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[Article]

Do Blue Crab Spawning Sanctuaries in North Carolina Protect the Spawning Stock?

David B. Eggleston,*[1] Geoffrey W. Bell, and Steven P. Searcy
Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina 27695-8208, USA

Abstract.—Spawning sanctuaries located at the five major inlets to Pamlico Sound, North Carolina, as well as various harvest controls, have not been adequate to protect the spawning stock of the blue crab *Callinectes sapidus*. We conducted an extensive trawl survey within Pamlico and Croatan sounds as well as five inlet spawning sanctuaries during 2002 to quantify the spatiotemporal use of spawning sanctuaries by mature female blue crabs and to identify potential migration corridors to spawning grounds. The abundance of mature females was highest along the northwestern portion of Pamlico Sound, suggesting this is an important staging area for females before their seaward migration; however, there was no clear evidence of specific migration corridors. Mature female abundance was no different inside inlet sanctuary boundaries versus 1–2 km outside sanctuary boundaries, and sanctuaries only protect 44.9% and 0.7% of the current local inlet and Pamlico Sound-wide spawning populations, respectively, of mature female blue crabs. In general, the abundance of mature female blue crabs was higher at inlets located to the extreme north or south in Pamlico Sound than at inlets located in the central portion of the sound. The results from this study suggest that the particular geometry and placement of inlet spawning sanctuaries are not adequate to protect the North Carolina blue crab spawning stock, and other management options should be considered, such as (1) a double sanctuary and migration corridor system located in northern and southern portions of Croatan and Pamlico sounds coupled with either (2) reduction of fishery effort on females or (3) seasonal closures.

Spawning sanctuaries closed to fishing are used in fisheries management worldwide to help conserve the spawning stock of intensively fished species (Bohnsack 1998; Luckenbach et al. 1999; Lipcius et al. 2003; Dew and McConnaughey 2005; Nemeth 2005; Lambert et al. 2006). A major postulated benefit of spawning sanctuaries is that they enhance recruitment from the protected segment of the spawning stock to local and metapopulations. The efficacy of these sanctuaries to protect a given spawning stock, however, will depend on their spatial and temporal design characteristics, as well as management practices. For example, when sanctuary boundaries matched the spatial footprint of aggregating red hind *Epinephelus guttatus* on spawning grounds, increases in the target population abundance at the spawning sites were observed (Nemeth 2005; Nemeth et al. 2006). Conversely, opening spawning sanctuaries to commercial fishing resulted in the collapse of Alaska's fishery for red king crab *Paralithodes camtschaticus* (Dew and McConnaughey 2005). Blue crab *Callinectes sapidus* spawning sanctuary boundaries in the Chesapeake Bay were initially too small to protect a significant portion of the spawning stock and have subsequently been expanded to include migration corridors that link subadult habitats to areas of larval release (Lipcius et al. 2003). A tag return study of mature female blue crabs inside and outside of the spawning stock sanctuary in Chesapeake Bay indicated that crabs were approximately five times more likely to be captured by the fishery outside than inside the sanctuary and that a significant portion of the spawning stock can spawn within the sanctuary (Lambert et al. 2006). For many species, protection of migration routes that are exploited by fishers (e.g., crabbers moving pots downriver to coincide with mature female blue crab migrations to inlets), coupled with adequate spawning sanctuaries, may be a critical component of effective conservation and management strategies.

The blue crab supports the world's largest fishery for crabs (Lipcius and Eggleston 2001); however, blue crab population size and commercial landings are declining in many areas throughout the east and Gulf coasts of the United States (Seitz 2005). For example, the blue crab spawning stock abundance and biomass in Chesapeake Bay have declined by 81% and 84%, respectively from 1992 to 2000, with a concurrent decline in larval and postlarval abundance (Lipcius and Stockhausen 2002). Similarly, in Pamlico Sound, North Carolina, blue crab spawning stock biomass and concurrent postlarval settlement have declined by

* Corresponding author: eggleston@ncsu.edu
[1] Present address: Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA.

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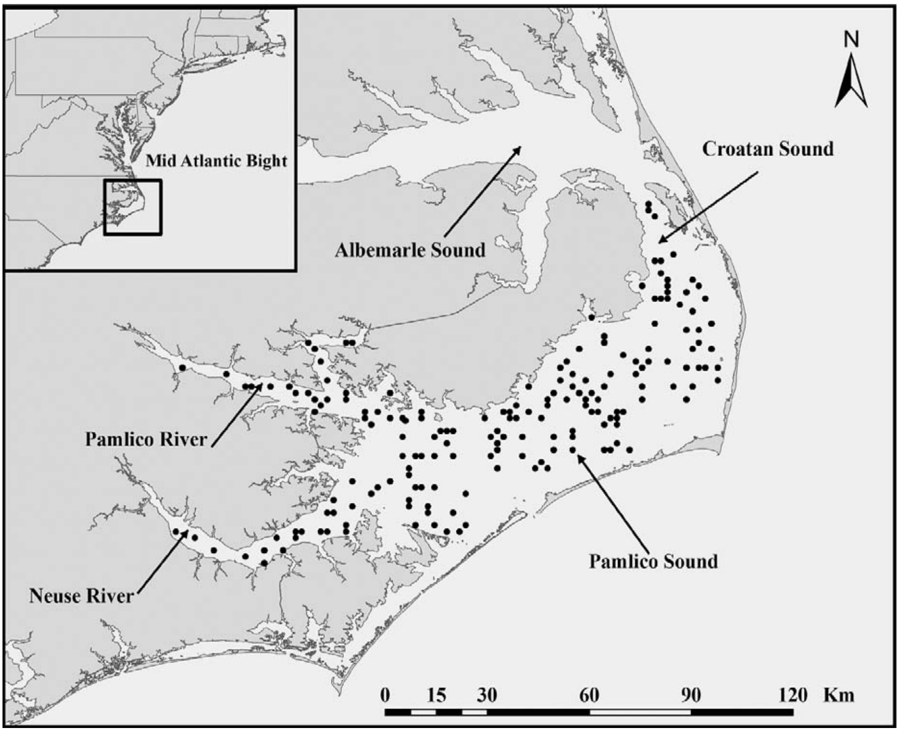

FIGURE 1.—Locations of trawl survey sampling sites for mature female blue crabs conducted by the North Carolina Division of Marine Fisheries (Program 195) during 2002. Inset shows North Carolina coastal waters in relation to the Mid-Atlantic Bight.

approximately 74% since 1999 (Eggleston et al. 2004). The spawning grounds for the blue crab have been partially protected from exploitation in Chesapeake Bay and Pamlico Sound, but the sanctuaries and various harvest controls have not been adequate to protect the spawning stock (Lipcius and Stockhausen 2002; Lipcius et al. 2003; Eggleston et al. 2004).

This study focuses on measuring the relative abundance of reproductive-stage female blue crabs within and outside of five inlet spawning sanctuaries connecting Pamlico Sound to the Atlantic Ocean in North Carolina. Blue crab mating typically occurs in the mesohaline and oligohaline zones of estuaries in North Carolina from May to October, and spawning occurs from April to November, with peak spawning in June through August (Dudley and Judy 1971; Epifanio 1995). The migration of inseminated females to inlet spawning grounds involves (1) movement to the lower estuary before brood production and (2) the subsequent migration of late-stage ovigerous females to the estuary mouth and adjacent coastal waters, where they release their fertilized eggs (Tankersley et al. 1998). After spawning, mature females may move back into the lower estuary or remain in coastal waters, where they may produce subsequent broods (Ballance and Ballance 2002; Forward et al. 2003; Medici et al. 2006).

Some of the key assumptions for establishing effective spawning sanctuaries and protected migration corridors are that the sanctuary boundaries encompass the target spawning stock and that the sanctuaries protect a substantial portion of the population from harvest. These assumptions have yet to be tested for North Carolina's blue crab spawning sanctuaries, which were established in 1965. The purpose of this research was to quantify spatiotemporal variation in abundance of mature female crabs (accounting for egg development) to determine spatial patterns of blue crab spawners and seasonality of spawning in relation to North Carolina spawning sanctuaries. We also wanted to identify potential migration corridors from the mesohaline and oligohaline areas throughout Pamlico Sound where females mate to the high-salinity inlets where they spawn.

Methods

During 2002, a total of 441 trawls for mature female blue crabs were conducted within Pamlico and Croatan sounds, which included the Pamlico and Neuse River estuaries (conducted in collaboration with the North Carolina Division of Marine Fisheries [NCDMF]), as well as the five inlet sanctuaries (Oregon, Hatteras, Ocracoke, Drum and Bardens inlets; Figures 1, 2).

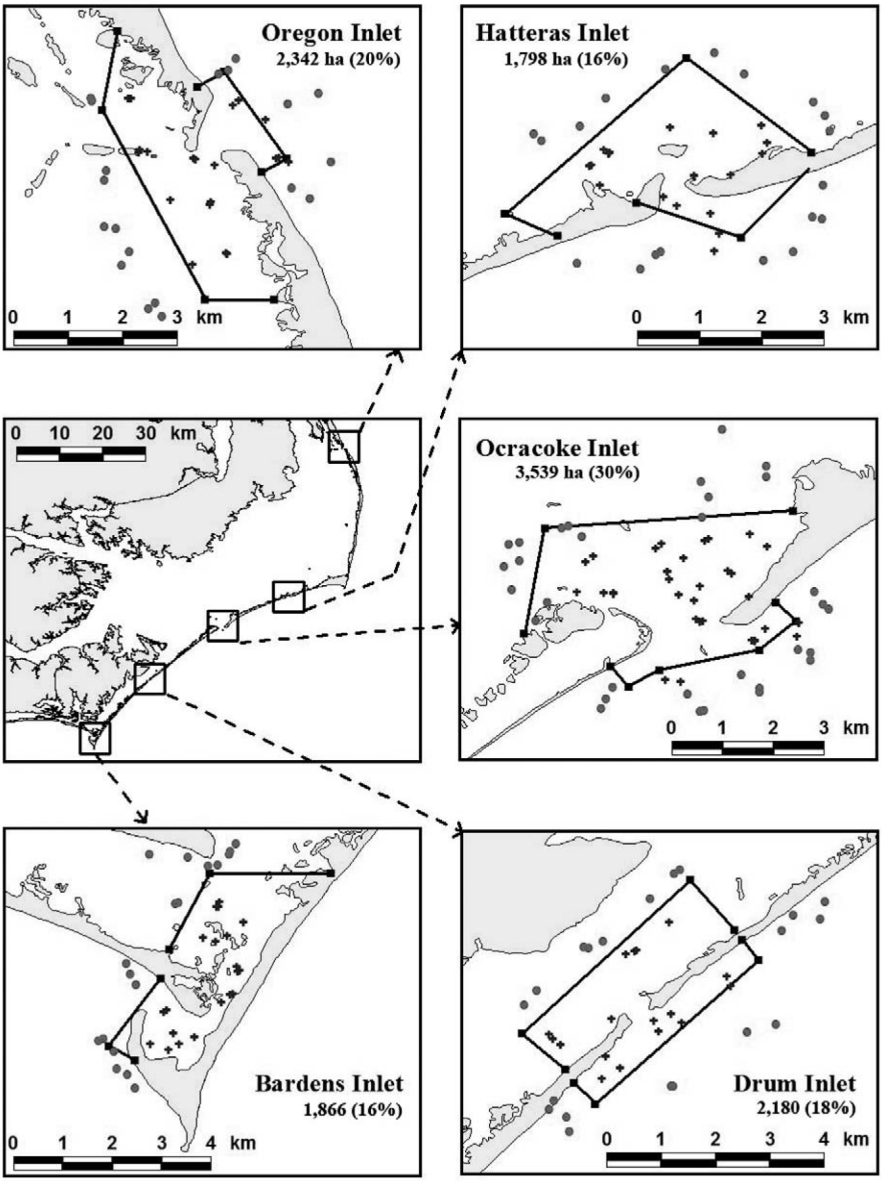

FIGURE 2.—Locations of five inlet blue crab spawning sanctuaries (dark lines) and trawl survey stations inside (crosses) and outside (circles) of spawning sanctuary boundaries in North Carolina. Total area (ha) of each sanctuary and the percentage of total surface area that was sampled are provided for each inlet.

Sampling was conducted during June, August, and September to coincide with the expected time for the spawning migration, which was based on evidence from the scientific literature (review by Millikin and Williams 1984), as well as from input from NCDMF staff (S. McKenna and L. Henry, personal communication) and crab fishers in North Carolina (R. Doxey and W. Phillips, personal communication). For each trawl tow, we recorded the carapace width (CW, mm) and sex of all captured crabs and whether females were mature. Sponge color on egg-bearing females was also recorded (i.e., orange, brown, or black). For mature female crabs collected at the inlets, we also recorded whether eggs had been recently released by pulling the telson down and examining the pleopods for eggs that had not hatched (D. Wolcott, North Carolina State University, personal communication). Latitude and longitude, water depth, dissolved oxygen (DO), temperature, and salinity were recorded at each sampling station.

Pamlico and Croatan sounds.—Trawl surveys in Pamlico and Croatan sounds were conducted in June, August, and September by the NCDMF and followed their fisheries-independent monitoring protocol for NCDMF Program 195 (P195). This program was initiated in 1987 as a deepwater (>2 m) survey of adult blue crabs in North Carolina. Our project supplemented the typical NCDMF P195 survey by adding 21 stations to their normal 54 stations in June and September and sampling the stations again in August when NCDMF does not normally sample (Figure 1). The P195 is a stratified random sampling program that uses paired, 9.1-m Mongoose trawls with a 1.9-cm-mesh cod end and a tow time of 20 min (Eggleston et al. 2004). Sampling stations in P195 are 1- × 1-min grid cells within Pamlico and Croatan sounds as well as the Neuse, Pamlico, and Pungo rivers that are stratified by water body and depth (seven strata total). For each sampling period, the number of randomly chosen sampling stations in each stratum was proportional to its surface area to ensure that sampling effort per unit area was equal among the strata. The response variable was the mean catch per unit effort (CPUE, number of crabs per tow) of mature females from the paired 20-min tows for a given station and month. We analyzed spatiotemporal variation in relative abundance of mature female blue crabs from Pamlico and Croatan sounds to determine the timing of migration down the estuary and identify potential migration corridors.

To determine whether the mean CPUE of mature female blue crabs was highest along the western shore and mid-sound areas of Pamlico Sound during the early reproductive period (i.e., June) and highest in the eastern region of Pamlico Sound during the late reproductive period (i.e., August and September), we used ArcView 3.2 software to generate figures that showed the geographic distribution and abundance patterns of mature female blue crabs within Croatan and Pamlico sounds. The mean CPUE (number of crabs per tow) of mature females at each sampling station's latitude and longitude was displayed as a circle, the diameter of which was proportional to CPUE. Therefore, we expected greatest female CPUE on the western shore of Pamlico Sound during June and greatest female CPUE on the eastern side of Pamlico Sound during August and September. If mature females used specific corridors to migrate to the inlet spawning sanctuaries, we expected to see relatively large CPUE values aggregated within specific geographic regions.

Inlet spawning sanctuaries.—The five inlet spawning sanctuaries (Oregon, Hatteras, Ocracoke, Drum, and Bardens) encompass approximately 11,792 ha and are closed to fishing from March 1 to August 31. A total of 75 stations were sampled across the five inlet spawning sanctuaries during June, August, and September 2002. For each trawl tow, we used a 6.7-m otter trawl with a 1.9-cm-mesh cod end (similar style of trawl net and same mesh size used by NCDMF for P195), which was towed for about 5–10 min by an 8.3-m vessel. Although trawl efficiencies can be relatively low for benthic species (15–20%; e.g., Gunderson 1993 and references therein) and can even vary spatially within the same substrate type (Kellison et al. 2003), the only gear that could reliably capture crabs in the hydrographically dynamic inlets were trawls and crab pots; the latter would have to be weighted heavily to stay in one place amid strong currents and also suffers from an inability to make inferences regarding crab density. Given that substrate type and depth ranges were similar across the inlet sanctuaries and that we consistently trawled against the prevailing current, we assumed that trawl gear efficiency would not vary among inlets and we used trawls instead of crab pots as a means to assess relative crab density.

The total sampling area at each inlet sanctuary was divided into 1- × 1-min grid cells covering zones within and 2 km outside (sound and ocean side) of the sanctuary boundaries. We then randomly picked cells to trawl within each of these three zones. A sample size of 75 was chosen for the five spawning sanctuaries because it provided for a minimum of 12 sampling stations at the smallest sanctuary (Hatteras Inlet), which, in turn, would permit taking three samples seaward and three samples inshore of the sanctuary boundaries. The sampling effort at each inlet sanctuary was generally split evenly between stations within and outside of the sanctuary boundaries. Stations located outside the sanctuary boundaries were further split evenly between stations located approximately 2 km seaward or 2 km soundward (inshore) of the sanctuary boundaries (Figure 2). The number of sampling stations per month at each inlet ranged from 12 to 23, such that the proportional area sampled at each sanctuary was the same (Figure 2). In many cases, we were unable to reach the exact coordinates of the center of each randomly chosen grid cell due to many shallow shoals within and near the inlets. Therefore, we sampled as close as possible to the center of each randomly chosen grid cell. The response variable was the CPUE of mature females (number per minute of tow time) for a given station and month.

To assess the effectiveness of the spawning sanctuaries to protect the local inlet population (only spawning sanctuary data included) and soundwide population (combined data for inlet spawning sanctuaries, Pamlico and Croatan sounds, and Pamlico and Neuse rivers) of mature female blue crabs, we calculated the percentage of mature females caught inside and outside the spawning sanctuary boundaries. Sampling effort, however, was not consistent between the inlet spawning sanctuary and the NCDMF P195 surveys; therefore, we adjusted our CPUE estimates from the P195 survey using the following equation:

$$\text{Adjusted CPUE} = (\text{CPUE} \div 20) \times 0.7362,$$

where 20 is the tow time (standardized to CPUE units used for the sanctuary trawls; i.e., number of crabs per minute of tow time) and 0.7362 is the ratio of the trawl widths (i.e., CPUE for the 9.1-m P195 trawl was scaled down by 73.6% of its length to standardize to the 6.7-m sanctuary trawl net). This linear scaling down of net size is appropriate for benthic species, such as the blue crab, because it is the width of the net (not volume) that probably controls the catch efficiency of bottom trawls (Gunderson 1993). All other factors that could affect catchability (e.g., mesh size, tow direction [into the prevailing current or wind], and tow speed) were consistent between the inlet and sounds surveys. Lastly, we calculated mean CPUE for each P195 stratum and each inlet sanctuary and multiplied by the total surface area of each stratum and inlet to get comparable abundance estimates between Pamlico Sound and the inlet sanctuaries. A detailed description of the calculations and assumptions used to estimate the percentage of mature female blue crabs protected by the inlet spawning sanctuaries in North Carolina is found in the Appendix.

To determine the spatiotemporal use of the spawning sanctuaries by mature female blue crabs, we used a split-plot analysis of variance (ANOVA) to examine how the mean CPUE was influenced by the interactive effects of sanctuary (within versus outside), inlet (5 inlets), and month (June, August, September). In a split-plot design, all levels of the split-plot factor (e.g., within versus outside and soundward versus seaward) are sampled within a replicate (month) of the whole-plot factor (inlet). Split-plot ANOVA models were also used to test whether the percentage of mature females was greater soundward or seaward of the sanctuary boundaries for each inlet and month, as well as to assess the potential benefits to the local female population of extending the sanctuary boundaries 2 km either soundward or seaward while accounting for inlet and month effects. To examine the interactive effects of inlet and month on the percentage of mature females that were sponge (egg-bearing) crabs, we used a two-way ANOVA model. Before all statistical analyses, the assumption of homogeneity of variance was tested with an F_{max} test. In instances where the data were nonnormal or the variances were heterogeneous, log or square-root transformations were successful in meeting model assumptions.

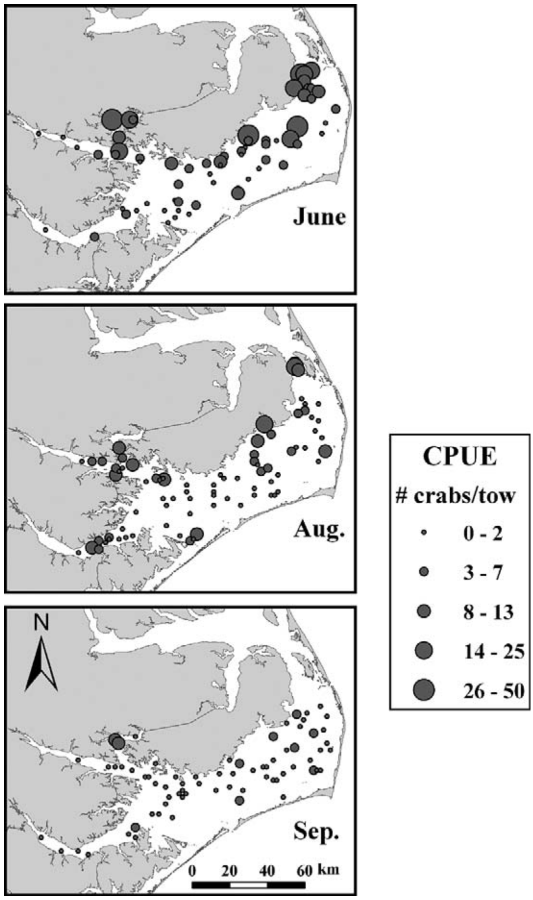

FIGURE 3.—Spatial distribution of mature female blue crabs throughout Pamlico and Croatan sounds, North Carolina, during June, August, and September. Diameter of circles represents relative catch per unit effort (CPUE; number of crabs per tow).

Results

Pamlico and Croatan Sounds

Mature female blue crabs were concentrated along the northwestern portion of Pamlico Sound between Croatan Sound and the lower Pamlico River (Figure 3). The hypothesized shift in the distribution of mature females from the western portions of Pamlico Sound to eastern sound spawning locations was not clearly evident by the crab distribution data from June to September 2002 (Figure 3), nor was there support for an easterly shift in crab distribution along a particular migration corridor (Figure 3). The only discernible seasonal pattern in abundance within Pamlico and

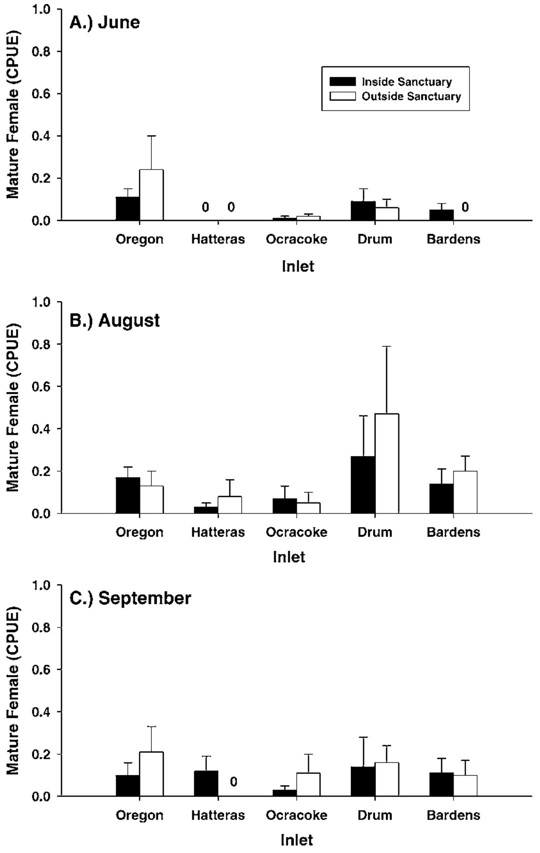

FIGURE 4.—Mean (+SE) catch per unit effort (CPUE; number of crabs per minute of tow time) of mature female blue crabs as a function of inlet, month (June, August, September), and spawning sanctuary (inside versus outside of sanctuary boundaries).

Croatan sounds was a 57% decline in CPUE from June to August and an 82% decline from June to September. Despite this large drop in soundwide spawning stock abundance, mature female abundance nearly tripled from June to August and was still twice as high in September compared with June (see next section) at the inlet spawning sanctuaries. The lack of a clear easterly shift in female crab distribution during summer or evidence of specific migration corridors could have been due to migration down the estuary taking place after September (Medici et al. 2006) or because the 82% decline in the overall population size of mature female blue crabs in Pamlico Sound from June to September 2002 made it difficult to discern spatial patterns. To account for this large seasonal decline in abundance and elucidate potential spatiotemporal patterns of abundance, we used two calculations to standardize our abundance data at each station by month. The first metric was the percent of the total monthly catch for each station, and the second was the percent deviation from the average monthly catch at each station. We were unable to discern any seasonal changes in mature female distribution and abundance patterns from either metric; therefore, we only present the raw CPUE data (Figure 3).

Inlet Spawning Sanctuaries

During June–September 2002, salinity at the five inlet blue crab spawning sanctuaries in North Carolina ranged from 22.7‰ to 31.7‰ (except for 11‰ at Oregon Inlet in September, which was in response to localized rainfall), temperature ranged from 23.9°C to 31.7°C, and DO ranged from 4.85 to 8.3 mg/L. Thus, during our 3-month sampling period, there was no evidence of any major freshwater outflow or hypoxic events that could have drastically altered blue crab movement patterns, except the drastically lower salinities at Oregon Inlet in September. Contrary to our original hypothesis, the mean CPUE of mature female blue crabs from our inlet surveys was not significantly higher inside than 2 km outside of designated spawning sanctuary boundaries (split-plot ANOVA: $F = 0.06$; df = 1, 12; $P = 0.81$; Figure 4). The percentage of mature female crabs caught inside versus 2 km outside of the boundaries of each sanctuary averaged 46.8 ± 5.3% (mean ± SE) across all inlets and varied little across months (Table 1). Moreover, total mature female abundance inside the sanctuaries only accounted for 0.7% of the Pamlico–Croatan Sound population of mature female blue crabs (Table 1). To determine whether expanding the spawning sanctuaries landward or seaward would protect a greater portion of mature female blue crabs, the percentage of mature females captured outside of the spawning sanctuary boundaries was compared between the sound side and ocean side. The percentage of mature female crabs captured by trawling was significantly greater outside and soundward of the sanctuary than seaward of the sanctuary, whereas the effects of inlet and month on the percentage of mature females captured were not statistically significant as determined by split-plot ANOVA (direction from sanctuary: $F = 8.10$; df = 1, 11; $P = 0.02$; month: $F = 0.18$; df = 2, 11; $P = 0.84$; inlet: $F = 0.41$; df = 4, 11; $P = 0.80$; Figure 5). Overall, mature females were nearly four times more abundant on the sound side of sanctuary boundaries than seaward of the boundaries (mean percentages of inlet populations across inlets = 41.9% and 11.3%, respectively; Table 1), with no mature females collected outside the ocean sanctuary boundary during June and only relatively low percentages collected during August and September (Table 1; Figure 5). In total, abundance of mature female blue crabs outside the sound boundary

TABLE 1.—Percentage of mature female blue crab abundance for local inlet and total Pamlico and Croatan Sound populations according to month and inlet. Soundwide population percentages are adjusted for differences in sampling effort between inlet sanctuaries and North Carolina Division of Marine Fisheries Program 195 trawls (see text for details). Inlet population percentages were not adjusted because sampling effort was consistent outside and inside sanctuary boundaries. Total values are percent abundance summed and averaged across all months and inlets. For example, in June 43.9% of mature females were captured inside the spawning sanctuaries as opposed to 1–2 km outside the boundaries, and this catch accounted for 0.12% of the soundwide population in Pamlico Sound.

	Percentage (%) inside boundaries		Percentage (%) outside boundaries			
			Soundside		Seaward	
Month or inlet	Inlet population	Soundwide population	Inlet population	Soundwide population	Inlet population	Soundwide population
Month						
Jun	43.9	0.12	56.1	0.28	0.0	0.00
Aug	42.5	1.14	47.8	2.26	9.7	0.41
Sep	42.6	1.83	36.0	3.28	21.4	1.21
Average	43.0	1.03	46.6	1.94	10.4	0.54
Inlet						
Oregon	40.0	0.85	41.2	1.98	19.1	0.65
Hatteras	64.3	0.33	35.7	0.43	0.0	0.00
Ocracoke	38.7	0.38	54.8	0.77	6.4	0.07
Drum	37.7	1.37	62.3	3.47	0.0	0.00
Bardens	53.9	0.60	15.4	0.28	30.7	0.66
Average	46.8	0.70	41.9	1.39	11.3	0.28

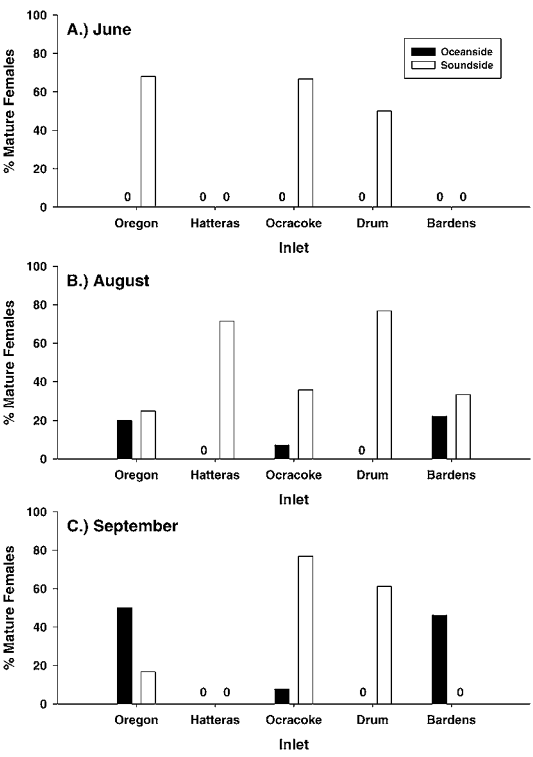

FIGURE 5.—Percentage of all mature blue crab females at each inlet in North Carolina collected outside the soundward (open bars) and seaward (closed bars) boundaries of the inlet spawning sanctuaries during **(A)** June, **(B)** August, and **(C)** September.

of the sanctuaries accounted for 1.39% of the total Pamlico–Croatan soundwide abundance, whereas CPUE outside the ocean side of the sanctuaries accounted for only 0.28% of overall soundwide abundance. Therefore, expanding the sanctuary boundaries 2 km seaward and soundward would only increase the protection afforded by the sanctuaries from 0.7% of the soundwide population of mature female crabs to 2.37% of the population.

Next, to determine whether there was spatiotemporal variation in the relative importance of the different inlet spawning sanctuaries, the relative abundance of mature female blue crabs was compared among the three collection months and five inlets. The mean CPUE of mature female blue crabs varied significantly according to month ($F = 8.39$; df = 2, 12; $P = 0.005$; Figure 6) and inlet ($F = 7.56$; df = 4, 12; $P = 0.003$; Figure 7), and was lowest in June (Figure 6; split-plot ANOVA contrasts, June versus August: $F = 16.43$; df = 1, 12; $P = 0.002$; June versus September: $F = 6.44$; df = 1, 12; $P = 0.03$; August versus September: $F = 2.30$; df = 1, 12; $P = 0.16$). The percentage of mature female abundance in Pamlico and Croatan sounds that was contained within the spawning sanctuaries was consistently low across months, ranging from 0.12% in June and increasing to 1.14% in August and 1.83% in September (Table 1).

There was evidence for spatial variation in the effectiveness of North Carolina's spawning sanctuaries as mature female blue crabs were more abundant inside the sanctuary boundaries than immediately outside the

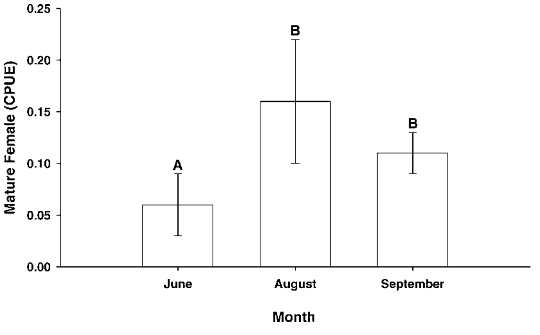

FIGURE 6.—Mean (±SE) catch per unit effort (CPUE; number of crabs per minute of tow time) of mature female blue crabs as a function of month. Different letters above each bar indicate statistically significant differences from multiple comparison tests. See text for additional results of statistical analyses.

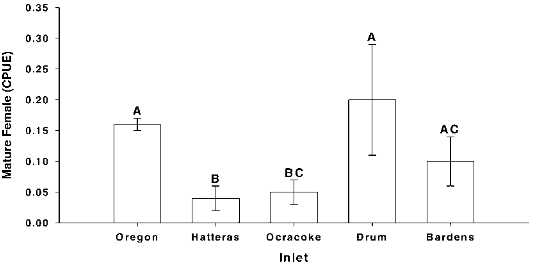

FIGURE 7.—Mean (±SE) catch per unit effort (CPUE; number of crabs per minute of tow time) of mature female blue crabs caught at each inlet in Pamlico Sound, North Carolina. Different letters above each bar indicate statistically significant differences from multiple comparison tests.

boundaries at Hatteras and Bardens inlets (64.3% and 53.9% of total inlet abundance, respectively) and less abundant inside than outside the sanctuary boundaries at Oregon, Ocracoke, and Drum inlets (40.0, 38.7, and 37.7% of total inlet abundance, respectively; Table 1). The relative importance of inlet spawning sanctuaries based on CPUE of mature females also varied. Mean CPUE of mature females was lowest at Hatteras and Ocracoke inlets, intermediate at Barden's Inlet, and highest at Drum and Oregon inlets (see Figure 7 for results of statistical contrasts). The three inlets (inside and outside sanctuary boundaries) with the greatest catches of mature females (Drum, Oregon, and Bardens inlets) accounted for 92.7, 81.4, and 72.0% of the total inlet abundance during June, August, and September, respectively.

The percentage of female crabs with sponges increased from June to September (June = 39%, August = 48%, September = 55%); however, the trend was not statistically significant (two-way ANOVA: $F = 0.13$; df = 2, 39; $P = 0.88$). The percentage of mature females that were sponge crabs showed no significant differences among inlets ($F = 1.10$; df = 2, 39; $P = 0.37$) and averaged 45.3% across all inlets. The developmental stage of the sponge also showed no pattern with respect to month or inlet.

Discussion

Spawning sanctuaries are the foundation of North Carolina's blue crab spawning stock protection strategy. Seasonal closure (March 1 through August 31) for commercial crab harvest at the five inlet sanctuaries was thought to afford protection to spawning mature females, allow for optimum yield of the resource, and have minimal effect on the majority of crab fishers (NCDMF 2004). However, evaluating the effectiveness of these sanctuaries is difficult because our study indicates that there are strong seasonal and spatial patterns in the level of protection these sanctuaries provide to the North Carolina blue crab spawning stock; the patterns are still poorly understood. Despite these spatiotemporal patterns, our study suggests that North Carolina spawning sanctuaries presently are too small to protect the blue crab spawning stock.

Spatial Patterns in Sanctuary Protection

In general, the abundance of mature female blue crabs was much higher at the three inlets located to the extreme north (Oregon Inlet) or south (Bardens and Drum inlets) in Pamlico Sound, compared with the inlets located in the central portion of Pamlico Sound (Hatteras and Ocracoke inlets; 85.7% of mature females collected in the spawning sanctuaries were from Oregon, Bardens, and Drum inlets versus 14.3% from Hatteras and Ocracoke inlets). This spatial pattern in abundance could be due to differences in catch efficiency among the inlets; however, our trawling protocol was consistent across inlets (e.g., trawling against the current at the same speed). Moreover, environmental conditions that may affect catchability (e.g., presence or absence of macroalgae and seagrass; depth; current speeds) were similar among all inlet sanctuaries. The higher relative abundance of mature females at the northern and southern edges of the Croatan–Albemarle–Pamlico Estuary System (CAPES) probably reflects crabs migrating to the closest inlet after mating. Therefore, Oregon Inlet would accumulate crabs migrating from Albemarle and northern Pamlico sounds, whereas Barden's and Drum inlets would accumulate crabs migrating from the Neuse and Pamlico rivers, as well as the southern portion of Pamlico and Core sounds. This hypothesis is consistent with tag–recapture studies in Pamlico Sound, which indicate that once mated, mature females migrate to the closest inlet (Medici et al. 2006). However, more detailed research on the soundwide movement patterns of migrating mature female crabs is required to determine where spawning females originate from and to identify potential migratory corridors in this relatively shallow estuary.

Despite the implications from this study and from Medici et al. (2006), which suggest that mature female blue crabs migrate along corridors in the CAPES, and the findings of Lipcius et al. (2003), which show that postcopulatory female blue crabs use deep basins in Chesapeake Bay to migrate to the mouth of the bay, our analysis of the NCDMF P195 survey data did not find clear evidence that female blue crabs use specific migration corridors to migrate to inlets for spawning. The lack of our ability to detect a distinct migration corridor may have been due to a sampling bias in the P195 sampling design or because the environmental cues blue crabs use to migrate to the inlets are patchily distributed throughout the CAPES. The P195 is designed to sample the relatively deep waters of North Carolina estuaries (>2 m); however, a recent biotelemetry study that tracked the movement patterns of a small number of postcopulatory mature female blue crabs suggests that newly inseminated mature females migrate down Chesapeake Bay along shallow nearshore areas (Turner et al. 2003). Therefore, the P195 depth bias may not have sampled potential shallow migratory routes of mature females.

The hypothesis of a shallow-water migratory route, however, is somewhat inconsistent with the yearly baywide trawl survey in Chesapeake Bay, which indicates that more than 50% of mature females in Chesapeake Bay are collected at depths greater than 10 m during the migratory months (Lipcius et al. 2003). Although it is difficult to infer movement patterns from trawl survey data (Bell et al. 2003), the distinct deep channel along the central north–south axis leading to the mouth of Chesapeake Bay could provide an effective orientation cue if mature females followed depth contours (Lipcius et al. 2003). Therefore, mature females migrating from the meso- and oligohaline tributaries would be funneled into the deeper channels of the bay and would eventually be concentrated at the mouth of the bay to spawn. Pamlico Sound, however, is a uniformly shallow (mean depth = 4.5 m, depth range = 1–6 m) system that contains several shoals, especially near the five inlets (Reyns et al. 2007). Thus, the spatially heterogeneous pattern in potential depth cues throughout Pamlico Sound may make it difficult for a trawl survey to detect a specific migratory route to the inlets and, thereby, make establishing a protective migration corridor untenable for North Carolina.

Temporal Patterns in Abundance in Spawning Sanctuaries

There was no clear qualitative evidence of a seasonal easterly shift in abundance of mature female blue crabs in Pamlico Sound during 2002. Rather, the most striking temporal pattern in abundance was the 82% decline in relative abundance from June to September of 2002. The historical P195 record indicates that this substantial seasonal decline in spawning stock has consistently occurred in North Carolina since 1978 (Eggleston et al. 2004). The decline in relative abundance of mature female blue crabs in Pamlico Sound from June to August ranges from 54% to 85%, which indicates that the relative decline in blue crab spawning stock during 2002 was one of the highest ever recorded. This decline could be due to mature female blue crabs moving to areas outside of our sampling area, including shallow nearshore zones (see previous section) and the coastal ocean. Some researchers have suggested that mature females may collect in the coastal ocean as they continually move seaward to produce additional broods (D. Ritchoff, Duke University, personal communication). Our trawl study, however, only detected a minor increase in relative abundance from June to September. Moreover, mature female blue crab abundance was consistently low during a 1990–1999 fishery-independent trawl survey program (SEAMAP South Atlantic 2002) off southern North Carolina in 4–10-m depths. Therefore, although mature female blue crabs may accumulate to some extent in the coastal ocean to spawn from June to September, the seasonal increase in their abundance in these waters probably would not account for the drastic decline in spawning stock biomass throughout the CAPES observed in this and other studies (Eggleston et al. 2004).

The most likely explanation for the dramatic seasonal decline in mature female abundance is fishing mortality. Although predation from large fishes, such as the red drum *Sciaenops ocellatus*, can be substantial for blue crabs (Boothby and Avault 1971), red drum selectively feed on crabs that are smaller (25–75 mm) than mature female (>130 mm CW) blue crabs (Scharf and Schlicht 2000). Fishing pressure for blue crabs is intense in all coastal North Carolina waters from spring through fall, and blue crabs are North Carolina's largest fishery in terms of total landings (~9.5 million kg [~21 million lb] in 2007) as well as monetary value. Nearly all mature females are larger than the current size limit imposed by the NCDMF; therefore, few mature females attain a size refuge from crabbers. Thus, it is likely that many mature female blue crabs are harvested by the fishery before they have had a chance to reach the protective boundaries of the sanctuaries, which probably explains the 82% decline in abundance of mature female blue crabs in Pamlico Sound from June to August 2002.

Despite this decline, the relative abundance of mature female blue crabs still increased by 73% at the inlet spawning sanctuaries during this same time period, suggesting that (1) some mature female blue crabs were successfully immigrating into inlet spawning sanctuaries during the summer, (2) resident subadult female crabs at the inlet spawning sanctuaries matured during summer, or (3) a combination of both. Therefore, the sanctuaries do protect some mature females; however, our data indicate that North Carolina blue crab spawning sanctuaries do not afford adequate protection to mature female blue crabs since, on average, only 0.7% of the mature female blue crab population in Pamlico and Croatan sounds was protected in 2002. Moreover, the proportion of female blue crabs tagged near two of North Carolina's spawning sanctuaries that were recaptured inside versus outside the sanctuaries were approximately equal, indicating that these two sanctuaries afforded little protection to spawners (Medici et al. 2006). Our estimates of sanctuary protection are probably conservative considering the shallowest areas of Pamlico Sound (<2 m), as well as Albemarle Sound, are not sampled by the NCDMF. For example, the Pamlico–Albemarle–Croatan Sound system in North Carolina encompasses a total of 559,300 ha of which nearly one-quarter (124,300 ha; in Albemarle Sound) is not sampled. The ineffectiveness of North Carolina's spawning sanctuaries raises the question, "How big do the sanctuaries need to be to maintain a viable spawning stock?"

The Chesapeake Bay spawning and migration corridor sanctuary, which was expanded to 240,376 ha in 2002, may be a useful benchmark for estimating the proportion of the spawning stock that needs to be protected. This sanctuary currently protects approximately 70% of mature female blue crabs in Chesapeake Bay (Lipcius et al. 2003; Lambert et al. 2006). It is difficult to estimate the extent to which the North Carolina sanctuary boundaries would need to be expanded to protect 70% of spawning stock because mature female abundance is spatially complex, with the greatest abundance occurring far from the inlets, such as along the western edge of Pamlico Sound and within the rivers (see Figure 3). Moreover, the spatial patterns in abundance we observed during our 1-year study may not be similar during other years since interannual variability in rainfall can shift the distribution of crabs within Pamlico Sound (Eggleston et al. 2004). Even if 70% of the spawning stock could be protected, it may not be sufficient to improve the current state of the blue crab population in North Carolina because the Chesapeake Bay sanctuary and associated harvest controls have not been able to reverse the major decline in the baywide population, spawning stock, and postlarval recruitment during the last two decades (Lipcius and Stockhausen 2002; Lambert et al. 2006).

Implications for Conservation and Management

Many exploited marine species, including blue crabs, have complex life histories whereby spatially separated ontogenetic stages are connected by dispersal. This poses a major challenge for scientists and managers when designing spawning sanctuaries because these areas must be larger than the scale of the animal's movement patterns (Medici et al. 2006) and protect the corridors that link juvenile–subadult nursery habitats with adult spawning sites (Beck et al. 2001; Lipcius et al. 2003). In the case of the North Carolina blue crab population, not only are the sanctuaries too small to protect mature females on the spawning grounds, but the lack of clear migration corridors makes it difficult to protect migrating mature females from the intense fishing pressure throughout Pamlico Sound and its tributaries. Thus, spawning sanctuaries coupled with protective corridors may be an untenable management strategy in North Carolina. Agencies currently using or considering spawning sanctuaries should use more traditional effort control measures (e.g., catch quotas, size limits, total or partial bans on collecting mature females) if there are no clear migration corridors connecting juvenile habitats to adult spawning grounds.

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Appendix: Calculation of Female Blue Crab Percentages

To calculate the percentages of the total population of mature female blue crabs in Pamlico and Croatan sounds and the major tributaries shown on Figure 1, the North Carolina Division of Marine Fisheries Program 195 trawl catch per unit effort (CPUE) estimates were averaged across all sampling stations within each of seven water bodies within Pamlico Sound. The seven water bodies within Program 195 are Pamlico Sound Deep East, Pamlico Sound Shallow East, Pamlico Sound Deep West, Pamlico Sound Shallow West, Neuse River, Pamlico River, and Pungo River (Table A.1). The mean CPUE for each water body stratum was then multiplied by the surface area of its corresponding body of water (Table A.1) to obtain a total relative CPUE estimate for each stratum (assuming an even distribution of mature females throughout each water body stratum). Relative CPUE was then averaged across months (for calculating water body strata percentages) and inlets (for calculating monthly percentages) and divided by the respective total mean CPUE to determine the percentage of soundwide mature females within each of the water body strata.

To calculate the percentages of the total population of mature female blue crabs in the inlet spawning sanctuaries, we summed all CPUE values for each of three inlet strata: (1) inside the sanctuary, (2) 2 km seaward of the sanctuary boundary, and (3) 2 km soundward of the sanctuary boundary ($n = 15$; Table A.1). Mean CPUEs for each inlet and month were calculated and divided by the respective total mean CPUE to determine percentage of the local inlet populations found within each of the Pamlico Sound water body or inlet strata.

TABLE A.1.—Descriptive details of water bodies used to determine percentages of mature female blue crabs in Pamlico and Croatan sounds, North Carolina.

Survey	Region	Stratum	Surface area (km^2)	Description
NCDMF P195[a]	Pamlico Sound	Deep east	1,551.2	Area calculated by multiplying estimated area of 1- × 1-min grid cells (2.8 km^2) by total number of grid cells in each water body stratum.
		Deep west	873.6	
		Shallow east	576.8	
		Shallow west	378.0	
	Pamlico River		179.2	
	Pungo River		50.4	
	Neuse River		260.4	
P195 total			3,869.6	
Inlet sanctuaries	Oregon Inlet	Inside sanctuary	23.4	Area inside sanctuaries from NCDMF (2004). Area soundward and seaward of sanctuary boundaries calculated using ArcView 3.2 software.
		Soundward of sanctuary	27.9	
		Seaward of sanctuary	17.9	
	Hatteras Inlet	Inside sanctuary	18.0	
		Soundward of sanctuary	31.2	
		Seaward of sanctuary	16.4	
	Ocracoke Inlet	Inside sanctuary	35.4	
		Soundward of sanctuary	29.0	
		Seaward of sanctuary	21.7	
	Drum Inlet	Inside sanctuary	21.8	
		Soundward of sanctuary	25.9	
		Seaward of sanctuary	23.8	
	Bardens Inlet	Inside sanctuary	18.7	
		Soundward of sanctuary	16.9	
		Seaward of sanctuary	14.7	
Inside total			117.3	
Soundward total			130.8	
Seaward total			94.5	

[a] North Carolina Division of Marine Fisheries Program 195.