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SPATIAL DYNAMICS AND VALUE OF A MARINE PROTECTED AREA AND CORRIDOR FOR THE BLUE CRAB SPAWNING STOCK IN CHESAPEAKE BAY

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ABSTRACT

In lower Chesapeake Bay, a 172,235 ha marine protected area and corridor (MPAC) was recently established to protect blue crab adult females either en route to or at the spawning grounds during the reproductive period. The MPAC was justified due to a recent substantial decline in spawning stock biomass. It was situated in waters deeper than 10 m throughout the lower bay due to the high abundances of adult females in this zone, and it was an expansion of a historical spawning sanctuary near the bay mouth to include northward extensions (upper and lower MPACs). We examined spatial dynamics of the blue crab spawning stock in relation to the MPAC through analyses of trawl survey data (abundances of adult females and egg-bearing females from 1989–1997 and 1995–1997, respectively) partitioned by water depth, time (month and year), and spatial zone (upper MPAC, lower MPAC, MPAC Historical Sanctuary) during the reproductive period (June–September). Adult female abundance peaked at 6–14 m water depths. Consequently, nearly half of all adult females in the lower bay were deeper than 10 m, and therefore protected by the MPAC during the reproductive period, whereas the historical sanctuary protected about ⅓ that of the MPAC. All MPAC segments were utilized by adult females at different times of the spawning season, without consistent use of any particular segment. In contrast, abundance patterns of egg-bearing females were consistent and did not differ by developmental stage of the eggs. Peak abundances of egg-bearing females shifted from the northern to southern portions of the MPAC as the spawning season progressed. Differences in distribution of adult females and egg-bearing females demonstrated the importance of the expanded MPAC to the conservation of the spawning stock, which requires an extensive area to cover seasonal and yearly alterations in distribution. The expanded MPAC is much more effective than the historical sanctuary at protecting a consistent fraction of the blue crab spawning stock over the full spawning season and every year. Both the lower MPAC and historical sanctuary contained high abundances of adult females and egg-bearing females, and these segments therefore potentially function as corridors and spawning grounds. In contrast, whereas adult females were equally abundant in all MPAC segments, egg-bearing females were rarely common in the upper MPAC segment. Hence, the upper MPAC serves primarily as a corridor for females migrating to spawn or hatch their egg masses in the lower MPAC and historical sanctuary. The MPAC protects a major fraction of the spawning stock and spawning grounds both seasonally and yearly, and it encompasses a dispersal corridor for adult females in the deeper waters of Chesapeake Bay. The MPAC therefore serves as a foundation for long-term protection of the blue crab spawning stock, and should be utilized concurrently with complementary management measures to conserve the blue crab population in Chesapeake Bay. Furthermore, the MPAC for the blue crab in Chesapeake Bay may serve as a model system for investigating the value of marine protected areas for exploited marine populations with ontogenetically disjunct stages in the life cycle that encompass diverse habitats.

A major postulated benefit of marine protected areas (e.g., sanctuaries) is that they will enhance recruitment from the protected segment of the spawning stock to the full population (Allison et al., 1998; Guenette et al., 1998). In addition, protected dispersal corridors are potentially necessary complements to marine protected areas when conserving migratory species (Rosenberg et al., 1997; Beier and Noss, 1998). The utility of marine protected areas and corridors (MPACs) remains generally untested and uncertain due to experimental and logistical difficulties in demonstrating population-level impacts (Hobbs, 1992; Inglis and Underwood, 1992; Simberloff et al., 1992; Allison et al., 1998; Lipcius et al., in press), despite the likely value of MPACs for species such as the blue crab, *Callinectes sapidus,* whose life cycle encompasses dispersal (e.g., spawning migration) via corridors (Rosenberg et al., 1997).

The blue crab, *Callinectes sapidus*, supports the world's largest crab fishery (Lipcius and Eggleston, 2000). The blue crab population in Chesapeake Bay is the biggest throughout its range along the Atlantic and Gulf coasts of North America (Williams, 1984; Rugolo et al., 1998), and fluctuates in abundance interannually (Hines et al., 1990; Lipcius and Van Engel, 1990; Lipcius and Stockhausen, 2002). A detailed account of the life history and fisheries for the blue crab in Chesapeake Bay is provided in Seitz et al. (2001). The relevant portion of the life history for this study deals with the reproductive segment of the population. After a terminal maturity molt and mating in the oligohaline and mesohaline segments of Chesapeake Bay and its tributaries, newly inseminated female crabs either migrate to the lower Chesapeake Bay spawning grounds in summer, or they migrate to the lower bay in fall, overwinter, and then spawn the following year (Van Engel, 1958; Tagatz, 1968). Egg extrusion and larval release occur from late spring through summer (Jones et al., 1990; Prager, 1996).

The blue crab in Chesapeake Bay has suffered a major reduction in the baywide population (Lipcius et al., in press) and in the spawning stock, recruitment, larval abundance, and size (Lipcius and Stockhausen, 2002), despite protection from exploitation by a spawning sanctuary in the spawning grounds (Seitz et al., 2001) and various catch or effort controls (Rugolo et al., 1998). A sustainable fraction of the spawning stock (Miller and Houde, 1998; Rugolo et al., 1998) has not been maintained (Seitz et al., 2001) to ensure maximal recruitment (Tang, 1985; Rothschild, 1986; Lipcius and Van Engel, 1990; Lipcius and Stockhausen, in press) under intense exploitation (Miller and Houde, 1998; Lipcius et al., 2002).

Consequently, an expansion of the spawning sanctuary and protection of a deep-water dispersal corridor as an MPAC (Figs. 1, 2) was planned for the lower bay where anoxia is not severe (R. Lipcius, unpubl.), because adult females concentrate in waters outside of the existing sanctuaries and deeper than 13 m (Fig. 2; Lipcius et al., 2001). These findings suggested that spawning activity outside the existing sanctuary was substantial and that females used a part of the bay mainstem as a dispersal corridor to the spawning grounds (Lipcius et al., 2001). The MPAC (Figs. 1, 2) was adopted (27 June 2000, Virginia Marine Resources Commission), and currently protects females in 172,235 ha of deep waters (mostly $>$10 m depth) in the lower bay from 1 June–15 September.

The previous investigation (Lipcius et al., 2001) was limited in that it did not examine abundance patterns of (i) egg-bearing females to determine probable spawning areas and dispersal corridors in the MPAC, (ii) adult females in separate segments of the MPAC to ascertain spatial variation in utilization of the MPAC, (iii) adult females by depth to estimate the fraction of the spawning stock protected by the MPAC, and (iv) adult females by time during the reproductive period to define seasonal utilization of the MPAC. The present study utilizes a different data set that permits evaluation of the preceding issues and an estimate of the probable value and function of the MPAC. Specifically, we measured spatial and temporal variation in abundance of egg-bearing and adult females throughout the MPAC during the reproductive period over several years to achieve the following objectives:

1. *Estimate the fraction of the spawning stock protected in the MPAC* by mea-

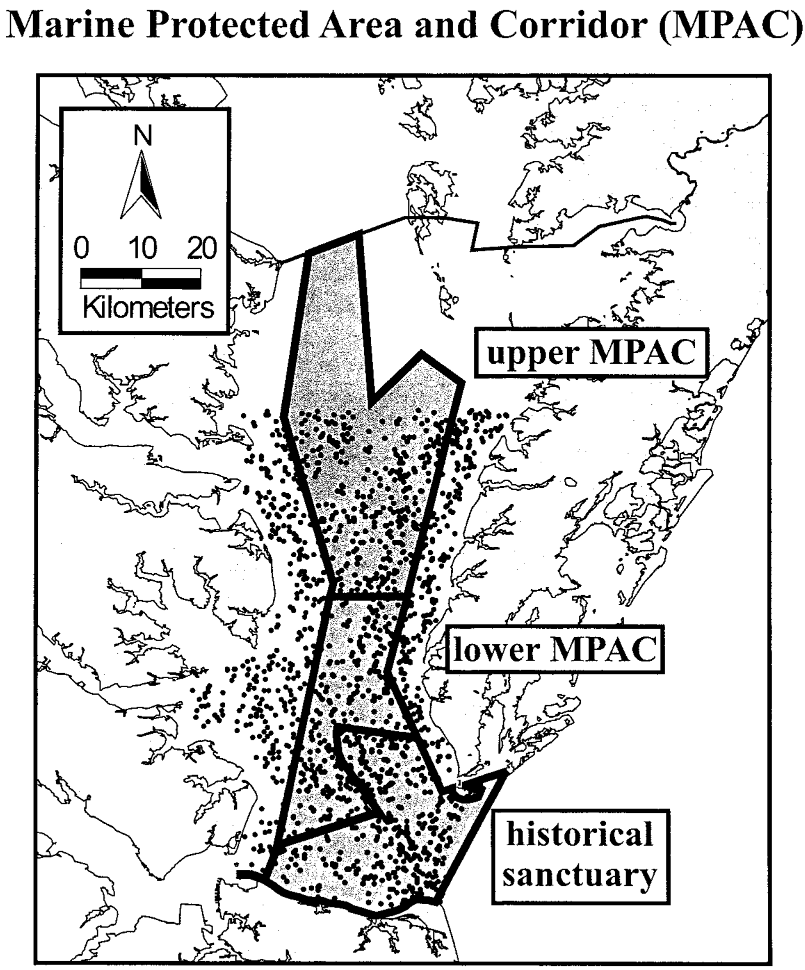

Figure 1. Chesapeake Bay marine protected area and corridor (MPAC, shaded area in bay), and trawl survey sampling stations (dots). Progressing from north to south in the MPAC, the first horizontal line splits the upper MPAC and lower MPAC. Near the southern end of the MPAC, the crooked boundary separates the upper MPAC from the historical spawning sanctuary. The line at the northern end of the MPAC defines the Maryland and Virginia border. The MPAC was expanded further in 2002; see Appendix Fig. 1.

suring the abundance of adult females by depth, since the MPAC follows the 10.7 m depth contour.

2. *Assess utilization of the MPAC as a spawning area and as a dispersal corridor* by contrasting the distribution patterns of egg-bearing and adult females as a function of location within the MPAC.
3. *Assess interannual variation in utilization of different segments of the MPAC,* to test the hypothesis that the value of each segment of the MPAC as a spawning sanctuary or corridor differs from year to year. For this we contrasted annual abundance patterns of egg-bearing and adult females as a function of location within the MPAC.
4. *Assess variation in utilization of different segments of the MPAC over the course of the reproductive period* to test the hypothesis that utilization of

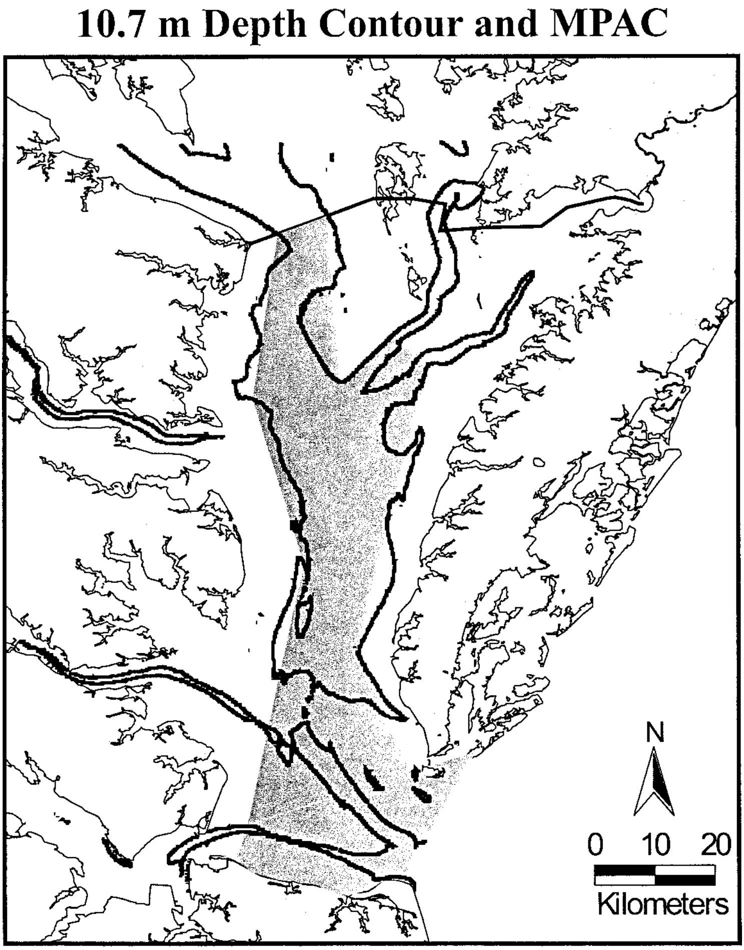

Figure 2. Chesapeake Bay marine protected area and corridor (MPAC, shaded area) and 10.7 m depth contour (based on NOAA depth charts), which generally bounds the MPAC. The line at the northern end of the MPAC defines the Maryland and Virginia border.

the MPAC varies predictably in space and time during the reproductive period. Abundance of egg-bearing and adult females as a function of month and MPAC segment was quantified to test this hypothesis.

Methods and Materials

Female blue crabs release larvae in the lower reaches of Chesapeake Bay each year from June through September (Van Engel, 1958; Jones et al., 1990). Hence, we sampled adult females in the spawning grounds of lower Chesapeake Bay from June through September during 1989–1997; egg-bearing status was recorded during 1995–1997. Crabs were sampled with a stratified random trawl survey, which minimizes spatial autocorrelation; each value from a single survey tow served as an independent datum (i.e., number of adult females tow^{-1}). Average sample sizes in the spawning grounds were 25 month^{-1} (minimum = 22) and 100 year^{-1} (minimum = 77); there were approximately equal proportions in each of the MPAC segments (Fig. 1). Temporal autocorrelation was minimized (i) monthly, because blue crab females have a residence time in the spawning grounds estimated at 2–4 wk (Prager, 1986; Seitz et al., 2001; J. R. McConaugha, pers. comm.), and (ii) yearly, because most of the females in the spawning grounds are of a new year class (Van Engel, 1958; Lipcius et al., in press). These circumstances reduced the probability of resampling females more than one month

Table 1. Egg mass stages for the blue crab. Characteristics of egg mass stages were originally derived for brachyuran crabs (Anderson, 1982) and applied to the blue crab (Jones et al., 1990). Egg yolk % represents the volume of egg yolk as a percentage of the total egg volume. na = not applicable.

Stage	Description	Egg yolk %	Egg mass color
1	No eggs present; no evidence of past spawning.	na	na
2	Early embryonic development; small embryonic disk; no invagination.	90	orange
3	Intermediate embryonic development; invagination completed; eye pigmentation and organogenesis proceeding.	50	brown
4	Fully developed embryos; eyes completely pigmented.	10	black
5	No eggs present; evidence of previous spawning (e.g., remnants of hatched eggs on pleopods).	na	na

or one year, respectively, and should have minimized temporal autocorrelation. Bottom water depth was recorded each tow.

The trawl survey has undergone minor changes in sampling protocol since 1979, which requires gear conversion factors to standardize abundance values (Hata, 1997). In our case, data from July 1989–September 1990 was standardized. Analyses with uncorrected data yielded equivalent statistical results; all analyses presented herein use the standardized data.

Abundance was analyzed in analysis of variance models as the log-transformed ($\log[10x + 1]$), standardized number of adult females tow^{-1} to normalize the data and reduce heterogeneity of variance (Underwood, 1997). The data were transformed as $10x + 1$ to avoid negative characteristics in the logarithms (Sokal and Rohlf, 1981). In all cases, variances were either homogeneous ($P > 0.05$, Cochran's C statistic) or the F-test in analyses of variance was rejected at an α level lower than that used in the test for homogeneity of variance (Underwood, 1997). All analysis of variance models used fixed factors (i.e., Year, Month, MPAC Segment, Egg Mass Stage). To examine differences between factor levels, either for main effects with multiple levels or in comparisons when interaction effects were significant, we used Student-Newman-Keuls a posteriori multiple comparison tests (Underwood, 1997).

For the analysis of abundance by water depth, we calculated the depth-specific and cumulative adult female abundance by 1.5 m depth intervals from 0–32 m using yearly (i.e., June–September) sums of adult females tow^{-1}. Values across depth strata were normalized annually to weight all years equally, and expressed as the depth-specific or cumulative percent of adult female abundance by depth. Given that the depth-specific means are expected to be distributed normally, a sigmoid function would best describe the cumulative percent distribution (Sokal and Rohlf, 1981). The mean across all years was therefore analyzed relative to depth with a sigmoid function using non-linear regression:

$$y = \frac{\alpha}{1 + e^{-(x-x_0)/\beta}}$$

where y = mean cumulative percent of adult female abundance in depth interval x. The resulting sigmoid curve was used to estimate the proportion of the spawning stock residing in the MPAC.

In 1995–1997, we also measured the incidence and developmental stages of egg masses on adult females from the trawl survey samples. The egg masses were characterized according to documented criteria for brachyuran crabs (Anderson, 1982), which have also been applied to the blue crab (Jones et al., 1990). These criteria relate the color of the egg mass to specific stages in the development of the embryos (Table 1). The number of females tow^{-1} that were bearing eggs (i.e., egg stages 2–4, Table 1) was used as the dependent variable in analysis of variance models. In these analyses, the data were not transformed since variances were not heterogeneous ($P > 0.05$, Cochran's C statistic). As for abundance, we used fixed factors (i.e., Year, Month, MPAC Segment, Egg Mass Stage) in analysis of variance models, and the Student-Newman-Keuls test in a posteriori multiple comparisons (Underwood, 1997).

RESULTS

ABUNDANCE OF ADULT FEMALES BY DEPTH.—The depth-specific mean of adult female abundance peaked at 6–14 m water depths (Fig. 3a). The sigmoid function relating the mean cumulative percent of adult female abundance to water depth (Fig. 3b) was:

Table 2. Analysis of variance for log-transformed adult female abundance tow^{-1}. Year (9 levels: 1989–1997), Month (4 levels: June–September), and MPCA Segment (3 levels: upper MPCA, lower MPCA, and historical sanctuary) served as fixed factors in the model.

Source of variation	SS	df	MS	*F*	*P*
Year (Y)	113.25	8	14.16	27.25	0.0005
Month (M)	16.38	3	5.46	10.51	0.0005
MPCA Segment (S)	6.67	2	3.34	6.42	0.002
Y × M	24.81	24	1.03	1.99	0.003
Y × S	16.91	16	1.06	2.04	0.009
M × S	13.07	6	2.18	4.19	0.0005
Y × M × S	36.75	48	0.77	1.47	0.022
Error	420.24	809	0.52		
Total	651.55	916			

$$y = \frac{107.10}{1 + e^{-[(x-10.36)/-2.67]}}$$

with $r^2 = 0.997$, $P < 0.0001$, df = 2, 17. Approximately 50% of all adult females sampled by the trawl survey in the lower bay was located deeper than 10 m, and therefore contained within the boundaries of the MPAC (Fig. 3b).

ADULT FEMALE DISTRIBUTION.—Although adult females were broadly distributed throughout the MPAC and adjacent shallow waters, most of the high abundances were in the MPAC (Fig. 4). Highest abundances were in the upper MPAC, MPAC historical sanctuary, and near the southern border of the lower MPAC (Fig. 4).

In the analysis of adult female abundance, there was a significant 3-way interaction effect of Year × Month × MPAC Segment, precluding singular conclusions about the main effects. We hypothesized that the interaction effect might be due to changing distribution patterns when female abundance was reduced significantly in 1992 and thereafter (Lipcius and Stockhausen, 2002), so we repeated the analysis separately for the 1989–1991 and 1992–1997 data sets. In both cases, the 3-way interaction effect was not significant (ANOVA; 1989–1991: $F = 1.15$, df = 12, 277, $P = 0.319$; 1992–1997: $F = 1.22$, df = 30, 532, $P = 0.198$). However, the Month × MPAC Segment interaction effect was significant for both time periods (ANOVA; 1989–1991: $F = 3.35$, df = 6, 12, $P = 0.003$; 1992–1997: $F = 4.33$, df = 6, 30, $P < 0.0005$), requiring examination of the effects of MPAC segment within each month, using SNK tests. The Year × MPAC Segment interaction effect was not significant (ANOVA; 1989–1991: $F = 1.35$, df = 4, 277, $P = 0.252$; 1992–1997: $F = 1.68$, df = 10, 532, $P = 0.081$).

There were some consistent patterns in abundance between MPAC segments by month (Fig. 5). In both 1989–1991 and 1992–1997, abundance during June did not differ significantly by MPAC segment (SNK tests, $P > 0.05$; Fig. 5a, b). In July of both time periods, abundance was significantly lower in the MPAC historical sanctuary than in the lower MPAC (Fig. 5c, d; SNK tests, c: $P < .05$, d: $P < 0.01$). In August, abundance did not differ by MPAC segment in 1989–1991 (Fig. 5e; SNK test, $P > 0.05$), whereas in 1992–1997, abundance in the lower MPAC was significantly higher than that in the upper MPAC (Fig. 5f; SNK test, $P < 0.01$). During September of both time periods, abundance was significantly higher in the upper MPAC than in the lower MPAC (Fig. 5g, h; SNK tests, $P < 0.05$); in 1992–1997 abundance was also significantly higher in the historical sanctuary than in the lower MPAC (Fig. 5h; SNK test, $P < 0.05$). Abundance patterns by MPAC segment reflected substantial variation in their utilization over

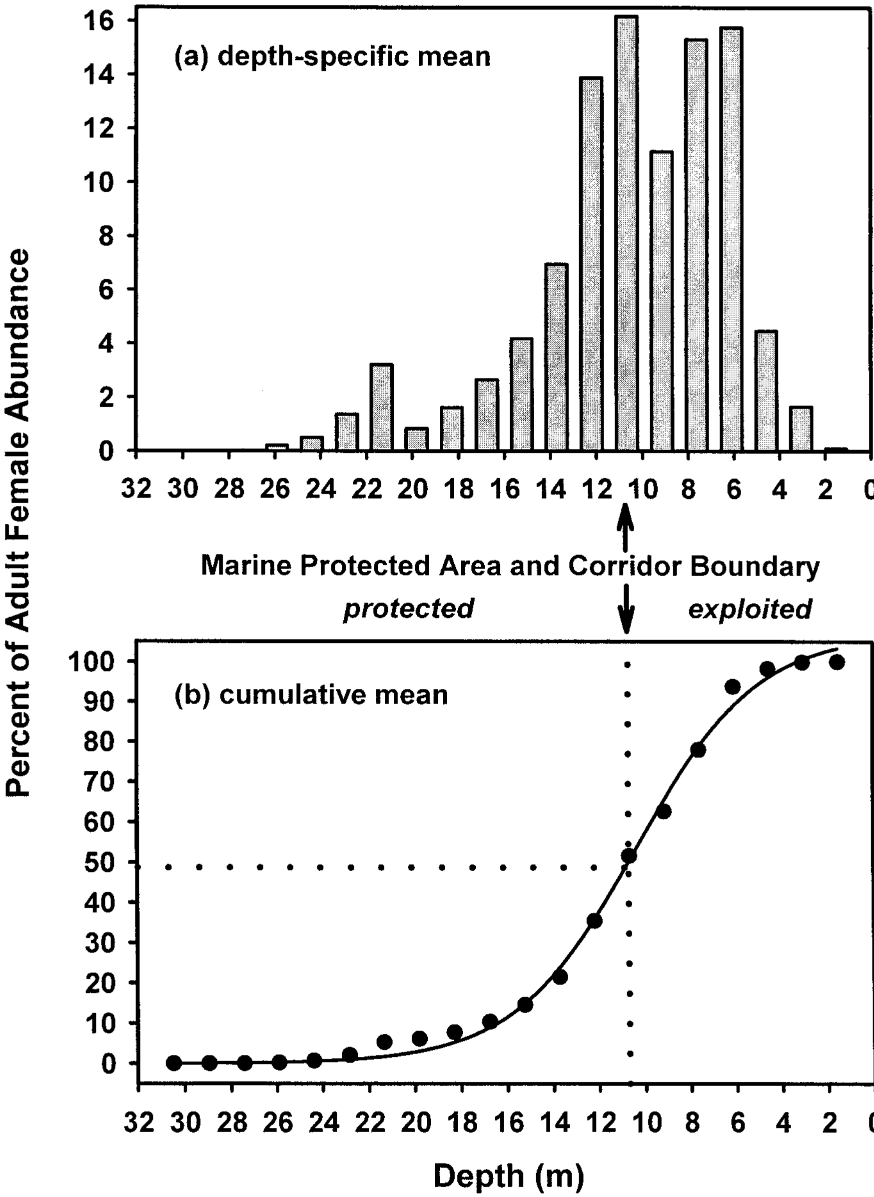

Figure 3. Depth-specific mean (a) and cumulative mean (b) percent of adult female abundance (normalized by year) as a function of water depth in lower Chesapeake Bay. The depth boundary of the marine protected area and corridor is indicated by the arrows between the two graphs, and by the vertical dotted line at 10.7 m depth in graph b.

the reproductive period; all segments of the MPAC were utilized at different times of the spawning season (Fig. 5).

EGG-BEARING FEMALE DISTRIBUTION.—Egg-bearing females were not as broadly distributed as all adult females throughout the upper MPAC, lower MPAC, and MPAC historical sanctuary and adjacent shallow habitats; highest abundances occurred in the southern portion of the upper MPAC through the MPAC historical

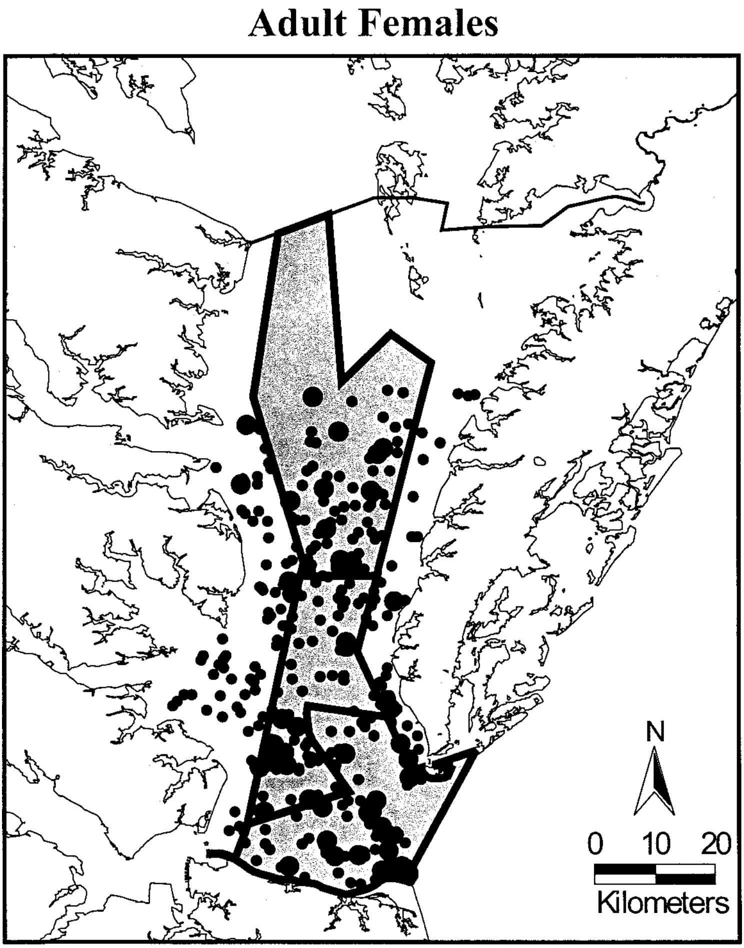

Figure 4. Distribution of adult female abundance throughout the marine protected area and corridor. Circle sizes represent abundances that were 1 and 2 standard deviations greater than the normalized mean in each year. See Figure 1 legend for further details, and the text for results of statistical analyses.

sanctuary (Fig. 6). Within the MPAC, highest abundances were evident in the lower MPAC and MPAC historical sanctuary (Fig. 6).

In the analysis of egg-bearing female abundance, we first determined whether there was a difference in the distribution of the different egg stages by MPAC segment by using Egg Stage (Stage 2, Stages 3–4), Year, Month, and MPAC Segment as fixed factors in a 4-way ANOVA model with the number of females in each egg stage as the dependent variable. None of the factor effects involving Egg Stage was significant (ANOVA; main effect: $F = 1.51$, df = 1, 526, $P = 0.219$; interaction effects: all $P > 0.713$). We therefore lumped all the egg stages and analyzed the remaining ANOVA models without Egg Stage as a factor.

In the 3-way ANOVA, neither the Year × Month × MPAC Segment (ANOVA, $F = 1.23$, df = 12, 263, $P = 0.260$) nor the Year × Month (ANOVA, $F = 1.33$, df = 6, 263, $P = 0.243$) interaction effects were significant. However, the Year × MPAC Segment (ANOVA, $F = 2.18$, df = 4, 263, $P = 0.072$) and Month × MPAC Segment (ANOVA, $F = 2.40$, df = 6, 263, $P = 0.028$) interaction effects

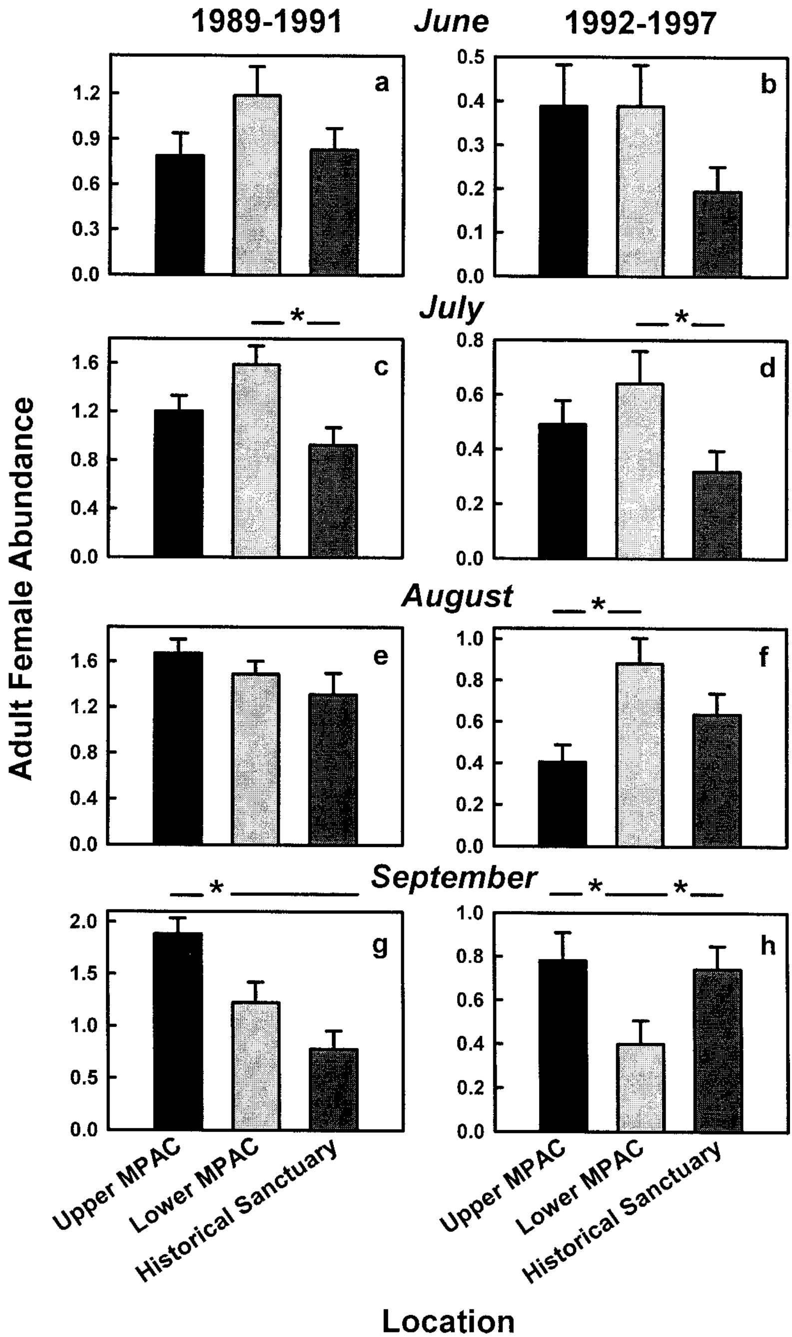

Figure 5. Adult female abundance (log-transformed number tow^{-1}) as a function of segment of the marine protected area and corridor (MPAC; upper MPAC, lower MPAC, MPAC Historical Sanctuary), time period (1989–1991, 1992–1997), and month (June–September). Vertical bars depict 1 SE. MPAC segments were compared statistically within each combination of time period and month using Student-Neuman-Keuls multiple comparisons, with equal sample sizes for all comparisons within a time period to equalize statistical power (Underwood, 1997). Non-significant comparisons (SNK tests, $P > 0.05$) are not distinguished. Significant comparisons are signified by asterisks. See text for results of statistical analyses.

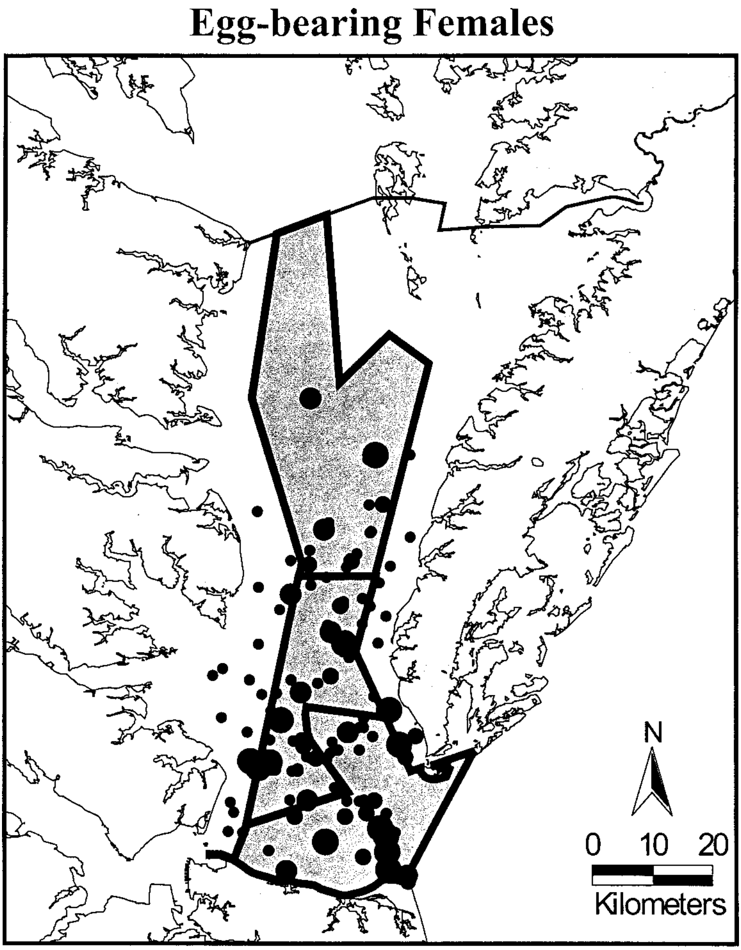

Figure 6. Distribution of egg-bearing female abundance throughout the marine protected area and corridor. Circle sizes represent abundances that were 1 and 2 standard deviations greater than the normalized mean in each year. See Figure 1 legend for further details, and text for results of statistical analyses.

were significant. We thus examined the effects of MPAC segment on egg-bearing female abundance within each level of month and year (Figs. 7, 8).

There was a consistent seasonal pattern in abundance of egg-bearing females by MPAC segment (Fig. 7). In June, most egg-bearing females were in the upper MPAC and lower MPAC (Fig. 7a), but the differences were not significant (SNK test, $P > 0.05$). In July and August, abundance of egg-bearing females shifted to the lower MPAC and MPAC historical sanctuary (Fig. 7b, c), with significantly higher abundances in the lower MPAC than in the upper MPAC (SNK tests, b: $P < 0.05$, c: $P < 0.01$). In September, egg-bearing females were significantly more abundant in the MPAC historical sanctuary than in both the lower MPAC and upper MPAC (Fig. 7d; SNK test, $P < 0.05$).

The distribution pattern of egg-bearing females across MPAC segments was variable interannually (Fig. 8). In 1995, there was no significant difference in abundance between the three segments (Fig. 8a; SNK test, $P > 0.05$). In contrast,

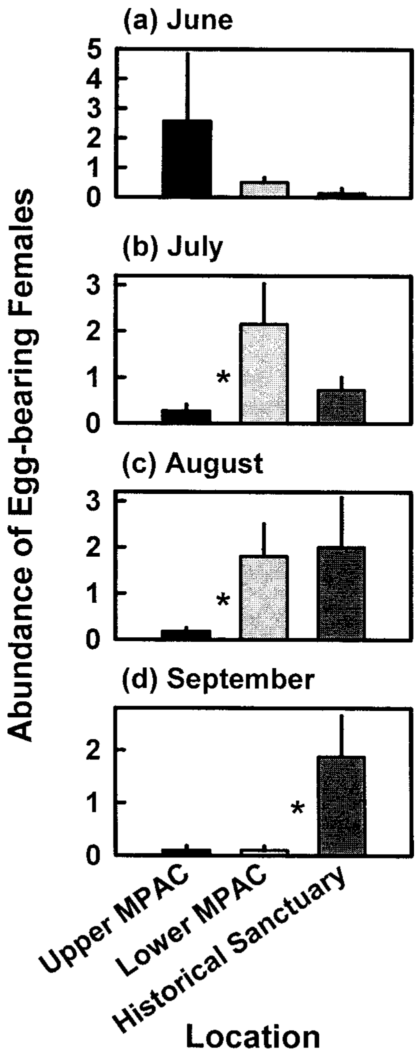

Figure 7. Abundance of egg-bearing females as a function of region of the marine protected area and corridor (MPAC; upper MPAC, lower MPAC, MPAC Historical Sanctuary) in each month, collapsed across year. Vertical bars depict 1 SE. Non-significant comparisons (SNK tests, $P > 0.05$) are not distinguished. Significant comparisons (SNK tests, $P < 0.05$) are indicated by asterisks. See text for results of statistical analyses.

during 1996 abundance was significantly higher in the lower MPAC than in the upper MPAC (Fig. 8b; SNK test, $P < 0.05$) and during 1997 abundance was significantly higher in the MPAC historical sanctuary than in the upper MPAC (Fig. 8c; SNK test, $P < 0.05$).

Discussion

We investigated the spatial dynamics of the blue crab spawning stock within a protected 172,235 ha marine protected area and corridor (MPAC) in lower Chesapeake Bay by partitioning the MPAC into upper, lower, and historical sanctuary (i.e., bay mouth) segments. Next, we determined the distribution of adult females

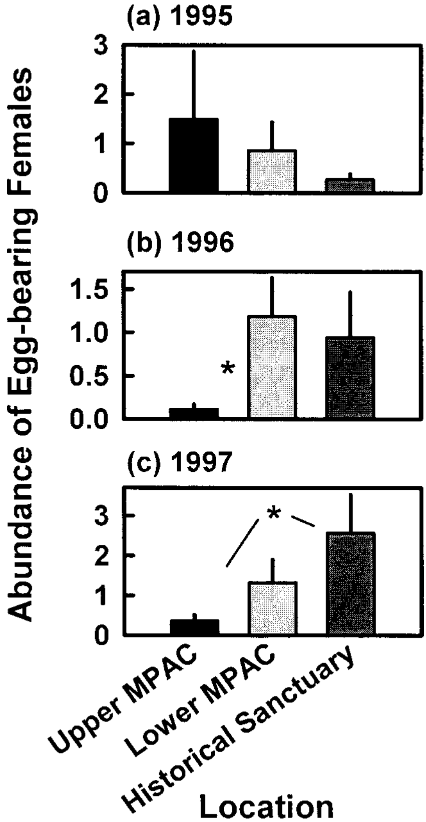

Figure 8. Abundance of egg-bearing females as a function of region of the marine protected area and corridor (MPAC; upper MPAC, lower MPAC, MPAC Historical Sanctuary) in each year, collapsed across month. Vertical bars depict 1 SE. Non-significant comparisons (SNK tests, $P > 0.05$) are not distinguished. Significant comparisons (SNK tests, $P < 0.05$) are indicated by asterisks. See text for results of statistical analyses.

as a function of water depth, specifically because the upper and lower MPAC are bounded approximately by the 10.7 m depth contour (i.e., waters deeper than 10.7 m are protected from crabbing). Finally, we assessed the probable function and effectiveness of each MPAC segment in conserving the blue crab spawning stock by quantifying variation in the distribution and abundance of adult females and egg-bearing females in the MPAC segments, both across years and as a function of time during the reproductive period.

Estimation of the Fraction of the Spawning Stock Protected in the MPAC.—Adult female abundance varied significantly as a function of water depth, such that peak abundances occurred at 6–14 m depths. Consequently, nearly half of all adult females in the lower bay were deeper than 10 m, and therefore protected by the MPAC during the reproductive period. Since peak abundance of adult females coincided closely with the depth boundary of the MPAC, the depth limits of the MPAC should be effective in protecting approximately 50% of the blue crab spawning stock in Chesapeake Bay. However, the effectiveness of the MPAC will be reduced if females in the MPAC do not remain resident in the MPAC before spawning (i.e., move to exploited areas), or if heavy exploitation outside the MPAC greatly reduces their numbers before entry of mature females into the MPAC. For instance, mature and egg-bearing females are exploited for a short time before and after the effective period of the MPAC in spring and fall, respectively. In other exploited marine species, such displaced fishing effort has limited the benefits of marine protected areas (Lipcius et al., in press), and may reduce the effectiveness of the MPAC in protecting the blue crab spawning stock.

ASSESSMENT OF INTERANNUAL AND MONTHLY VARIATION IN UTILIZATION OF MPAC SEGMENTS.—Adult females were distributed throughout the upper, lower, and historical sanctuary MPAC segments, as well as adjacent shallow waters, but with highest abundances in the MPAC. Distribution patterns of adult females in the MPAC segments differed in the two time periods (i.e., 1989–1991 and 1992–1997) between which spawning stock abundance declined over 80% (Lipcius and Stockhausen, 2002). In both 1989–1991 and 1992–1997, abundance during June (early in the reproductive period) was equivalent across MPAC segments. From July through September, abundance was not consistently higher or lower in any one of the MPAC segments. Abundance patterns by MPAC segment reflected substantial variation in their utilization over the reproductive period, without consistent use of any particular segment; all segments of the MPAC were utilized at different times of the spawning season and during the two time periods (1989–1991 and 1992–1997). Moreover, the historical sanctuary at times had significantly lower abundances than the other MPAC segments, reinforcing the importance of an expanded MPAC.

Egg-bearing females were not as broadly distributed as all adult females throughout the MPAC segments and adjacent shallow habitats; highest abundances occurred in the southern portion of the upper MPAC through the historical sanctuary. Abundances of egg-bearing females followed a much more consistent and generalized pattern through time than that of adult females. Highest abundances of egg-bearing females typically shifted from the northern to southern portions of the MPAC as the spawning season progressed. In June, most egg-bearing females were in the upper and lower MPAC segments. In July and August, the distribution of egg-bearing females shifted to the lower MPAC and historical sanctuary. By September, egg-bearing females were abundant only in the historical sanctuary. Surprisingly, this pattern held irrespective of the developmental stage of the eggs (i.e., early- or late-stage egg masses). The consistency in the seasonal shift in spatial distribution of egg-bearing females demonstrates the importance of the expanded MPAC to the conservation of the spawning stock, which by virtue of its spatial variation requires an extensive area to cover the seasonal alterations in abundance of egg-bearing females. For instance, whereas the MPAC protects egg-bearing females throughout the spawning season, the historical sanctuary only protected egg-bearing females during the latter half of the spawning season. Hence, the expanded MPAC is much more effective than the historical sanctuary at protecting a consistent fraction of the blue crab spawning stock over the full spawning season and across years.

ASSESSMENT OF UTILIZATION OF THE MPAC AS A SPAWNING AREA AND AS A DISPERSAL CORRIDOR.—We compared the distributions of adult females (i.e., females with or without eggs) and egg-bearing females to assess the functions of each of the MPAC segments. Both the lower MPAC and historical sanctuary contained high abundances of adult females and egg-bearing females, and these therefore potentially function as corridors and spawning grounds. In contrast, whereas adult females were equally abundant in all MPAC segments, egg-bearing females were rarely common in the upper MPAC segment. We therefore conclude that the upper MPAC serves primarily as a corridor for females migrating to spawn or hatch their egg masses in the lower MPAC and historical sanctuary.

Further investigations of the migration pathways and spawning behavior of blue crab females are required to discern the exact functions of each of the MPAC segments.

We conclude that (i) the blue crab spawning stock shifts spatially both during the reproductive period and between years; (ii) the historical spawning sanctuary did not protect a consistent fraction of the spawning stock, whereas the expanded MPAC protects a major fraction of the spawning stock both seasonally and yearly; and (iii) the expanded MPAC encompasses a dispersal corridor for adult females as well as most of the spawning grounds in the deeper waters of Chesapeake Bay. The MPAC therefore serves as a foundation for long-term protection of the blue crab spawning stock in Chesapeake Bay, and should be utilized concurrently with complementary conservation measures, such as effort controls, to prevent displaced fishing effort from negating the benefits of the marine protected area and corridor.

APPLICABILITY TO CONSERVATION OF EXPLOITED MARINE POPULATIONS.—Populations such as the blue crab in Chesapeake Bay, whose benthic life-history stages are disjunct (e.g., juveniles in shallow nurseries and adults in deeper waters), require protection not only in the spawning grounds, but also in dispersal corridors that link nursery habitats with the spawning grounds (Lipcius et al., in press). As with the displaced fishing effort that plagues migratory populations (Lipcius et al., in press), redirected fishing effort towards either earlier or other exploitable stages in the life history will likely negate the benefits of marine protected areas for these ontogenetically disjunct populations. For instance, the blue crab life history in Chesapeake Bay involves reinvasion of shallow-water nurseries by postlarvae from the continental shelf, followed by growth and dispersal throughout the tributaries and upper Bay. Mating takes place in the tributaries and in some upper portions of the Bay, after which mature females migrate to the Bay's mouth to spawn their egg masses and hatch their larvae in the higher salinities of the lower Bay. Hence, juveniles, subadult females, and mature males are distributed throughout the Bay, predominantly in shallow habitats where they are exploitable. Mature females must traverse the fishing gauntlet in the tributaries and bay mainstem as they migrate via shallow waters or deep-water dispersal corridors to the lower bay MPAC. Thus, protection from exploitation within the spawning grounds alone is not sufficient. Similarly, other types of marine protected areas are ineffective when they do not protect all exploitable stages in the life history prior to their maturation into the spawning stock (Allison et al., 1998; Lipcius et al., in press). The current MPAC protects a significant fraction of the spawning stock, and therefore serves as the foundation for future expansion of the MPAC into shallow habitats. In addition, the MPAC for the blue crab in Chesapeake Bay may also serve as a model system for evaluating the utility of marine protected areas for ontogenetically disjunct marine populations.

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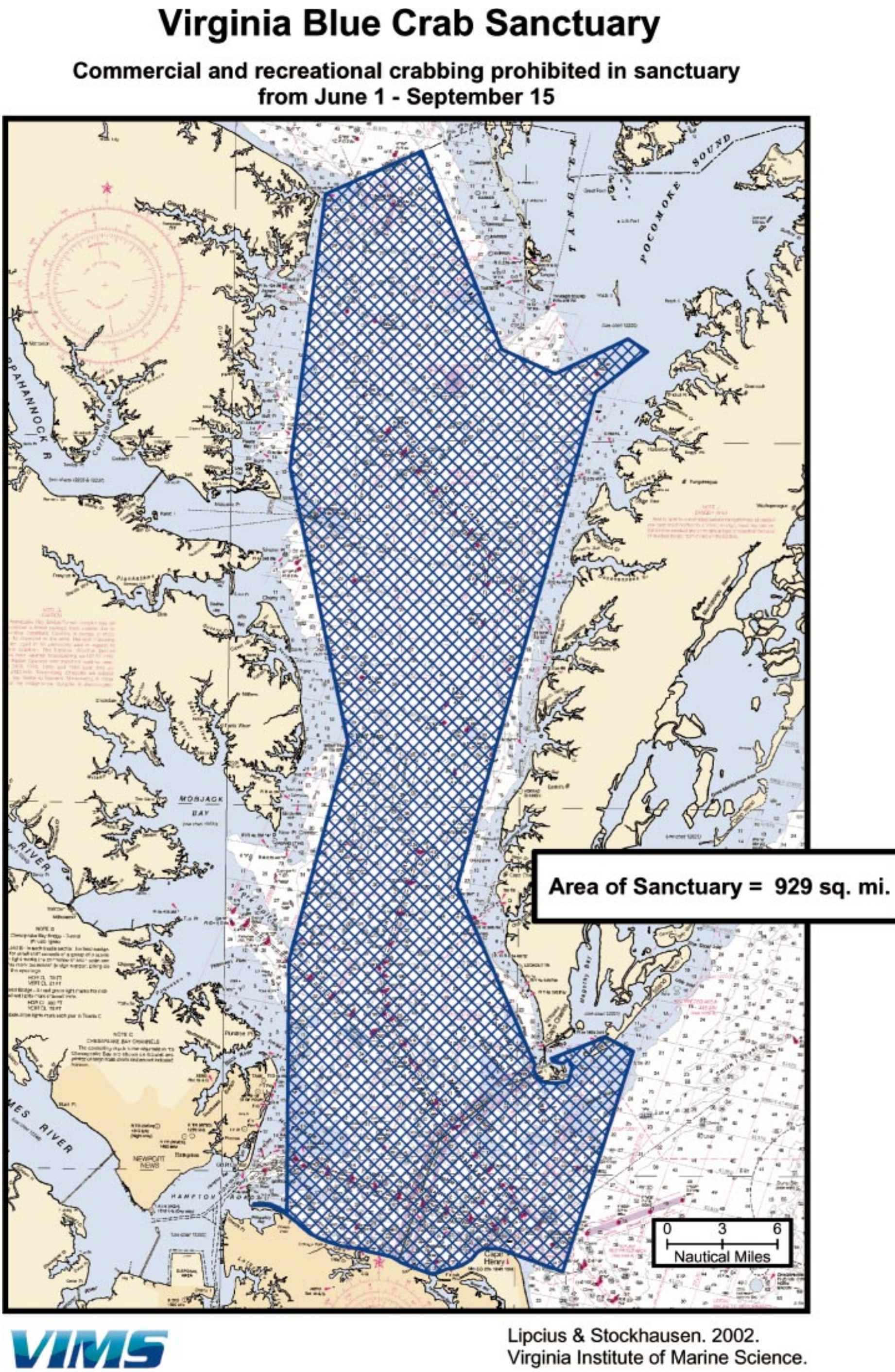

Appendix Figure 1. The MPAC was expanded in 2002 as shown to an area of 240,376 ha.