected area along the Outer Banks. As demonstrated by the gill net and trawl survey data, most of the females caught in east Pamlico Sound during the spring and summer months have eggs, whereas very few crabs caught in the central and western areas of the sound have eggs. Again, Outer Banks crabbers would be disproportionately affected by this rule. In addition, a no-sponge crab rule would not address the issue of how to ensure that crabs get a chance to reproduce in the first place. Expanding the ban to include non-ovigerous females would protect mature females en route to and on the spawning grounds.

In considering a partial or total ban on the harvest of females, managers should first evaluate the potential impacts of such a ban on different regions of the fishery. Since the crab population in eastern Pamlico Sound consists primarily of females (males do not migrate), crabbers who place their pots in the eastern areas of the Sound would be most affected by such a ban. But if the goal is to protect the spawning stock, some limits on the take of females that are en route to and on the spawning grounds will have to be imposed.

In assessing the spawning stock in Pamlico Sound, I recommend the NCDMF consider using the east gill net data. The trawl survey only samples two months out of the year, and provides very little coverage of east Pamlico Sound. The mature females caught in this survey represent potential spawning stock, not actual spawning stock. Since blue crabs migrate continually from spring to fall, leaving the estuary to spawn in coastal waters, any estimation of spawning stock abundance based on data collected in the sound should be cumulative. We need data that is collected on the spawning grounds on a monthly basis throughout the spawning season (April – September). While the gill net survey is not designed to target blue crabs, it is the most spatially and temporally comprehensive dataset of blue crabs on the spawning grounds. Seasonal patterns in cumulative CPUE mature females in the east gill net survey correspond well with patterns in megalopal settlement in the estuary.

This study was strictly qualitative, but the next step would be to determine whether cumulative CPUE is capable of predicting post-larval settlement in Pamlico

Sound. If it is possible to fit stock-recruitment relationships with the gill net data, than the gill net survey may provide a better index of spawning stock than the trawl survey.

If the NCDMF continues to use the trawl survey to assess the blue crab spawning stock, the limitations of this survey should be taken into account. Unfortunately, expanding the trawl survey to include areas adjacent to the Outer Banks is not feasible. These areas are predominantly seagrass beds and are not trawlable because (1) trawling would damage these critical habitats and (2) it has been demonstrated that samples collected in seagrass beds are not representative (K. West, pers. comm.). Without sampling on the spawning grounds, however, the trawl survey is limited to assessing only the potential spawning stock, not the actual spawning stock. If a ban were placed on the take of mature females, then abundance of mature females throughout the sound in spring and summer months would be a good estimate of abundance on the spawning grounds. A better understanding of how mature females migrate in the western non-tidal areas of the sound would also help managers use potential spawning population as an estimate of actual spawning population.

The greatest limitation of the trawl survey is that it is only conducted two months out of the year. Since crabs spawn from spring to fall, we need to be able to account for mature females as they move out of the estuary. The NCDMF should therefore consider sampling more frequently in order to develop a cumulative index. If only two months can be sampled due to resource constraints, then I recommend sampling in May and July, when we generally find peak numbers of spawning crabs in the estuary. The index of spawning stock should be cumulative rather than monthly.

In summary, in developing measures to protect and assess the blue crab spawning stock in Pamlico Sound, we should take into account that (1) blue crabs typically do not extrude their first clutch of eggs until they reach high salinity water ~ 21 ppt, (2) migration of mature females is in one direction – once they reach the ocean, crabs do not reenter the estuary, (3) by September, most spawning crabs are gone from the estuary. Spawning continues in the ocean as long as temperatures are warm enough – as late as November, and (4) post-larval abundance in the estuary in the fall is a function of continual spawning from spring to fall and is best represented by mature females in the ocean in September.

Recent declines in commercial landings and value in the blue crab fishery indicate that a partial and/or total ban on the take of females should soon be implemented in order to ensure sufficient numbers of females survive to contribute to larval production. The NCDMF should continue to evaluate blue crab catch in the gill net survey, particularly in the eastern survey region, and consider using data collected in this survey in assessments of the spawning stock.

Acknowledgements

Special thanks to Katy West and Sean McKenna of the NCDMF for providing the gill net and trawl survey data, and Matt Ogburn for providing the megalopae data. Thanks to Matt Ogburn, Zack Darnell and my advisor Dan Rittschof at the Duke University Marine Lab for sharing their extensive knowledge and advice in this project. Thanks to Dan Eggleston for sharing with me his paper, *Assessment of spawning sanctuaries and possible migration corridors for the blue crab spawning stock in North Carolina*.

References

Atlantic States Marine Fisheries Commission (ASMFC) (2007). Southeast Area Monitoring and Assessment Program (SEAMAP). http://www.asmfc.org/seamap.htm.

Atlantic States Marine Fisheries Commission (ASMFC) (2000). SEAMAP-SA 10-Year Trawl Report: Results of Trawling efforts in the coastal habitat of the South Atlantic Bight, FY 1990-1999. Special Report No. 71.

Carr, S.D., Tankersley, R.A., Hench, J.L., Forward, R.B., and R.A. Luettich, Jr. (2004). Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration. Estuarine, Coastal and Shelf Science 60: 567-579.

Chaves, J.C., and D.B. Eggleston (2003). Blue crab mortality in the North Carolina soft-shell industry: biological and operational effects. J. Shellfish Res. 22: 241-249.

Dickinson, G.H., Rittschof, D., and C. Latanich (2006). Spawning Biology of the Blue Crab, *Callinectes Sapidus*, in North Carolina. Bulletin of Marine Science 79(2): 273-285.

Dudley, D.L. and M.H. Judy (1971). Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. U.S. Dept Commer, NOAA Tech Rep NMFS SSRF-637, 10 p.

Eggleston, D.B., Johnson, E.G., and J.E. Hightower (2004). Population dynamics and stock assessment of the blue crab in North Carolina. Final Report for Contracts 99-FEG-10 and 00-FEG-11 to the North Carolina Fishery Resource Program, North Carolina Sea Grant, and the North Carolina Department of Environmental Health and Natural Resources, Division of Marine Fisheries.

Eggleston, D.B., Bell, G.W., and S.P. Searcy (unpub.). Assessment of spawning sanctuaries and possible migration corridors for the blue crab spawning stock in North Carolina. North Carolina State University, Dept of Marine, Earth & Atmospheric Sciences, Raleigh, NC.

Epifanio, C.E. (1995). Transport of blue crab (*Callinectes sapidus*) larvae in the waters off Mid-Atlantic States. Bulletin of Marine Science 57(3): 713-725.

Epifanio, CE (2003). Spawning behavior and larval ecology: a brief summary. Bulletin of Marine Science 72(2): 352-330.

ESRI. 2006. ArcMap 9.2 [computer program]. ESRI, Redlands, Calif.

Etherington, LL, Eggleston, DB (2003). Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. Can. J. Fish. Aquat. Sci. 60: 873-888.

Forward, R.B., Jr., Cohen, J.H., Irvine, R.D., Lax, J.L., Mitchell, R., Schick, A.M., Smith, M.M., Thompson, J.M. and J.I. Venezia (2004). Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary 269: 237-247.

Forward, R.B., Cohen, J.H., Darnell, M.Z., and A. Saal (2005). The circatidal rhythm in vertical swimming of female blue crabs, *Callinectes sapidus*, during their spawning migration: a reconsideration. J. Shellfish Res. 24: 587-590.

Hench, J.L, Forward, R.B., Carr, S.D., Rittshof, D., and R.A. Luettich (2004). Testing a selective tidal-stream transport model: observations of female blue crab (*Callinectes sapidus*)vertical migration during the spawning season. Limnol. Oceanogr. 49: 1857-1870.

Lipcius, R.N. and W.T. Stockhausen (2002). Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar Ecol Prog Ser 226: 45-61.

Lipcius, R.N., Stockhause, WT, Seitz, R.D. and P.J. Greer (2003). Spatial dynamics and value of a marine protected area and corridor for the blue crab spawning stock in Chesapeake Bay. Bulletin of Marine Science 72(2): 453-469.

Medici, D.A., Wolcott, T.G., and D.L. Wolcott (2006). Scale-dependent movements and protection of female blue crabs (*Callinectes sapidus*). Can. J. Fish. Aquat. Sci. 63: 858-871.

Milikin, M.R., and A.B. Williams (1984). Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, FAO Fisheries Synopsis No. 138.

North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries (2004). North Carolina Fishery Management Plan: Blue Crab.

North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries (2005). The North Carolina Pamlico Sound Survey.

North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries (2005). Biological Program Documentation, Program 915: Presence/Absence of Disease Sampling, Pamlico Sound Independent Gill Net Survey & Pamlico and Neuse Watershed Gill Net Survey, Independent Fishery. Masterfile NER.NMA900-1.MISC.

North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries (2007). Stock Status of the Blue Crab in North Carolina, 2007. http://www.ncfisheries.net/stocks/index.html.

Tankersley, R.A., Wieber, M.G., Sigala, M.A., and K.A. Kachurak (1998). Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: evidence for selective tidal-stream transport. Biol. Bull. 195: 168-173.

Tilburg, C.E., Dittel, A.I. and C.E. Epifanio (2007). Retention of crab larvae in a coastal null zone. Estuarine, Coastal and Shelf Science 72: 570-578.

Uphoff, J.H., Jr. (1998). Stability of the blue crab stock in Maryland portion of Chesapeake Bay. J. Shellfish Res. 17: 519-528.

Van Engel, W.A. (1958). The blue crab and its fishery in the Chesapeake Bay, Part 1: Reproduction, early development, growth, and migration. Commer. Fish. Rev. 20: 6-17.

Warner, W.W. and J. Barth (1976). Beautiful Swimmers: Watermen, Crabs, and the Chesapeake Bay. Boston: Back Bay Books.