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A Deepwater Dispersal Corridor for Adult Female Blue Crabs in Chesapeake Bay

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Abstract

In marine ecosystems, there is no empirical evidence for the utility of dispersal corridors in conservation, despite widespread migrations by mammals, fish, and invertebrates. We investigated the potential for a deepwater dispersal corridor (> 13 m depths) in protecting adult females of the blue crab, *Callinectes sapidus*, en route from shallow-water nursery and mating areas to the spawning sanctuary in lower Chesapeake Bay. We used existing survey data for the population, both baywide before spawning occurs (winter dredge survey), and in the spawning grounds during reproduction (spring-fall trawl survey) over several years. Survey catches (CPUE, catch per unit of effort) were standardized and stratified by depths shallower and deeper than 13 m, and areas within and outside the spawning sanctuary. The key findings were: (1) the CPUE of adult females was significantly higher in the corridor than in adjacent shallow-water habi-

tats, both prior to the reproductive period and during the migratory and reproductive period; (2) the corridor was selective for adult females; and (3) a sanctuary-corridor complex, composed of the spawning sanctuary and protected corridor, had higher abundances and lower variation in abundance of the spawning stock between years than either the sanctuary or the corridor alone. Hence, a sanctuary-corridor complex should promote a less variable and more abundant spawning stock interannually, if displaced fishing effort is controlled. In contrast, adult males, juvenile males, and juvenile females were most dense in habitats shallower than 13 m. A protected, deepwater dispersal corridor coupled to the spawning sanctuary in the lower bay would therefore selectively conserve adult females either en route to or resident in the spawning grounds, whereas the remainder of the stock would remain susceptible to exploitation.

Introduction

Marine reserves and sanctuaries (= protected areas) may conserve and enhance exploited populations, thereby resulting in their establishment worldwide under the assumption that they facilitate long-term, sustainable exploitation (Bohnsack 1993, Roberts 1997, Allison et al. 1998, Guenette et al. 1998). Dispersal corridors may complement reserves in the conservation of species and diversity (Rosenberg et al. 1997, Beier and Noss 1998), though their utility remains uncertain due to the paucity of supporting empirical evidence (Hobbs 1992, Inglis and Underwood 1992, Simberloff et al. 1992). Experimental and logistical difficulties have precluded the necessary experimental evidence to validate the utility of corridors in conservation (Hobbs 1992, Inglis and Underwood 1992, Simberloff et al. 1992). The application of corridors will most likely be suited to particular landscapes, habitats, and species (Rosenberg et al. 1997), with the most promising species being those for which dispersal (e.g., spawning migration) is a key feature of the life cycle, such as the blue crab.

In the marine environment, there is widespread use of migration pathways by marine mammals, fish, and invertebrates (Herrnkind 1980, Rose 1993, Morreale et al. 1996, Colbourne et al. 1997, Estrella and Morrissey 1997, Acosta 1999, Micheli and Peterson 1999), though no conclusive evidence exists for the utility of marine dispersal corridors in conservation. Hence, we assessed the efficacy of a deepwater dispersal corridor for females of the blue crab, *Callinectes sapidus*, as they migrate from shallow-water nursery and mating areas to the spawning grounds in Chesapeake Bay.

Blue Crab in Chesapeake Bay: Life History, Exploitation, and Sanctuaries

The blue crab, *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Portunidae), is dispersed widely along the Atlantic and Gulf coasts of North

America (Williams 1984), is abundant throughout Chesapeake Bay (Hines et al. 1990, Lipcius and Van Engel 1990), and supports the world's second largest crab fishery in tonnage (Lipcius and Eggleston 2000). A detailed description of the life history and fisheries for the blue crab in Chesapeake Bay is provided in Seitz et al. (2001). The relevant portions of the life history deal mostly with the reproductive segment of the population. After a terminal maturity molt and mating in the oligohaline and mesohaline portions of Chesapeake Bay, adult females migrate to lower Chesapeake Bay to spawn in the summer, or overwinter and then spawn the following spring and summer (Van Engel 1958, Tagatz 1968). In Chesapeake Bay, maximal egg extrusion and larval release occur in summer, principally from July through mid-September either as a single midsummer peak or as bimodal early summer and late summer peaks (Jones et al. 1990, Prager 1996).

For decades, the blue crab spawning stock in Chesapeake Bay has been partially protected from exploitation from 1 June to 15 September by a sanctuary in the lower bay spawning grounds (Seitz et al. 2001). However, the sanctuary and various catch or effort controls have not protected a sufficiently large fraction of the spawning stock (Seitz et al. 2001) to avert an approximate 70% reduction in the baywide population (Lipcius and others, unpubl. manuscript), nor a 84% decrease in spawning stock biomass from 1994-1999 (Lipcius, unpubl. manuscript). Despite the need to protect a minimal proportion of the spawning stock for future recruitment (Tang 1985, Rothschild 1986, Lipcius and Van Engel 1990, Miller and Houde 1998, Rugolo et al. 1998), the spawning sanctuary apparently has not maintained the spawning stock at sustainable levels due to the intense exploitation of the population (Miller and Houde 1998, Lipcius and others, unpubl. manuscript) prior to its arrival in the spawning sanctuary (Seitz et al. 2001). Similarly, marine reserves 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). The blue crab spawning stock therefore requires supplementary protection of all stages in the life history and throughout critical habitats in Chesapeake Bay for effective conservation. Thus, we have examined a potential extension of the existing spawning sanctuary into a sanctuary-corridor network, with this investigation emphasizing a deepwater dispersal corridor (>13 m depths) from nursery and mating areas to the spawning sanctuary in the lower bay (Fig. 1). Depth of the corridor was chosen due to anecdotal fishery observations of concentrations of adult females at depth.

Specifically, we first characterized the size structure and interannual CPUE of female blue crabs in lower Chesapeake Bay, and then examined hypotheses that:

1. The CPUE of adult females is significantly higher in the deepwater dispersal corridor than in adjacent shallow-water habitats during the migratory and reproductive period;

Chesapeake Bay

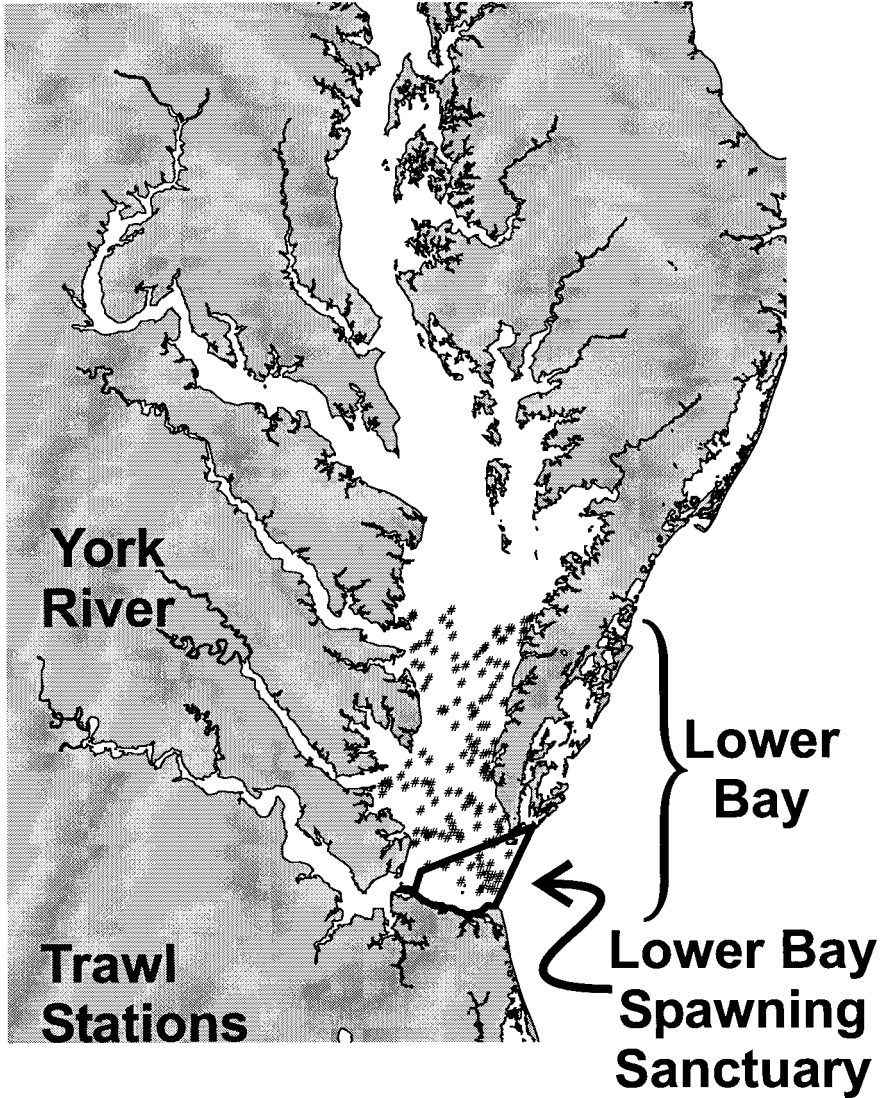


Figure 1. Chesapeake Bay spawning sanctuary. The spawning sanctuary is displayed as the outlined area near the bay mouth. Representative sampling stations are displayed for the trawl survey in the lower Chesapeake Bay spawning grounds during 1997. Approximately 50 stations were sampled monthly from July through September each year.

2. The deepwater dispersal corridor is selective for adult females (i.e., no other life-history stages, such as juveniles and adult males, are dense in the deepwater corridor); and
3. The CPUE of adult females is also significantly higher in the deepwater dispersal corridor than in shallow-water habitats during winter prior to the reproductive period.

Furthermore, we compared CPUE and variation in CPUE in the existing spawning sanctuary, the proposed deepwater corridor, and a sanctuary-corridor complex integrating the spawning sanctuary and deepwater corridor, to assess the hypothesis that:

4. A sanctuary-corridor complex produces lower variation and higher abundance interannually in the protected spawning stock than either the spawning sanctuary or the deepwater corridor alone.

Methods

CPUE of Adult Females in the Corridor and Shallow-Water Habitats during Reproduction

Adult female blue crabs were sampled monthly in the lower bay spawning grounds (Fig. 1) from spring through fall. Details of sampling are given by Lipcius and Van Engel (1990) and Lipcius (unpubl. manuscript). Each CPUE and size value came from single tows, which were collected with similar methods throughout the study period, and which served as independent data points (i.e., number or mean size of adult females per tow); annual sample sizes usually averaged about 50 tows.

CPUE was analyzed as the log-transformed, standardized number of adult females per tow. Log ($10x + 1$) transformation was used to normalize the data and reduce heterogeneity of variance (Underwood 1997). In all cases, variances were either homogeneous (Cochran's C statistic) or, if heterogeneous, the F test in analyses of variance was rejected at an alpha level lower than that used in the test for homogeneity of variance (Underwood 1997). Abundance was calculated as the product of mean CPUE, corrected for efficiency (Seitz et al. 2001), and area of each region.

In addition, we examined the size structure of females in the region of the sanctuary and corridor. Mean size per tow was used in size analyses, rather than all individual sizes, because the mean size per tow provided an independent data value which could be used in parametric analyses (e.g., analysis of variance), whereas each individual size was not independent of tow and invalid as an independent value in the parametric analyses. Further details of size analyses are provided by Lipcius (unpubl. manuscript). Size data did not require standardization nor transformation to meet assumptions of normality and homogeneity of variance. Size structure of

females in the spawning grounds was characterized by monthly size frequencies.

Selectivity of the Corridor

Juveniles, immature males, immature females, and adult males were sampled monthly in the lower bay (Fig. 1) from spring through fall, as for adult females. Juveniles are < 60 mm cw (= carapace width), immature males < 120 mm cw, and mature males > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. All females with the circular abdomen are adults, regardless of size.

CPUE of Adult Females in the Corridor and Shallow-Water Habitats before Reproduction

We sampled the blue crab population in winter (late November-March) by a baywide winter dredge survey using a stratified random design, which divided Chesapeake Bay into three geographic strata (Fig. 2). The advantages of sampling in winter over summer are: (1) blue crabs are not exploited in most areas of Chesapeake Bay during the winter, except in the lower Chesapeake Bay by the winter dredge fishery, and (2) blue crabs bury in the sediments during the winter, thereby sharply restricting their movement, which justifies the assumption of negligible immigration and emigration in the estimation of abundance.

Each year, 1,500 sites were selected randomly, and apportioned by the area of each stratum. The upper bay stratum included the tributaries, creeks, and upper mainstem of Chesapeake Bay, which are characterized by lower salinities, except near the mouths of tributaries in the lower bay. The middle bay stratum encompassed the middle mainstem of the bay, whereas the lower bay stratum circumscribed the spawning grounds (Fig. 2). Further details of sampling are provided by Lipcius and others (unpubl. manuscript). Each crab was measured (mm cw), and the sex, maturity, and overall condition recorded. At each sampling site, depth, salinity, water temperature, and dissolved oxygen were recorded and a sediment sample was collected.

Variation and Abundance in the Sanctuary, Corridor, and Sanctuary-Corridor Complex

The CPUE and abundance data for the spawning sanctuary and deepwater corridor were used in the comparison of (1) the existing spawning sanctuary, (2) the proposed deepwater corridor, and (3) a sanctuary-corridor complex integrating the sanctuary and deepwater corridor. Coefficients of variation were derived from the annual mean CPUEs in each zone for 1990-1997.

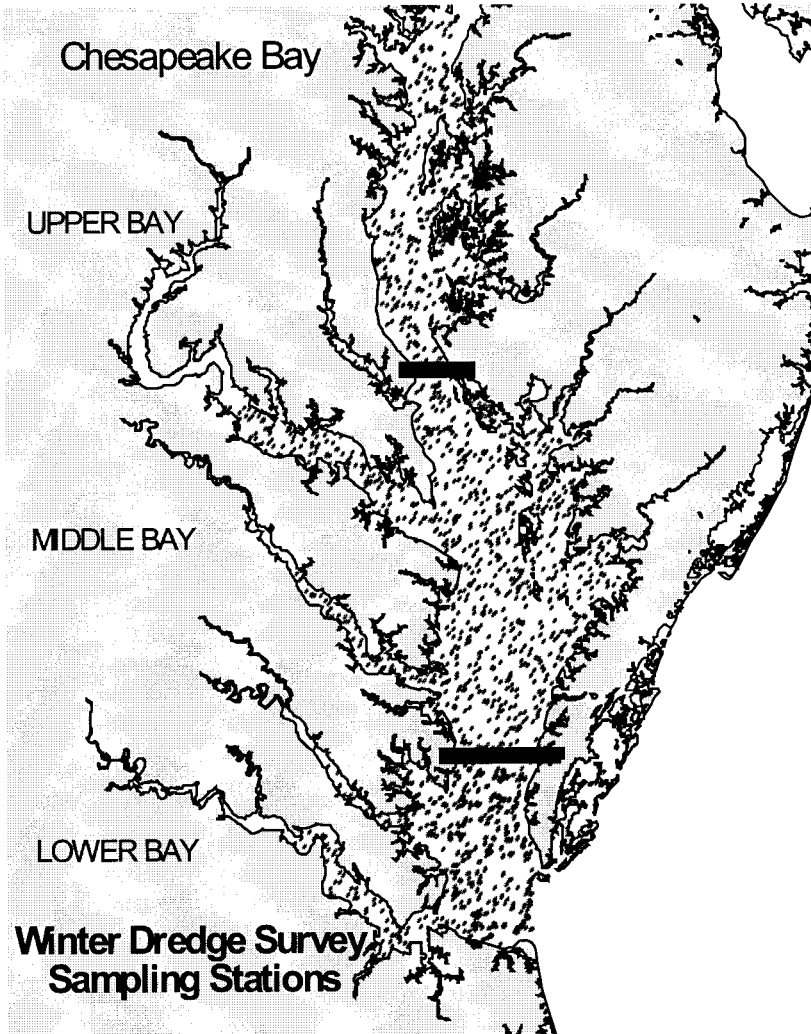


Figure 2. Representative sampling stations for the dredge survey during the 1990-1991 winter season. Sampling strata, divided by solid horizontal lines, included: upper bay mainstem and all tributaries, middle bay mainstem, and lower bay mainstem. Usually 1,500 stations were sampled annually.

Results

Size Structure and Interannual CPUE in Lower Chesapeake Bay

In April, females comprised at least two year classes ($t-1 = 0+$ and $t-2 = 1+$ and greater; t is the current year). The $0+$ year class had a mean size near 30 mm cw, and the $1+$ approximately 140 mm cw (Fig. 3). The $0+$ year class would have recruited in year $t-1$, and the $1+$ year class in year $t-2$, or before. Most growth occurred after June, when the $0+$ year class began to merge with the $1+$ year class (Fig. 3). Adult females in the $1+$ year class generally do not molt and grow after their pubertal molt to maturity (Van Engel 1958), thereby maintaining a relatively constant size distribution (Fig. 3). In September the new $0+$ year class was evident, resulting in a population composed of at least three year classes which recruited in years t , $t-1$ and $t-2$ (Fig. 3). Much of the $0+$ year class had entered the $1+$ year class by November so that the adult female segment of the population was composed of at least two year classes (from years $t-1$ and $t-2$). Migration by adult females to the lower bay spawning grounds occurs between May and November (Fig. 3), with peaks subsequent to the spring and fall “peeler runs” whereby pubertal or recently matured and mated females migrate down the tributaries and bay toward the spawning grounds (Van Engel 1958).

Adult female CPUE (Fig. 4a) and size (Fig. 4b) declined significantly during 1994-1997, both within the nominal deepwater corridor, in the lower bay outside the sanctuary, and in the spawning sanctuary (ANOVA, $P < 0.05$). Without regard to depth, there was no consistent trend toward greater CPUE or mean size of adult females in the sanctuary or outside the sanctuary (Fig. 4a,b), although mean size was larger outside the sanctuary in some years (Fig. 4b), probably due to size-selective exploitation of adult females before reaching the spawning grounds (Lipcius and others, unpubl. manuscript).

CPUE of Adult Females in the Corridor and Shallow-Water Habitats during Reproduction

In summer, adult females had a higher CPUE in deep water, both significantly so in the deepwater corridor zone outside the sanctuary (Fig. 5a, ANOVA, $P < 0.05$), and as a trend within the spawning sanctuary (Fig. 5b, ANOVA, $P > 0.05$). Within the spawning sanctuary, adult females represented the only segment of the population captured at moderate to high levels (Fig. 5b).

Selectivity of the Corridor

Outside the sanctuary, only adult females were characterized by high CPUE values in the deepwater corridor (Fig. 5a). Juveniles and immature males and females had significantly higher CPUE values in shallow-water habitats

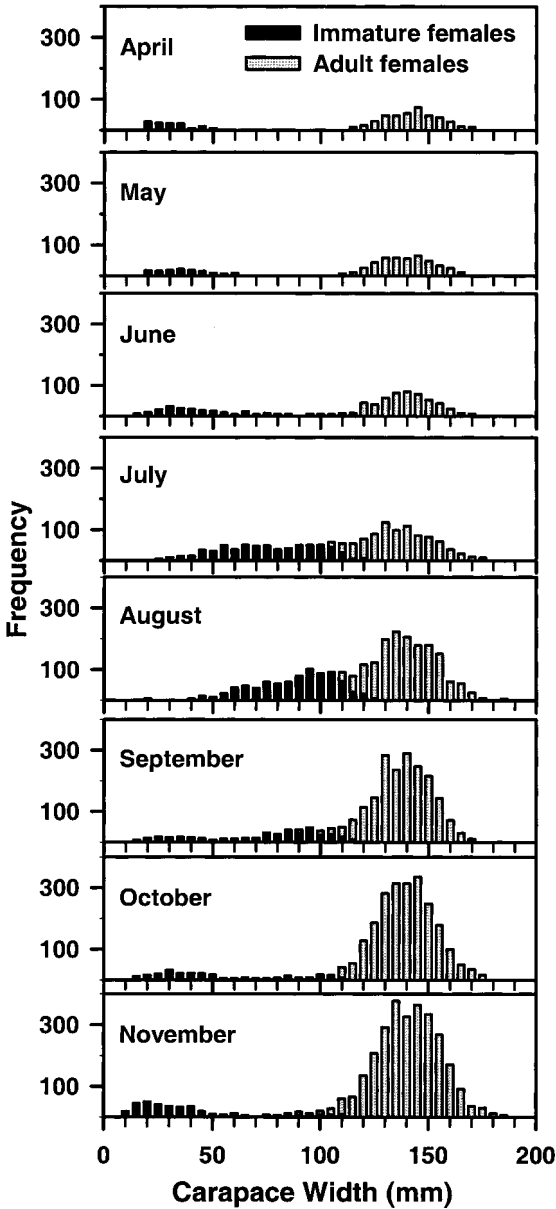


Figure 3. Composite of size frequencies of females captured by the trawl survey in the mainstem spawning grounds from 1990 to 1997, July-September; approximately 50 trawl tows were taken monthly. Mature females (= adults) are differentiated by their rounded abdomens. Note that adult females generally cease to grow after their pubertal molt, resulting in a static size distribution for adult females through time.

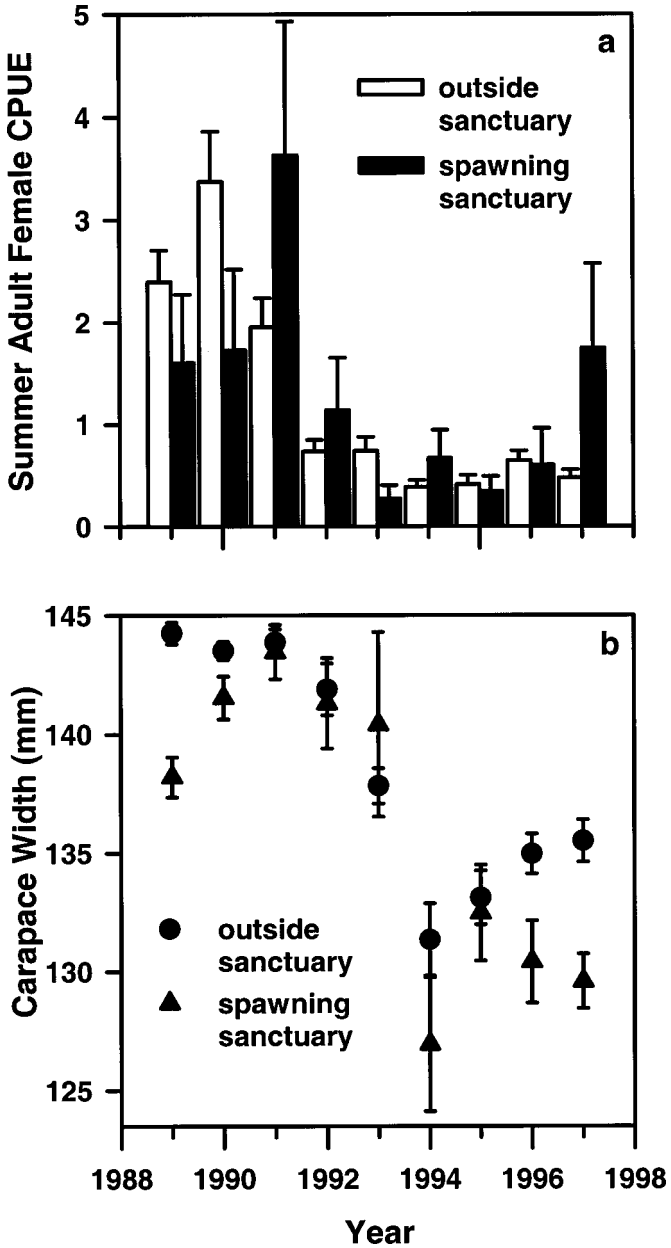


Figure 4. Interannual mean CPUE (a) and size (b) of adult females during summer in lower Chesapeake Bay, as sampled by the trawl survey, both inside and outside the spawning sanctuary. Vertical bars depict 1 S.E.

than in the deepwater corridor, where they were sparsely distributed (Fig. 5a, ANOVA, $P < 0.05$). Adult males were sparse and equally distributed in shallow and deep waters (Fig. 5a, ANOVA, $P > 0.05$).

CPUE of Adult Females in the Corridor and Shallow-Water Habitats before Reproduction

In winter, adult females had significantly higher CPUE values in deep than shallow habitats (Fig. 6, ANOVA, $P < 0.05$) in all years (Fig. 7), whereas total abundance was greater in the shallower habitats due to their much greater area (Fig. 8). A considerable and consistent fraction (approximately 20-25%) of all adult females resided within the boundaries of the deepwater corridor (Fig. 8). In contrast, CPUE and abundance levels of adult males, juvenile males, and juvenile females were significantly higher in habitats shallower than 13 m (Fig. 6, ANOVA, $P < 0.05$).

Variation and Abundance in the Sanctuary, Corridor, and Sanctuary-Corridor Complex

Highest abundances alternated between the spawning sanctuary and deepwater corridor with no apparent pattern (Fig. 9), other than the general increase in abundance in late summer as females migrated to the spawning grounds (Figs. 3 and 9). Highest abundances could be in the spawning sanctuary (Fig. 9: 1994, 1996-1997), in the deepwater corridor (Fig. 9: 1993, 1995), or in both areas (Fig. 9: 1990-1992).

The average fraction of adult females in the spawning sanctuary was 20.4%, in the deepwater corridor it was 26.7%, and in the shallow habitats outside the sanctuary 52.9%. The fractions in the deepwater corridor and spawning sanctuary did not differ significantly (ANOVA, $P > 0.05$), whereas these were significantly lower than that in the shallow-water area outside the sanctuary (ANOVA, $P < 0.05$). Hence, the abundances and fractions of adult females in the spawning sanctuary and deepwater corridor were generally complementary.

We also characterized and contrasted the variation in abundance in the spawning sanctuary, in the deepwater corridor, and in the collective zone encompassing the spawning sanctuary and deepwater corridor (= sanctuary-corridor complex) (Fig. 10) during years of low abundance (1992-1997). Abundance varied least in the sanctuary-corridor complex, with a coefficient of variation of 38% (Fig. 10a). In contrast, the coefficients of variation in the sanctuary and corridor were substantially higher at 90% and 64%, respectively (Fig. 10b,c), mostly due to interannual alternation of abundance between the sanctuary and corridor. For instance, abundances were high in the sanctuary and low in the corridor during 1996 and 1997, and conversely, low in the sanctuary and high in the corridor during 1993 and 1995 (Fig. 10b,c). Consequently, annual abundance in the sanctuary-corridor complex (Fig. 10a) was much more constant from year to year than in either the sanctuary (Fig. 10b) or the corridor (Fig. 10c).

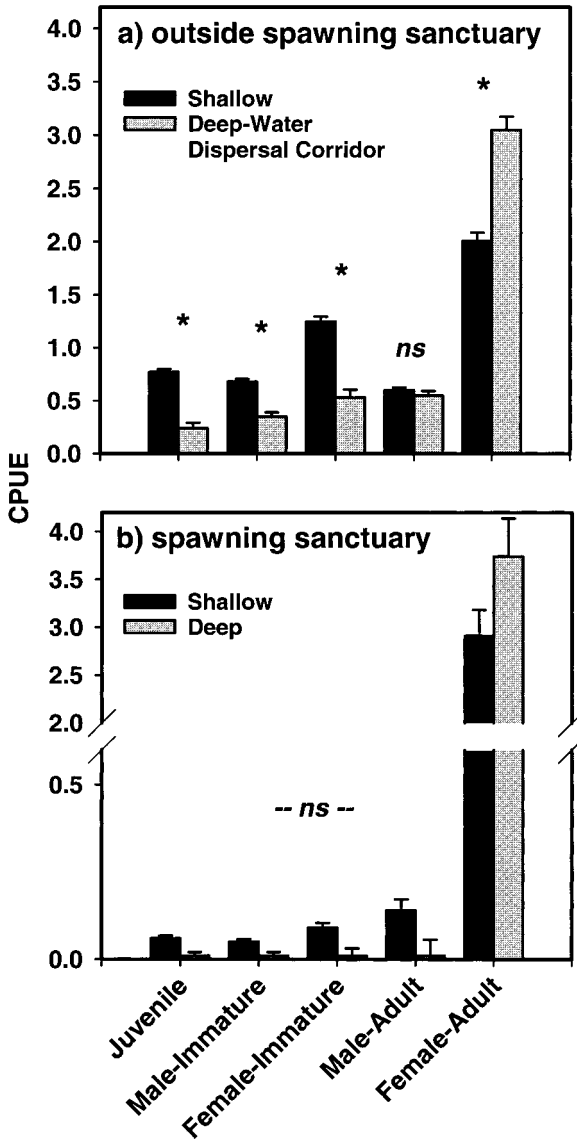


Figure 5. Mean CPUE of blue crab life-history stages during summer, as sampled by the trawl survey, both outside (a) and within (b) the spawning sanctuary in lower Chesapeake Bay. Shallow depths are < 13 m; deep habitats and the deepwater dispersal corridor are > 13 m. Juveniles are those crabs < 60 mm cw, immature males are < 120 mm cw, and mature males are > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. Vertical bars depict 1 S.E. * $P < 0.05$; ns $P > 0.05$ for comparisons of depth zones.

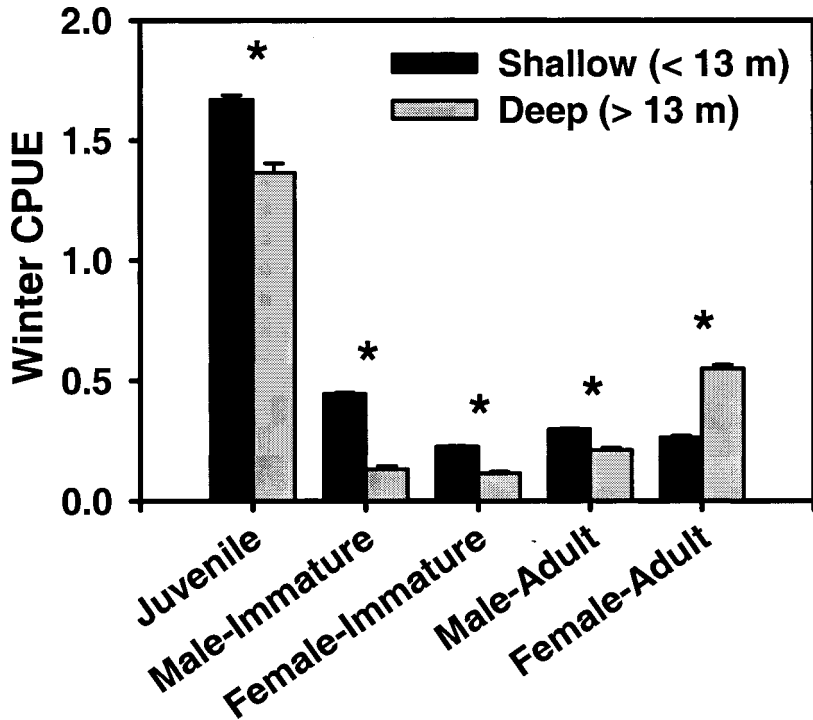


Figure 6. Mean CPUE of blue crab life-history stages in Chesapeake Bay during winter, as sampled by the baywide dredge survey. Juveniles are those crabs < 60 mm cw, immature males are < 120 mm cw, and mature males are > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. Vertical bars depict 1 S.E. * $P < 0.05$; ns $P > 0.05$ for comparisons between depth zones.

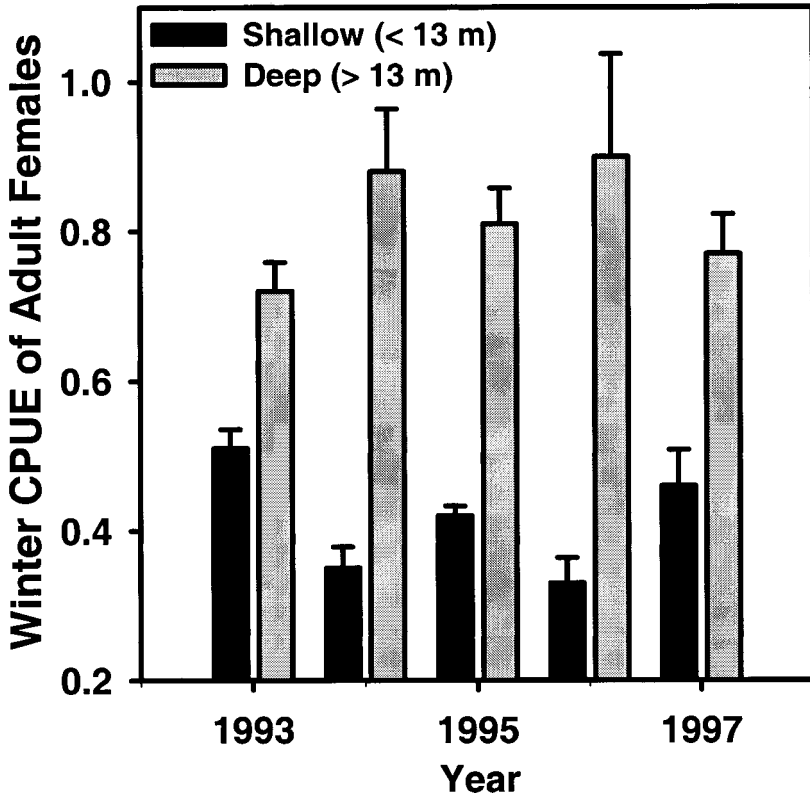


Figure 7. Mean CPUE of adult females baywide during winter, both in shallow (< 13 m depths) and deep (> 13 m depths) habitats. Vertical bars depict 1 S.E. CPUE in the deep habitats was significantly higher than that in shallow habitats (ANOVA, $P < 0.05$).

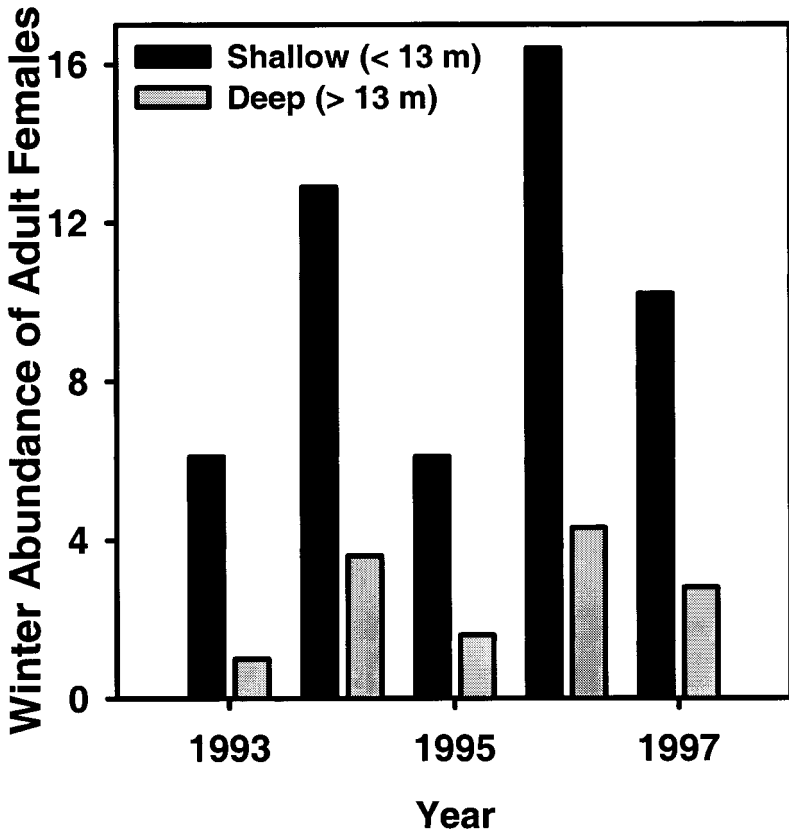


Figure 8. Abundance of adult females baywide during winter, both in shallow (< 13 m depths) and deep (> 13 m depths) habitats. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone.

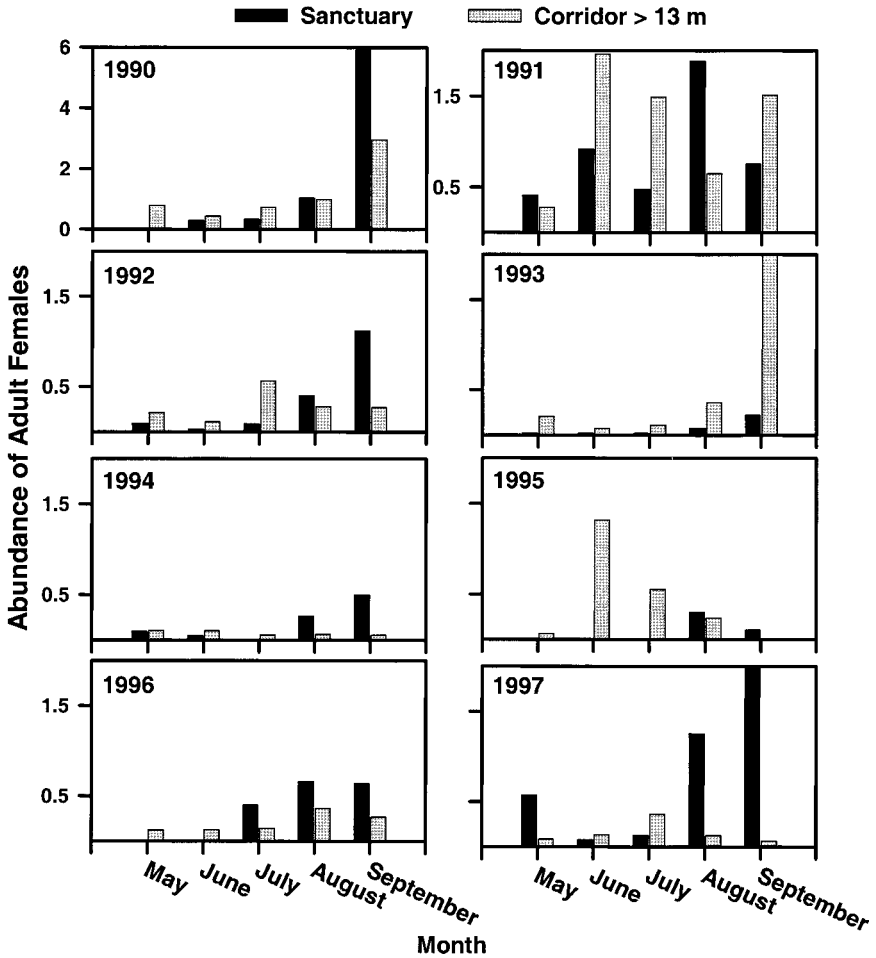


Figure 9. Monthly abundance of adult females during summer in lower Chesapeake Bay, residing either in the spawning sanctuary or within the deepwater (> 13 m depth) corridor outside the spawning sanctuary. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone.

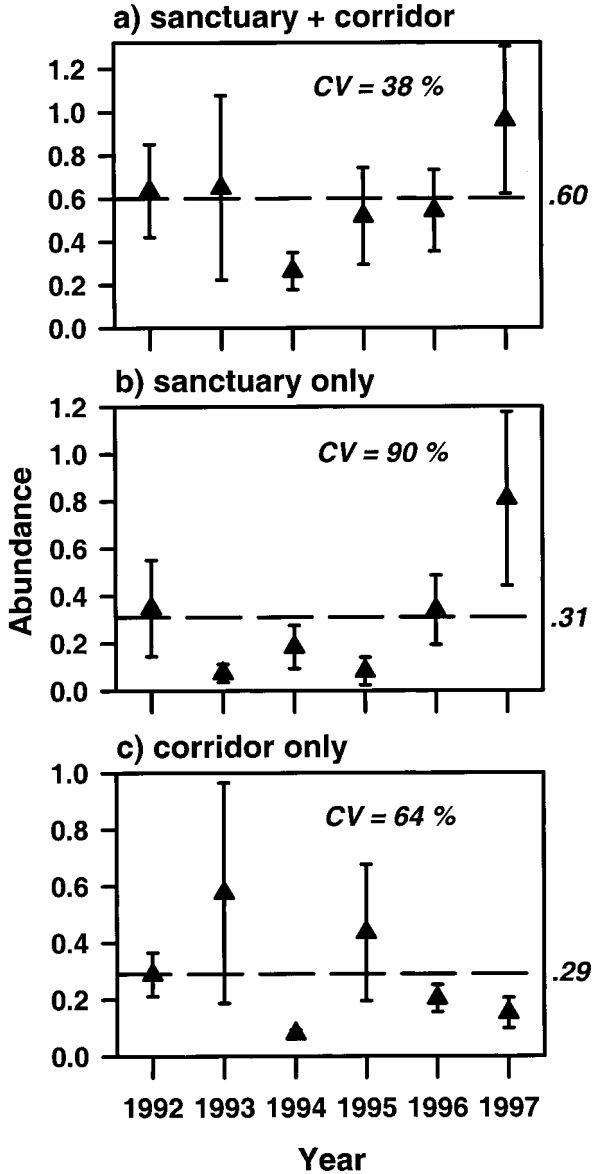


Figure 10. Annual CPUE of adult females during summer in lower Chesapeake Bay, residing in the (a) collective zone encompassing the spawning sanctuary and deepwater (> 13 m depth) corridor, (b) spawning sanctuary only, and (c) deepwater corridor only. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone. Coefficients of variation (C.V. = S.D./mean × 100%) are indicated, as well as the mean (dashed line) for each zone.

Discussion

Dispersal corridors may be useful in conserving species or diversity, although the effectiveness of corridors remains uncertain due to the paucity of empirical evidence. In the marine environment, there is no conclusive evidence that corridors facilitate faunal conservation, despite the widespread existence of migration pathways between divergent habitats utilized by marine mammals, fish, and invertebrates (Herrnkind 1980, Rose 1993, Morreale et al. 1996, Colbourne et al. 1997, Estrella and Morrissey 1997, Acosta 1999, Micheli and Peterson 1999). Herein we investigated the potential for a deepwater dispersal corridor (> 13 m depths) in protecting a key fraction (i.e., adult females) of the blue crab population en route from shallow-water nursery and mating areas to the spawning sanctuary in lower Chesapeake Bay. Adult female CPUE and size declined significantly after 1993, both within the corridor and in the spawning sanctuary, similarly to that observed previously (Lipcius and others, unpubl. manuscript; Lipcius, unpubl. manuscript). In addition, the existing spawning sanctuary has not protected a sufficient fraction of the spawning stock for long-term, sustainable exploitation (Seitz et al. 2001). Hence, further protection of the spawning stock, such as that potentially provided by a sanctuary-corridor network, is needed to conserve a sustainable exploited population in Chesapeake Bay.

Our key findings were: (1) the CPUE of adult females was significantly higher in the corridor than in adjacent shallow-water habitats, both prior to the reproductive period and during the migratory and reproductive period; (2) the corridor was selective for adult females; and (3) a sanctuary-corridor complex, composed of the spawning sanctuary and protected corridor, had higher abundances and lower variation in abundance of the spawning stock between years than either the sanctuary or the corridor alone. Hence, a sanctuary-corridor complex would protect a less variable and more abundant spawning stock interannually, provided that fishing effort is not redirected markedly.

Adult females were the only segment of the population at moderate to high CPUE within the spawning sanctuary and in the deepwater corridor outside the sanctuary. Outside the sanctuary, adult females had higher CPUE values in the deepwater corridor than in shallow habitats, as they migrated to the lower bay spawning grounds. Furthermore, CPUE in the corridor might be higher than that measured, if exploitation were eliminated and fishing effort were not displaced to intercept those females migrating to the corridor and sanctuary. Juveniles and immature males and females had significantly higher CPUE values in shallow-water habitats outside the sanctuary; adult males were approximately equally distributed in shallow and deep waters. None of these constituents of the population had high CPUE within the deepwater corridor. A protected, deepwater dispersal corridor in the lower bay coupled to the spawning sanctuary would therefore selectively conserve adult or maturing females either en route to

or resident in the spawning grounds, whereas the remainder of the stock (adult males, juvenile males, juvenile females) would remain susceptible to exploitation.

In different years, highest abundances vacillated between the spawning sanctuary and deepwater corridor. In addition, the average fraction of all adult females in the lower bay that resided in the spawning sanctuary was 20.4% and in the deepwater corridor it was 26.7%, which did not differ significantly. Hence, the abundances and fractions of adult females in the sanctuary and deepwater corridor were complementary. Moreover, the interannual variation in abundance was lowest in the sanctuary-corridor complex, with a coefficient of variation of 38%, whereas the respective coefficients of variation in the sanctuary and corridor were substantially higher at 90% and 64%, mostly due to the interannual alternation of abundance between the sanctuary and corridor. Consequently, annual abundance in the sanctuary-corridor complex was not only higher, but also much more constant from year to year than in either the sanctuary or the corridor.

The utility of a deepwater corridor in the middle and upper bay is questionable. Summertime hypoxia (Diaz and Rosenberg 1995) likely precludes utilization of the deepwater corridor in the middle and upper bay during the migratory and reproductive period. However, if females utilize the deepwater corridor during spring and early summer prior to the onset of summertime hypoxia, or during the fall after hypoxia dissipates, then protection of the deepwater corridor throughout the bay during the spring and fall migrations may be warranted. Further sampling of the deepwater corridor during spring, summer, and fall in the middle and upper bay is necessary to test these assertions.

Conclusions and Recommendations

Adult females are consistently found in substantial numbers within the confines of the deepwater migration corridor, whether during the overwintering period or during the spawning season. A protected deepwater migration corridor (Fig. 11) would nearly selectively protect adult females en route to the spawning grounds, whereas the remainder of the exploitable segment of the stock (i.e., adult males, juvenile males, juvenile females) would be minimally impacted and remain susceptible to the crab fisheries. Consequently, we propose that a protected deepwater dispersal corridor is an effective means of protecting adult females as they migrate to the spawning grounds, particularly in those middle bay and lower bay regions that are impacted negligibly by summertime hypoxia.

We therefore suggest that to conserve and enhance the blue crab spawning stock, the existing spawning sanctuary should be expanded into a sanctuary-corridor network. The first step in the development of a sanctuary-corridor network involves protection of the proposed deepwater corridor (Fig. 11) in summer. Concurrently, there should be (1) consider-



Figure 11. Proposed initial extension of the spawning sanctuary into the deepwater corridor in lower Chesapeake Bay and 13-m depth contour (based on NOAA depth charts). The sizes of the arrows reflect the densities of adult females in the different areas. Note that we assume that there are relatively few females during the reproductive period in deep waters of the middle and upper portions of Chesapeake Bay due to summertime hypoxia and anoxia, though this assumption remains untested. The spawning sanctuary is displayed as the shaded area near the mouth of the bay. The proposed sanctuary-corridor complex was adopted by the Virginia Marine Resources Commission on 27 June 2000.

ation of complementary effort controls to preclude displaced effort, which might nullify any benefits of a protected corridor, as well as (2) simulations of the impact of the network upon exploitation rates and population growth rates (e.g., Miller and Houde 1998). Second, there should be an examination of other critical habitats deserving protection, such as shallow-water corridors and habitats utilized by other benthic phases in the life cycle; these include settlement habitats, nursery grounds for young juveniles (e.g., seagrass beds and marshes), feeding sites of juveniles and adults (e.g., marshes and mud flats), and mating areas, all of which might be linked into the network by protected dispersal pathways. The network could also incorporate pelagic habitats used by the planktonic stages (i.e., larvae, postlarvae, and young juveniles). Some of the habitats are presently protected (e.g., spawning sanctuary in the lower bay, de facto sanctuaries such as shipping channels), and should be integrated into the network. Ultimately, the baywide sanctuary-corridor network could be used as a permanent management tool to protect that fraction of the stock which will maintain the blue crab population in Chesapeake Bay at long-term sustainable levels, as well as to protect critical shallow-water habitats such as seagrass beds and fringing marshes.

Advantages of a sanctuary-corridor network include efficient enforcement, reduction of fishing mortality, and preservation of critical Chesapeake Bay habitats (e.g., seagrass beds). The use of a sanctuary-corridor network does not preclude other effective management measures, but it may allow for the abolition of ineffective regulations that hinder exploitation and conservation alike. Finally, we posit that the blue crab in Chesapeake Bay serves as a model marine system for the study of the efficacy of sanctuaries and dispersal corridors for sustainable resource use in the marine environment.

Addendum

The sanctuary-corridor complex was adopted, with some modifications, by the Virginia Marine Resources Commission on 27 June 2000.

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References

- Acosta, C.A. 1999. Benthic dispersal of Caribbean spiny lobsters among insular habitats: Implications for the conservation of exploited marine species. *Conserv. Biol.* 13:603-612.
- Allison, G.W., J. Lubchenco, and M.H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* 8(1):S79-S92.
- Beier, P., and R.F. Noss. 1998. Do habitat corridors provide connectivity? *Conserv. Biol.* 12:1241-1252.
- Bohnsack, J.A. 1993. Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36:63-71.
- Colbourne, E., B. deYoung, and G.A. Rose. 1997. Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the northeast Newfoundland shelf. *Can. J. Fish. Aquat. Sci.* 54(Suppl. 1):149-157.
- Diaz, R.J., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Annu. Rev.* 33:245-303.
- Estrella, B.T., and T.D. Morrissey. 1997. Seasonal movements of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts. *Fish. Bull., U.S.* 95:466-476.
- Guenette, S., T. Lauck, and C. Clark. 1998. Marine reserves: From Beverton and Holt to the present. *Rev. Fish Biol. Fish.* 8:251-272.

- Herrnkind, W.F. 1980. Movement patterns in palinurid lobsters. In: J.S. Cobb and B.F. Phillips (eds.), *The biology and management of lobsters*. Vol. 1. Physiology and behavior. Academic Press, New York, pp. 349-407.
- Hines, A.H., A.M. Haddon, and L.A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67:105-126.
- Hobbs, R.J. 1992. The role of corridors in conservation: Solution or bandwagon? *Trends Ecol. Evol.* 7:389-392.
- Inglis, G., and A.J. Underwood. 1992. Comments on some designs proposed for experiments on the biological importance of corridors. *Conserv. Biol.* 6:581-586.
- Jones, C.M., J.R. McConaughy, P.J. Geer, and M.H. Prager. 1990. Estimates of spawning stock size of blue crab, *Callinectes sapidus*, in Chesapeake Bay, 1986-1987. *Bull. Mar. Sci.* 46:159-169.
- Lipcius, R.N., and D.B. Eggleston. 2000. Ecology and fishery biology of spiny lobsters. In: B.F. Phillips and J. Kittaka (eds.), *Spiny lobster management*. Blackwell Scientific, Oxford, pp. 1-41.
- Lipcius, R.N., and W.A. Van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River, 1972-1988) and stock-recruit functions. *Bull. Mar. Sci.* 46:180-194.
- Micheli, F., and C.H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conserv. Biol.* 13:869-881.
- Miller, T.J., and E.D. Houde. 1998. Blue crab target setting. Final Report to Chesapeake Bay Program. University of Maryland Center for Environmental Sciences, Chesapeake Biological Laboratory. Ref. No. [UMCES] CBL 98-129.
- Morreale, S.J., E.A. Standora, J.R. Spotila, and F.V. Paladino. 1996. Migration corridor for sea turtles. *Nature* 384:319-320.
- Prager, M.H. 1996. A simple model of the blue crab, *Callinectes sapidus*, spawning migration in Chesapeake Bay. *Bull. Mar. Sci.* 58:421-428.
- Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278:1454-1457.
- Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366:458-461.
- Rosenberg, D.K., B.R. Noon, and E.C. Meslow. 1997. Biological corridors: Form, function, and efficacy. *BioScience* 47:677-687.
- Rothschild, B.J. 1986. *Dynamics of marine fish populations*. Harvard University Press, Cambridge, Massachusetts.
- Rugolo, L.J., K.S. Knotts, A.M. Lange, and V.A. Crecco. 1998. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). *J. Shellfish Res.* 17:493-517.

- Seitz, R.D., R.N. Lipcius, W.T. Stockhausen, and M.M. Montane. 2001. Efficacy of blue crab spawning sanctuaries in Chesapeake Bay. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell (eds.), *Spatial processes and management of marine populations*. University of Alaska Sea Grant, AK-SG-01-02, Fairbanks. (This volume.)
- Simberloff, D., J.A. Farr, J. Cox, and D.W. Mehlman. 1992. Movement corridors: Conservation bargains or poor investments? *Conserv. Biol.* 6:493-504.
- Tagatz, M.E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull.*, U.S. 67:17-33.
- Tang, Q. 1985. Modification of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. *Fish. Res.* 3:13-21.
- Underwood, A.J. 1997. *Experiments in ecology*. Cambridge University Press, Cambridge, United Kingdom.
- 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.
- Williams, A.B. 1984. *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, D.C.