

Geostatistical Analysis of the Abundance and Winter Distribution Patterns of the Blue Crab *Callinectes sapidus* in Chesapeake Bay

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Abstract.—Spatial heterogeneity is a striking life history feature of the blue crab *Callinectes sapidus* in the Chesapeake Bay. Spatial patterns of sex- and age-specific habitat use have been well documented and affect the fisheries in the bay. However, a quantitative assessment of the spatial distribution of blue crabs during winter, when they are generally buried in the sediments, has been lacking. We applied geostatistical techniques (variogram modeling and kriging) to 13 years of winter dredge survey (WDS) data to map patterns of blue crab winter abundance. These maps were then quantified to derive a time series of baywide abundance and to examine changing patterns of habitat use and aggregation. Geostatistical abundance estimates were generally similar to those calculated from design-based methods but were more highly correlated with fishery catch per unit of effort. Both abundance time series showed a large and significant decline from 1990 to 2002. Changes in spatial distribution were evaluated using trend maps and a density-weighted centroid. Interannual variation in the latitude of the weighted centroid was positively correlated with baywide abundance, suggesting possible density-dependent changes in distribution. The southward shift in winter distribution at low stock size may increase the vulnerability of blue crabs to exploitation in a winter dredge fishery that occurs only in the southern portion of the bay. Such quantitative and spatially explicit information provides a potentially useful base for constructing population models and evaluating alternative management options.

There is increasing recognition of the importance of space and the need for spatially explicit information for understanding the ecology, population dynamics, and management of marine resources (Nishida and Booth 2001). This is not only because of a growing awareness of the risks of not accounting for the spatial distribution of exploited populations (Hutchings 1996; Walters 2003), but also because new methods have enabled space to be incorporated into a variety of stock assessment models (Caddy 1975; Walters et al. 1999; Pelletier et al. 2001). These spatial models and spatially explicit management strategies, such as time-area closures and marine protected areas, are being used increasingly to manage fisheries. Although the goals and data requirements of these modeling and management approaches differ substantially, all require a quantitative description of the distribution of the species in question and most could benefit from an understanding of how that distribution

may change over time or with changes in stock size.

An accurate quantitative description of a species' spatial distribution requires a spatially intensive survey of the entire study region conducted over a short enough time interval that the distribution can be assumed to have remained static. Assessing changes in distribution requires several such surveys conducted over different seasons, years, or stock sizes. The baywide winter dredge survey (WDS) of blue crabs *Callinectes sapidus* in Chesapeake Bay (Sharov et al. 2003) provided a unique opportunity for implementing data-intensive spatial analysis because it represents a relatively long time series (13 years) of spatially intensive (about 900–1,500 stations annually) sampling conducted over a wide range of blue crab abundances. Baywide abundance estimates have been developed from the WDS (Sharov et al. 2003), and time series of blue crab relative abundance are available from other fishery-independent surveys, including the Maryland and Virginia trawl surveys (Lipcius et al. 2003) and the Calvert Cliffs pot survey (Abbe and Stagg 1996). However, the spatial analysis of these surveys has been conducted only at a very coarse scale, information usually being limited to two geographic categories,

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upper bay or lower bay or Maryland or Virginia (e.g., Miller 2003).

Blue crabs are an important estuarine benthic predator and scavenger (Laughlin 1982; Millikin and Williams 1984; Hines et al. 1990; Mansour 1992) that provide a link between benthic and pelagic food webs (Baird and Ulanowicz 1989). The ecological role of the blue crab in Chesapeake Bay varies both spatially and temporally as a result of its complex life history (Miller 2001, 2003). Blue crabs spawn in mid to late summer in the high salinity waters of the lower Chesapeake Bay (Van Engel 1958; Jones et al. 1990). The larvae are advected offshore where they develop through seven to eight larval stages before returning to the bay as megalopae to settle in structured habitats in the lower bay (Lipcius and Van Engel 1990; Metcalf et al. 1995). In late fall, blue crabs in Chesapeake Bay undertake a migration to deeper water where they overwinter in the sediment. Migration patterns and winter habitat use are sex-specific and age-specific. Males and immature females predominate in the lower salinity waters of tributaries and the upper bay and make shorter migrations to nearby channels for overwintering (Abbe and Stagg 1996). Mature females migrate greater distances toward the lower bay spawning habitat (Hines et al. 1995; McConaugha 1995; Turner et al. 2003; Aguilar et al. 2005).

Chesapeake Bay blue crab fisheries reflect the spatial and temporal aspects of the blue crab life history. A diversity of gear and techniques exist to target seasonal aggregations and specific molt stages (Rugolo et al. 1998). For example, a winter dredge fishery targeting mature females exists in the lower bay; modified bottom trawls (called "crab scrapes") are used to target molting crabs, and pots and trot lines are used to catch hard-shell crabs of both sexes from spring through fall. Management efforts have responded to the spatial and temporal variability of blue crabs and their fisheries with regulations that are regionally and seasonally specific. For example, pot fishing is restricted to open waters of the main stem of the bay in Maryland, whereas trotlines are used in the tributaries and shallow bays. A blue crab spawning sanctuary designed to protect mature females in the lower bay has been in place for decades (Van Engel 1958) and has been extended several times, most recently in 2003 when it was enlarged from approximately 1,500 km² to 2,400 km² (Lipcius et al. 2001; Virginia Marine Resources Commission 2004). This sanctuary, however, protects crabs only during the summer (June 1 to September 15)

and is open to the dredge fishery in the winter. Recent declines in the Chesapeake Bay blue crab stock and decreases in spawning stock biomass (Lipcius and Stockhausen 2002) indicate that current restrictions, including the lower bay sanctuary, may be insufficient to ensure the long-term sustainability of the blue crab fishery. Although modeling studies show that reductions in the lower bay winter dredge fishery alone are not enough to ensure a sustainable fishery (Miller 2001), the lower bay sanctuary boundaries could probably be improved by using maps of blue crab winter distribution.

Classical statistical approaches to analyzing survey data are based on the underlying design of the survey (e.g., simple random, stratified random, systematic, etc.). However, these design-based approaches fail to take advantage of the information represented in the spatial autocorrelation structure and, in some cases (e.g., systematic surveys, Aubry and Debouzie 2000) may result in biased estimates of the variance. Aubry and Debouzie (2000, 2001) demonstrated the superiority of model-based geostatistical techniques when spatial autocorrelation is present in the data. Millar and Anderson (2004) give common examples of fishery survey designs that can lead to pseudoreplication due to temporal or spatial autocorrelation and suggest appropriate methods for analyzing data from these designs. Rossi et al. (1992) and Legendre (1993) showed that although spatial autocorrelation is a common source of problems for many design-based statistical methods, it is also a source of valuable information provided that the appropriate statistical tools are used.

Geostatistical methods are an approach for conducting finer-scale analyses of distributional patterns that have been gaining popularity in ecology and the environmental sciences in general (Rossi et al. 1992; Legendre 1993) and within fisheries science specifically (Petitgas 1993; Rivoirard et al. 2000). The two main components of a geostatistical analysis are variogram modeling followed by spatial prediction and interpolation. Empirical variograms show the decrease in relatedness between pairs of points as a function of distance. A variogram model fit to the empirical variogram describes small-scale variability and measurement error (the nugget parameter), broad-scale variability (the sill), and the distance at which points become statistically independent (the range). Kriging is a commonly used interpolation method that makes use of the spatial structure defined in the variogram to predict values of a variable at un-

sampled sites. Kriging can be used for descriptive purposes, such as mapping (e.g., Comeau et al. 1998), as well as for abundance estimation (Petitgas 1993; Rivoirard et al. 2000) based on physical sampling (Maynou et al. 1998) or acoustic surveys (Sullivan 1991).

Improvements in abundance estimation are not the only rationale for applying spatial modeling techniques to data on blue crab winter distributions. The ability to detect changes in the distribution of an exploited stock can be an important asset for fishery management. One explanation for the unexpected collapse of some fished populations involves undetected changes in distribution (Hutchings 1996). Many stock assessment models assume that fishery catch per unit of effort (CPUE) is directly proportional to stock abundance (Quinn and Deriso 1999). The coefficient of proportionality is termed the catchability coefficient, q . When this direct proportionality fails, stocks are said to be hyperdispersed or hypodispersed. This is often the case in a spatially structured (i.e., nonrandomly distributed) population, such as schooling fish or invertebrates with a patchy distribution, which may be caught very efficiently even as the total biomass and total number of aggregations declines (e.g., Rose and Kulka 1999; Die and Ellis 1999). In such cases, landings, which may remain high despite serious decreases in the population, do not accurately reflect population size. Thus, in spatially structured populations, changes in distribution may provide an early warning of stock depletion (Hutchings 1996).

Quantitative maps of blue crab distributions would allow managers to evaluate the potential effectiveness of time–area closures and marine reserves and provide an objective, biologically based criterion for setting reserve boundaries. Such maps may also provide input for predicting the potential impacts to the blue crab population of changes to the environment, such as dredging and disposal of dredged material. Quantitative maps allow researchers to develop and test hypotheses about habitat use and ecological relationships. Finally, distribution maps derived from a time series of data allow for the examination of potential changes in habitat use and aggregation through time. When the distribution maps are derived from data collected over a range of population sizes (as they are in our study), they also permit the examination of potential density-dependent changes in distribution.

We developed winter distribution maps of the Chesapeake Bay blue crab stock based on 13 years

of fishery-independent survey data. These maps were then used to derive a time series of geostatistical abundance estimates and to determine whether distributional changes were correlated with changes in stock size. We evaluated the results in the context of three hypotheses: (1) geostatistical methods provide a useful alternative to the stratified random-design-based methods that have previously been used to estimate abundance of blue crabs, (2) changes in spatial structure and distribution accompany changes in abundance, and (3) changes in the blue crab distribution result in changes in their vulnerability to exploitation in the winter dredge fishery.

To evaluate the first hypothesis, geostatistical and stratified random-design-based abundance time series were compared using two criteria: standard error of the estimates and correlation with a time series of CPUE from the winter dredge fishery. Because we did not know the true abundance of blue crabs in Chesapeake Bay, we did not attempt to determine which method is better—a question more suited to simulations.

The second hypothesis we addressed by (1) comparing variogram parameters and the location of the density-weighted centroid of blue crab distribution to the baywide abundance time series, and (2) through qualitative evaluation of a map of temporal trends in blue crab abundance. Evaluating changes in spatial distribution is challenging because no single metric summarizes all aspects of an organism's distribution. Maps representing the density of an organism over a two-dimensional space have many characteristics that may be relevant to understanding fisheries (Swain and Sinclair 1994), and distribution patterns can be evaluated using a variety of methods (e.g., Petitgas 1998). Variogram parameters are used here because they summarize a great deal of information about spatial autocorrelation structure, including large-scale (sill) and small-scale (nugget) variability and patch size (range). In addition, we use the density-weighted centroid, analogous to the center of gravity of an object, as a simple spatial measure of central tendency (Rose et al. 1994; Rose and Kulka 1999).

The final hypothesis we evaluated by comparing the location of the density-weighted centroid to the catchability coefficient of the winter dredge fishery.

Methods

Data source.—All data analyzed in this study were from the WDS of the blue crab population

- 1998 Sample locations

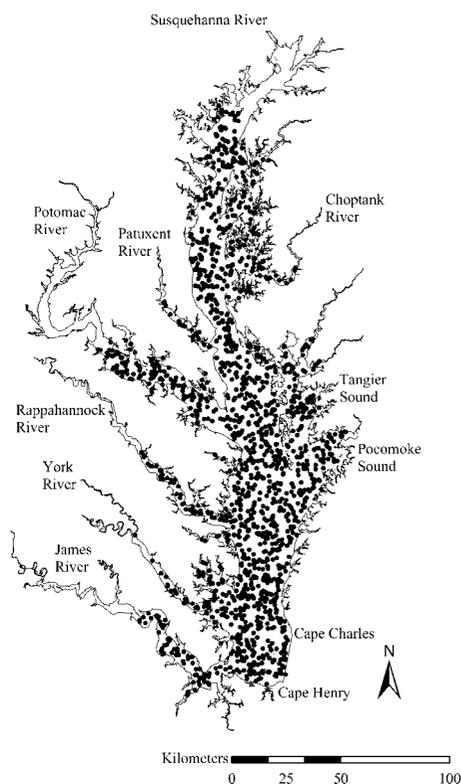


FIGURE 1.—The distribution of sample locations in 1998, which typified the locations used to analyze blue crab abundance and distribution patterns in the Chesapeake Bay between 1990 and 2002.

in Chesapeake Bay, which has been conducted annually since the winter of 1989–1990 (survey years will henceforth be referred to by the year in which the survey was completed). The WDS samples crabs during the dormant winter period when crabs lie buried in the sediment, thus limiting potential bias due to movement. Full details of the survey design and implementation are provided by Vølstad et al. (2000) and Sharov et al. (2003), and are summarized here. Briefly, the survey consisted of a 1-min tow of a 1.83-m wide crab dredge at each station. For most years, stations were chosen randomly within three strata. During the first 2 years of the survey, however, 22 and 25 strata were used, each of the major tributaries and embayments forming a separate stratum. Sample size ranged from approximately 900–1,500 stations annually during the period 1990–2002. A representative distribution of sample points for 1 year (1998) is shown in Figure 1. Depletion experiments (Zhang et al. 1993; Vølstad et al. 2000), in

which the same area was dredged repeatedly, were conducted yearly to determine the fraction of blue crabs sampled by a single dredge tow (i.e., the catchability coefficient for the survey, q_{survey}). Based on these experiments, Vølstad et al. (2000) used an exponential model to estimate vessel-specific and year-specific catchability coefficients and transform catch at each station into an estimate of absolute abundance. The variable we analyzed was the density of blue crabs (number/1,000 m²), calculated by dividing the absolute abundance estimate by the dredge area swept.

The spatial analyses we employed were based on sample coordinates defined by the starting location of each tow. The tow distance was calculated from the start and end coordinates as determined by Loran-C in early years and differential global position system since 1996. Tows shorter than 50 m and longer than 500 m (1.7% of the total data) were not used in this analysis. All coordinates were projected to universal transverse mercator zone 18 before analysis so that a unit in the east–west (easting) direction is equal to a unit in the north–south (northing) direction. For easier interpretation, plots show equivalent latitude and longitude coordinates.

Geostatistical analysis.—Although some researchers (Little et al. 1997; Rathbun 1998) have suggested that a landscape-based distance metric that measures distances between sample points through the water is more appropriate for kriging in estuaries, the results of these studies have not shown a consistent improvement in prediction accuracy compared with traditional kriging methods based on Euclidean distance. Use of a landscape-based distance metric for kriging blue crab density in Chesapeake Bay resulted in only small and inconsistent differences in prediction accuracy (Jensen et al., in press). Consequently, the Euclidean distance metric is used in this analysis.

To satisfy the assumption of stationarity (i.e., no large-scale trend in the mean or variance) required in geostatistical analyses, data were spatially detrended. A second-order two-dimensional spatial trend with all possible X (longitude or easting) and Y (latitude or northing) interactions was fit for each year (Cressie 1993). This trend model was then simplified using backward elimination at $\alpha = 0.01$ to stay in the model. This relatively stringent significance level threshold was used to avoid overfitting the trend. Variogram modeling and kriging were then conducted on the residuals. The large-scale trend was added back to the kriged estimates for mapping and abundance estimation.

Robust empirical variograms (Cressie 1993) were calculated in version 8 of SAS (VARIOGRAM procedure, SAS Institute, Inc., Cary, North Carolina). Variogram estimation was limited to stations separated by up to 40 km and a lag size of 250 m. Spherical, exponential, and Gaussian variogram models were fit to the empirical variogram (SAS version 8, NLIN procedure), and the best-fitting model was chosen, except in cases where one variogram model resulted in unrealistic variogram parameters (such as a negative nugget). In 1993 all three models failed to converge, and a Gaussian model was fit by eye. Following variogram selection, ordinary kriging was conducted (SAS version 8, KRIGE2D procedure) with a kriging neighborhood of the 10 nearest sample points. Although the choice of neighborhood size is arbitrary, use of a neighborhood limits the impact of outliers and speeds computation (Cressie 1993). Blue crab density was mapped at a 1-km grid scale by adding the kriged predictions (residuals) to the trend at the center point of every mapped grid cell.

Blue crab density was mapped for all grid cells in the bay south of the northernmost sample station. This cutoff was used to avoid extrapolation into the northernmost region of the bay, an area that was not sampled because it is believed to be outside the range of suitable winter habitat for blue crabs (G. Davis, Maryland Department of Natural Resources, personal communication). Kriging variance maps were also created. Mapping was conducted in version 8.3 ArcView (ESRI Corp., Redlands, California). Map cell densities were transformed to cell-specific abundance estimates by multiplying the density by the cell area. These local abundance estimates were summed across all mapped cells to estimate baywide abundance. The standard error of the baywide abundance estimate was calculated via a global variance estimator for point kriging (M. Christman, University of Florida, personal communication). This method was used in place of the global block kriging variance estimator (Kern and Coyle 2000; Rivoirard et al. 2000) because the complex shoreline of the Chesapeake Bay and its tributaries prevents the region from being easily divided into a small number of blocks.

To examine potential geographic differences in density trends over the 13-year time series, the temporal trend for each grid cell was calculated. For each grid cell, we fit a linear regression of within-cell blue crab abundance against time. The values for the slope of the regression were then mapped to visually evaluate patterns of change in

blue crab density. Although the large number of regressions (1/grid cell or 11,189 in total) and the presence of spatial autocorrelation prevent rigorous significance testing, a probability cut-off of 0.05 was used to limit the possibility of displaying spurious trends. Cells meeting the $P < 0.05$ criterion were classified as increasing (positive trend), moderate decline (negative trend of <0.1 crabs per 1,000 m²/year), and strong decline (negative trend of >0.1 crabs per 1,000 m²/year).

The relationship between winter blue crab abundance and CPUE from the winter dredge fishery was assessed by linear regression of CPUE against geostatistical and stratified random design-based (G. Davis, Maryland Department of Natural Resources, unpublished data) abundance estimates. The geostatistical abundance estimates calculated here were based on an area of 11,189 km², whereas the design-based estimates used an area of 9,812 km² (Sharov et al. 2003). Although both areas were estimated in a geographical information systems (GIS), different shoreline files or map projections may result in different area estimates. To facilitate comparison, the design-based abundance estimates were rescaled by the percent difference of the two areas (12.3%).

Detailed trip-level effort data for this fishery are only available from 1994 to the present. Information on dredge fishery license sales, however, is available for the entire 1990–2002 period (S. Iverson, Virginia Marine Resources Commission, unpublished data). Consequently, CPUE was calculated as landings per license. A strong correlation ($r = 0.96$) exists between landings per dredge day and landings per license (Jensen and Miller, unpublished), indicating that landings per license is a reasonable proxy for CPUE calculated from the more detailed effort data.

Changes in blue crab distribution.—A density-weighted centroid was calculated from the distribution maps for each year. This summary metric is simply the mean location of all grid cells weighted by the estimated blue crab density in each cell. It is possible to calculate a centroid from the raw data, but this estimate reflects the distribution of samples and the distribution of values. This is not true of centroids calculated from the abundance predicted for each cell of a grid. Because the same grid cells are used in all years in the map-based calculation of the centroid, the result reflects changes in the distribution of crabs rather than the distribution of samples.

To identify factors that may be responsible for changes in the distribution of blue crabs, the lat-

TABLE 1.—Summary of the number of dredge sites (*N*), variogram parameters (nugget, partial sill, and range), variogram models, and geostatistical and design-based baywide abundance estimates for blue crabs (>15 mm carapace width) in the Chesapeake Bay. The 1993 variogram was fit by eye; hence, there are no SEs.

Year	<i>N</i>	Model	Nugget		Partial sill		Range		Geostatistical abundance (10 ⁶)		Design-based abundance (10 ⁶)	
			Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1990	919	Gaussian	12,749	598	12,502	647	13,710	948	1,110	0.035	920	0.014
1991	947	Gaussian	11,272	395	25,144	8,686	45,037	10,962	1,454	0.041	957	0.017
1992	1,340	Spherical	731	25	1,008	101	52,532	8,221	403	0.006	427	0.006
1993	1,194	Gaussian	5,000		8,000		25,000		708	0.016	988	0.017
1994	1,382	Gaussian	2,631	89	6,168	243	26,409	1,268	714	0.011	599	0.011
1995	1,523	Gaussian	908	30	4,950	554	43,144	3,505	406	0.012	564	0.010
1996	1,523	Gaussian	3,304	95	8,557	549	32,278	1,982	1,000	0.016	856	0.014
1997	1,506	Spherical	1,664	70	15,467	26,459	196,671	345,102	670	0.012	781	0.010
1998	1,510	Gaussian	754	24	1,424	119	31,194	2,597	425	0.007	408	0.007
1999	1,457	Gaussian	407	13	1,383	98	34,206	2,170	335	0.007	357	0.009
2000	1,421	Exponential	260	16	3,754	1,883	147,284	84,953	322	0.006	341	0.006
2001	1,464	Gaussian	192	8	797	31	28,676	1,242	313	0.005	298	0.006
2002	1,457	Gaussian	254	9	866	57	33,048	2,037	259	0.005	362	0.008

itude of the centroid was compared with characteristics of the population (baywide abundance and the percent of mature females) and freshwater flow. Longitudinal (east–west) changes were initially considered, as well; however, no patterns were found and thus the results from these analyses are not presented. This finding is not surprising because many environmental gradients (e.g., salinity) also show a predominantly north–south orientation. Density-dependent changes in distribution were evaluated by regressing the latitude of the centroid against the geostatistical estimate of baywide abundance of all blue crabs. Because mature females are known to have different winter habitat preferences than males and immature crabs (Schaffner and Diaz 1988), the proportion of mature females in the population was tested as an alternative explanation for changes in distribution. Because geostatistical estimates of mature female abundance are not feasible given the high number of tows in which no mature females were caught (zero inflation), the proportion of mature females was calculated from design-based estimates of ma-

ture female and total blue crab abundance (G. Davis, unpublished data). The impact of changes in freshwater flow (and therefore the location of the salt front) due to interannual differences in precipitation was evaluated by regressing the latitude of the centroid against the mean flow rate of the Susquehanna River measured at Conowingo, Maryland, (USGS 2004) for the preceding fall (October–December). The effect of changes in the distribution of blue crabs on their vulnerability to the winter dredge fishery was examined by regressing q_{dredge} , the fishery catchability coefficient, against the latitude of the centroid. The catchability coefficient was calculated by dividing dredge fishery CPUE by the geostatistical baywide abundance estimate.

Results

Gaussian variogram models were chosen in all years except in 1992 and 1997, where a spherical model provided a better fit, and in 2000, where the best-fitting model was exponential (Table 1). The variogram-fitting routine failed to converge in 1993, and a Gaussian model was fit by eye. The nugget and sill parameters were significantly positively correlated with each other, and both parameters showed significant positive correlations with abundance and negative correlations with year (Table 2). The range parameter was not significantly correlated with any other variables. In summary, small-scale and large-scale variability decreased through time along with baywide abundance, whereas patch size did not show consistent patterns.

Spatial patterns of blue crab density in Ches-

TABLE 2.—Spearman’s rank correlation coefficients among variogram parameters (nugget, sill, and range), survey year, and the geostatistical baywide abundance estimate for blue crabs in the Chesapeake Bay. Significant ($P < 0.05^*$) and highly significant ($P < 0.01^{**}$) correlations are indicated. All other correlations are insignificant.

Variable	Nugget	Sill	Range	Year	Abundance
Nugget		0.89**	-0.31	-0.85**	0.97**
Sill			0.03	-0.65*	0.88**
Range				0.20	-0.27
Year					-0.81**

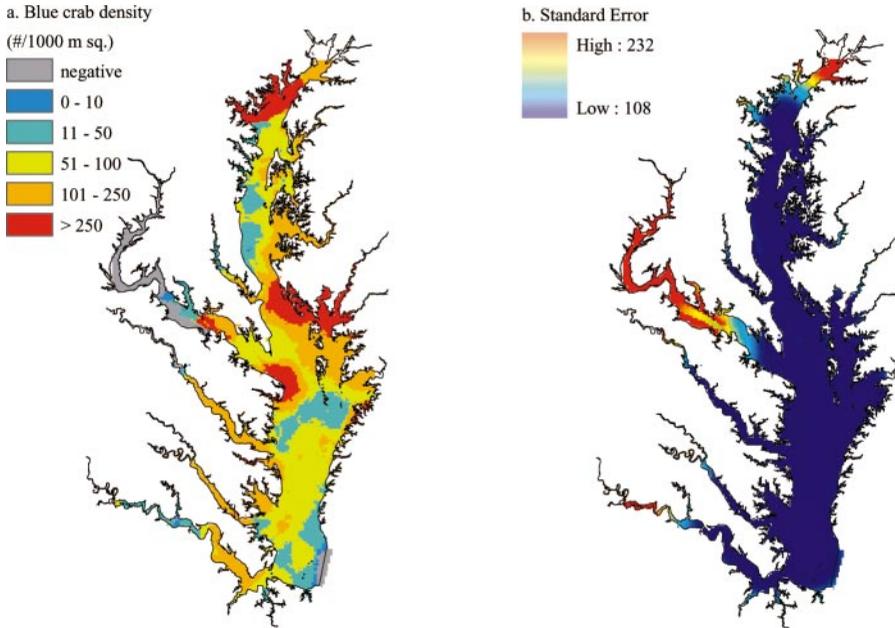


FIGURE 2.—Maps of Chesapeake Bay showing (a) blue crab (>15 mm carapace width) winter density (number/1,000 m²) and (b) standard error of density estimates based on geostatistical interpolation of winter dredge survey data from the winter of 1990–1991. The density indicated by NA indicates regions outside of the prediction area or cells for which negative values, an artifact of the two-stage process (detrrending before kriging), were predicted.

peake Bay showed a great deal of interannual variability, but areas of consistently high or low density were also evident. Distribution maps are presented for the year of highest (1991, Figure 2a) and lowest (2002, Figure 3a) abundance; maps for other years are available at <http://hjort.cbl.umces.edu/crabs/crabgeostat.html>. Predicted densities in the upper reaches of many tributaries and in the northernmost part of the main stem should be viewed with caution because few samples exist in these areas, and consequently, the uncertainty of predictions in these regions was high (Figures 2b, 3b). The map of average blue crab density over the 13-year study period (Figure 4a) showed complex patterns, high density occurring in many lower bay tributaries and eastern shore embayments (as labeled on Figure 1). Crab abundance in the deeper channels north of the Patuxent River and south of the Potomac River in the main stem was consistently below average. Tangier and Pocomoke sounds always exhibited above average abundances. Temporal trends in blue crab density over the 13-year study period differed throughout the bay, much of the lower bay main stem and the eastern shore experiencing declines and the upper Potomac showing some indication of increased in crab density (Figure 4b). The upper Potomac, how-

ever, falls in an area of consistently high variance, indicating that the significance of the temporal trend in this area is highly uncertain.

Trends in the time series of baywide blue crab abundance (all individuals of both sexes >15 mm) estimated using geostatistical methods (Figure 5a) generally agreed well with design-based estimates of abundance (G. Davis, unpublished data). Notable exceptions to this general agreement were apparent, however, in the first 2 years (1990 and 1991), where the respective geostatistical estimates were 21% and 52% higher. Standard errors of the abundance estimates were small for both methods and did not differ consistently (Table 1). Both abundance estimates showed significant negative trends from 1990 to 2002, specifically, a decrease in baywide abundance of 80% for geostatistical estimates ($R^2 = 0.53$, $P = 0.005$) and 66% for design-based estimates ($R^2 = 0.55$, $P = 0.004$). Winter dredge fishery CPUE was significantly related to both geostatistical ($R^2 = 0.59$, $P = 0.002$) and design-based ($R^2 = 0.31$, $P = 0.049$) abundance estimates (Figure 5b), but the correlation was stronger for the geostatistical model.

The centroid of blue crab density in Chesapeake Bay exhibited substantial interannual variability. Consistent with the north–south orientation of the

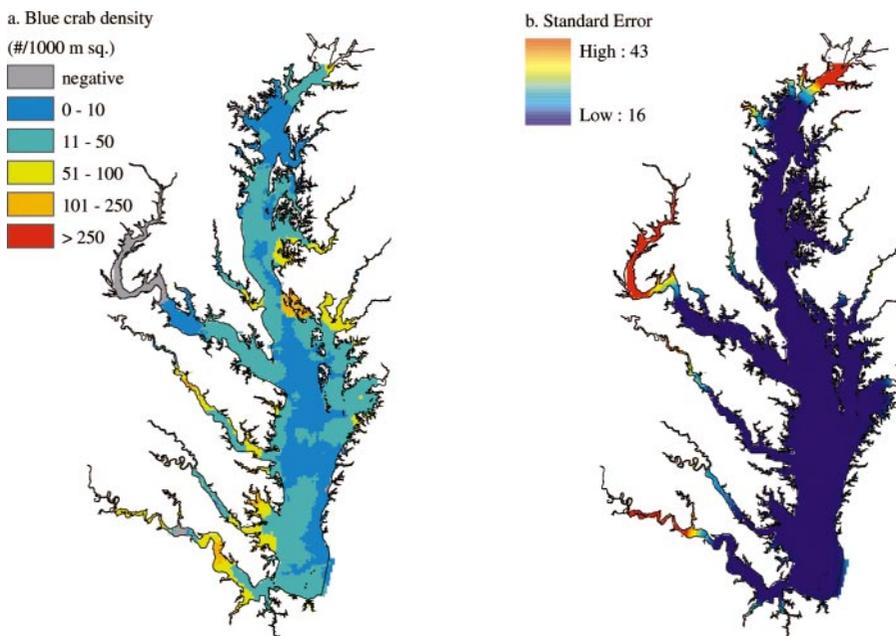


FIGURE 3.—Maps of Chesapeake Bay showing (a) blue crab (>15 mm carapace width) winter density (number/1,000 m²) and (b) standard error of density estimates based on geostatistical interpolation of winter dredge survey data from the winter of 2001–2002. The density indicated by NA indicates regions outside of the prediction area or cells for which negative values, an artifact of the two-stage process (detrrending before kriging), were predicted.

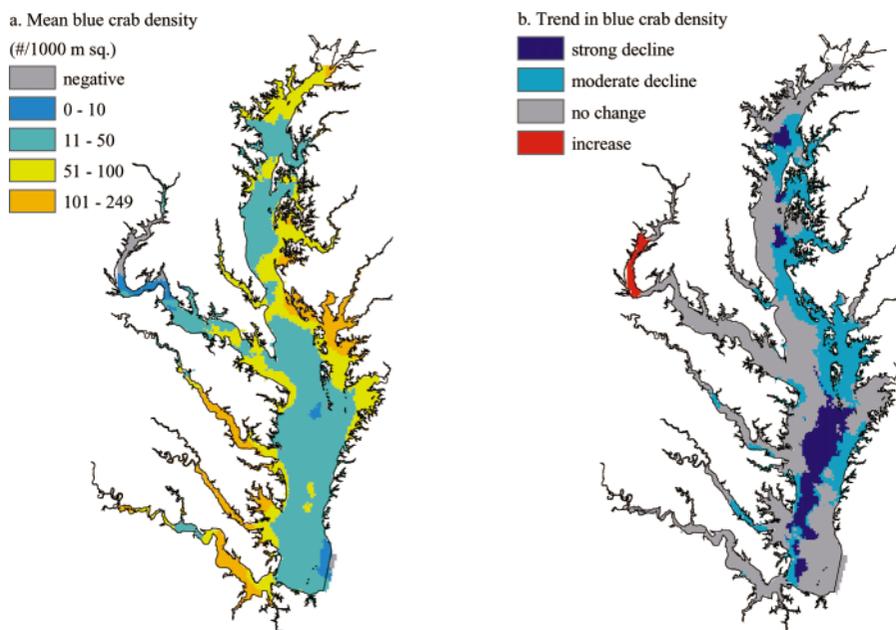


FIGURE 4.—Maps of Chesapeake Bay showing (a) the mean winter density of blue crabs (>15 mm carapace width; number/1,000 m²) and (b) trends in density (slope of linear regression) indicated by areas of strong decline (decrease in density of 0.1–0.32 crabs/1,000 m² per year), moderate decline (decrease of 0.01–0.1), and moderate increase (increase of 0.04–0.07) based on geostatistical interpolation of winter dredge survey data from 1990 to 2002. The density indicated by NA indicates regions outside of the prediction area or cells for which negative values, an artifact of the two-stage process (detrrending before kriging), were predicted.

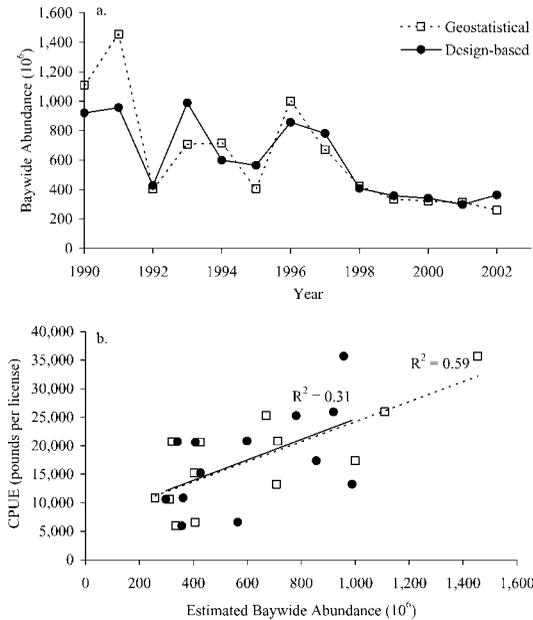


FIGURE 5.—(a) Time series of geostatistical (open squares, dashed line) and design-based (filled circles, solid line; G. Davis, unpublished data) estimates of blue crab (>15 mm carapace width) abundance throughout the Chesapeake Bay and (b) winter dredge fishery catch per unit of effort (CPUE [pounds of blue crabs landed per license; 1 lb = 0.454 kg]; S. Iverson, unpublished data) plotted against baywide abundance based on winter dredge survey data from 1990 to 2002. Error bars are absent because they were too small to be distinguished from symbols.

bay and of many environmental gradients, variation in the location of the centroid was more pronounced in the north–south than in the east–west direction (Figure 6). Generally, the centroids for earlier years fell to the north of those from later years; this temporal trend in the latitude of the centroid (Figure 7a) was statistically significant ($R^2 = 0.47$, $P = 0.01$). An even stronger relationship was found between the latitude of the centroid and the estimated baywide blue crab abundance, the centroid moving southward in years of low abundance (Figure 7b, $R^2 = 0.78$, $P < 0.001$). There was no apparent relationship between the latitude of the centroid and the percentage of mature females in the Chesapeake Bay blue crab population (Figure 7c, $R^2 = 0.02$, $P = 0.484$). Marginally significant relationships were found between flow rate of the Susquehanna River during fall of the previous year and the latitude of the centroid (Figure 7d, $R^2 = 0.32$, $P = 0.041$) and between q_{fishery} and the latitude of the centroid (Figure 8, $R^2 = 0.27$, $P = 0.068$).

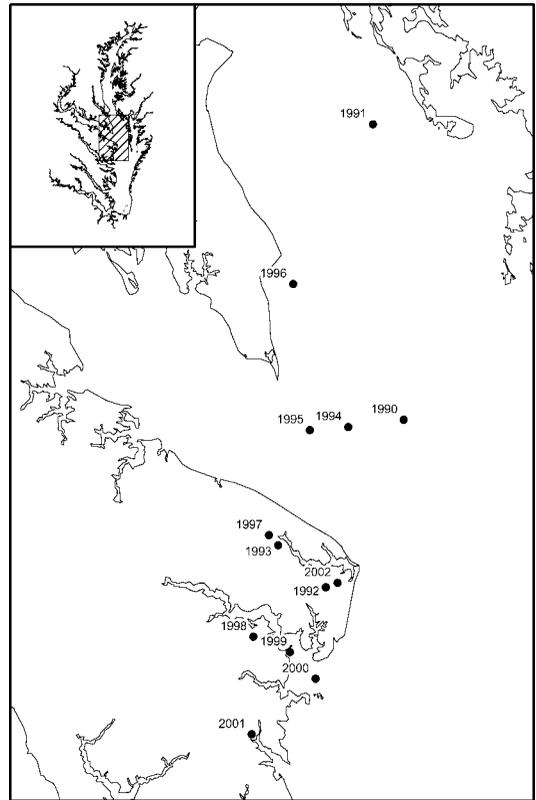


FIGURE 6.—Location of density-weighted centroid of blue crab (>15 mm carapace width) distribution in Chesapeake Bay for 1990–2002.

Discussion

For the period over which the WDS survey data were analyzed (1990–2002), the Chesapeake Bay blue crab stock has undergone a substantial and significant decline. This decline is evident in both the design-based (G. Davis, unpublished data) and geostatistical time series of the WDS and is consistent with observations of decreasing abundance and smaller size of mature females on the spawning grounds over roughly the same period (1988–2000, Lipcius and Stockhausen 2002). Coincident with this decline, the winter distribution of crabs has exhibited marked interannual variability and a significant southward shift. However, the pattern of decline was not spatially uniform. Consistent with the overall decline in blue crab abundance, most areas of the Chesapeake Bay exhibit either decreasing density or no significant change. Decreases in density are apparent in some of the highest-density regions of the bay, including the eastern shore from the Choptank River south through Tangier Sound. Generally, the major western shore

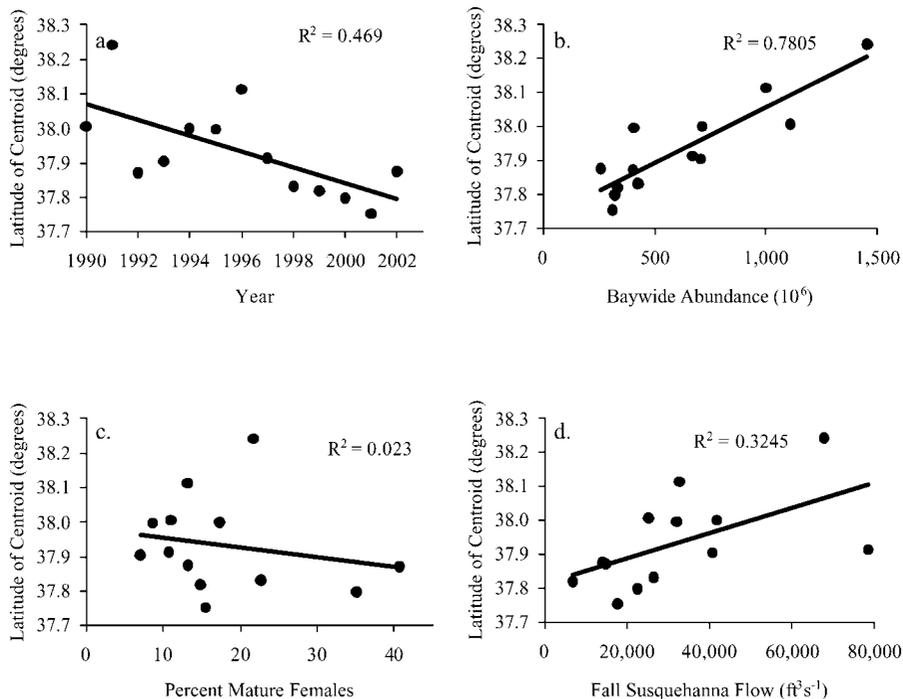


FIGURE 7.—Changes in the latitude of the centroid of blue crab density in the Chesapeake Bay as a function of (a) survey year, (b) the geostatistical estimate of baywide blue crab abundance, (c) the percentage of mature females (G. Davis, unpublished data), and (d) the average flow (ft^3/s ; 1 ft = 30.5 cm) of the Susquehanna River at Conowingo, Maryland (USGS 2004) in the preceding fall (October–December).

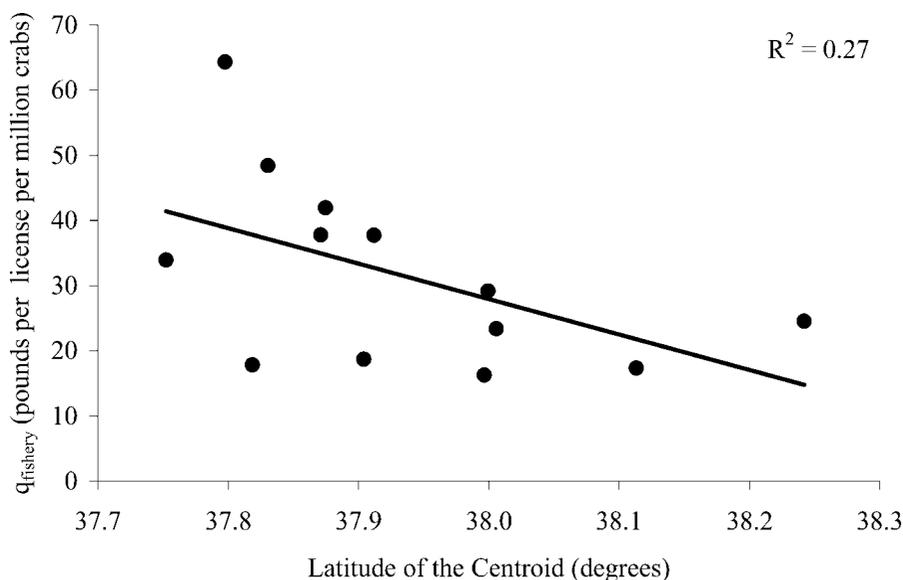


FIGURE 8.—Relationship between the winter dredge fishery catchability coefficient (q_{dredge} [pounds per license per million blue crabs; 1 lb = 0.454 kg]) and the latitude of the centroid of blue crab density in the Chesapeake Bay.

tributaries (the Patuxent, Potomac, Rappahannock, York, and James Rivers) do not show large areas of declining abundance. Although the overall distribution of blue crabs shifted toward the south, substantial regions of declining density were observed in the main stem of the lower bay, a region known to contain disproportional numbers of mature females and the site of a winter dredge fishery. The one area of increasing density, the upper part of the Potomac River, occurs in an area of high variance, which makes any conclusions about trends in this area highly uncertain.

Despite the overall pattern of decline, blue crab densities in some regions remain consistently above average (e.g., Tangier Sound and the lower portions of the three major lower Bay tributaries: Rappahannock, York, and James rivers), and some areas exhibit occasional high densities in some years (e.g., the uppermost mapped portion of the bay and the uppermost portions of many tributaries, particularly the Potomac River). Estimates of crab density in these regions are often associated with a higher degree of uncertainty. An important area of relatively high crab density is often found in the deep waters of the lower bay mainstem. The precise location of this high-density region, which is thought to be a particularly important overwintering habitat for mature females (Schaffner and Diaz 1988; Jensen et al. 2005), shows substantial interannual variation.

Both the design-based and geostatistical approaches to estimating crab abundance showed a pattern of declining abundances over the 13-year period from 1990 to 2002. Geostatistical estimates of baywide blue crab abundance were generally similar to estimates derived from the stratified random design-based method, except for the first 2 years of the time series. Differences in the abundance estimates between design-based and model-based methods are not unexpected, because the assumptions of the two methods differ. Furthermore, the accuracy of either estimate will be influenced by the degree to which its assumptions are met and the extent to which it can make use of patterns in the data. The strongest assumptions of the geostatistical methods used here are the stationarity of both mean and variance and that the fitted variogram models are an accurate description of the spatial autocorrelation structure. Examination of the residuals after detrending indicated that, although local trends remained, there was no broad-scale trend in the mean or variance. Although some variogram fits were problematic (e.g., 2 years showed an unusually high range and in 1

year the fitting routine failed to converge), all variograms showed strong evidence of spatial autocorrelation—a source of information that design-based methods fail to utilize.

A further important reason for the differences in the two estimates is the assumptions each method makes about unsampled areas. The design-based approach effectively assigns a density equal to the mean stratum density to all areas of a stratum, including poorly sampled areas, and then multiplies this mean by the area of the stratum. The geostatistical approach explicitly assigns values to unsampled areas based on the values of the nearest sampled locations. Accordingly, sample points in sparsely sampled regions are given disproportional weight in the geostatistical method. If these samples are representative of the region, the geostatistical approach may be more accurate. Conversely, if the observations are unrepresentative outliers, they can skew the resulting abundance estimate. This phenomenon is well illustrated in some of the density maps where extreme values are present in the sparsely sampled extremities of many tributaries and in the northernmost part of the main stem.

Without knowing the true abundance, it is not possible to determine which abundance estimation method more accurately estimates the size of the blue crab stock in Chesapeake Bay. The relationship between winter dredge fishery CPUE and the two abundance time series, however, provides stronger support for the accuracy of the geostatistical method. The higher coefficient of determination between fishery CPUE and the geostatistical abundance estimate suggests that this method may do a better job of capturing interannual fluctuations. Interestingly, in the years that the two methods differed most dramatically, 1990 and 1991, geostatistical abundance estimates fell close to the regression line in Figure 5a, indicating that these unusually high estimates may accurately reflect higher crab abundance in the first 2 years of the survey. This comparison only addresses pattern, however, not the scale of the estimates. A strong correlation between fishery CPUE and fishery-independent abundance estimates could be found even if the abundance estimates were consistently higher or lower than true abundance. Standard errors for both estimation methods were extremely small and did not consistently favor one approach over the other.

The large number of sample points and their extensive coverage of the winter range of blue crab within Chesapeake Bay make the WDS data well

suites to spatial analysis. This survey was not designed with such an analysis in mind, however, and some relatively minor modifications could greatly improve the accuracy of both the distribution maps and, potentially, the abundance estimates. Two problems are apparent: zero-inflation (i.e., the large number of tows in which no crabs were caught), and the lack of samples in the upper reaches of some tributaries and in some portions of the main stem.

Zero inflation can be handled effectively in a regression (Lambert 1992) or generalized additive model framework (Maravelias 1997; Jensen et al. 2005) by two-stage approaches that model presence-absence and abundance separately. Equivalent two-stage approaches for geostatistics have yet to be developed; however, the robust variogram (Cressie 1993) we used or cross-validation approaches to variogram fitting (e.g., Maravelias et al. 1996) are effective methods for describing the spatial autocorrelation structure of the highly skewed data that typically results from surveys of fish and crustacean populations. This problem could also be addressed in the survey design by increasing the length of tows in order to reduce the number of zero catches.

The problem of uneven distribution of sampling effort is evident in the maps of blue crab density and the kriging standard error (Figures 2, 3). The maps show negative densities (obviously impossible) and high variability in the upper reaches of the Potomac River because few samples were taken in this area. The addition of a few nonrandomly placed stations could greatly improve the spatial coverage of the survey at little additional cost. The remaining randomly placed stations could still be used to calculate abundance via design-based methods for a stratified random survey.

Spatial analysis techniques, including geostatistics and GIS-based approaches, are increasingly being used to estimate the abundance of exploited fish and invertebrate stocks (Rivoirard et al. 2000) and, when coupled with data from spatially extensive surveys conducted over different seasons and stock sizes, to examine both seasonal (Giannoulaki et al. 2003; Rueda and Defeo 2003; Axenrot and Hansson 2004; Perez-Castaneda and Defeo 2004) and density-related (Die and Ellis 1999; Abella et al. 2005) changes in distribution patterns. Studies of interannual changes in distribution patterns are less common (but see Bailey et al. 1998; Abella et al. 2005; and several studies on the collapse of cod in the western Atlantic, including Rose et al. 1994, 2000; Hutchings 1996; Atkinson et al. 1997;

Warren 1997; and O'Driscoll et al. 2000) because they require an adequate time series of spatially extensive survey data. Such studies may be essential, however, if we are to anticipate changes in abundance and vulnerability to exploitation in populations that show a patchy spatial distribution.

Despite the fact that trend and variogram models were allowed to vary among years, two of the variogram parameters (the nugget and sill) showed strong and significant correlations with abundance. This pattern indicates that both small-scale and large-scale variability increase with increasing abundance. Patch size, as estimated by the range parameter, displayed little correlation with abundance. A study of a penaeid shrimp fishery in Australia found that average patch size (i.e., biomass), number of patches, and total biomass decreased much more rapidly than fishery CPUE within a fishing season (Die and Ellis 1999). The apparent lack of a relationship between the range parameter and baywide blue crab abundance may be due to the fact that 2 years (1997 and 2000) displayed anomalously high ranges due to variograms that showed nearly linear increases. Other geostatistical studies of fish and crustacean distributions that have looked at variation in variogram parameters have shown mixed results. For example, Giannoulaki et al. (2003) found that the range of spatial autocorrelation for small pelagic fish in the eastern Mediterranean Sea was unrelated to coastal topography, whereas the nugget was negatively correlated with depth. They interpreted this pattern as evidence that pelagic fish exist in patches that are size-independent of topography but form less structured aggregations in shallower waters. Although this explanation appears plausible, the biological implications of differences in variogram parameters are not well understood. The positive correlation we observed between abundance and the nugget and sill may simply reflect the commonly observed pattern of variability increasing with the mean.

One of the most striking patterns that emerged from analysis of the crab density maps was the positive relationship between the latitude of the centroid of blue crab density and the abundance of blue crabs in Chesapeake Bay. In years of lower blue crab abundance, the distribution shifted notably southward. The mechanism underlying this apparent relationship is unclear, but one intriguing possibility is density-dependent habitat selection (DDHS). Theories of DDHS, such as MacCall's (1990) "basin model," predict that at low population density, individuals should concentrate

themselves in the most suitable habitat. As population density increases, the realized suitability in the best habitat declines, and individuals spread out to other habitats that were initially less suitable but that now have equal or better realized suitability. Although DDHS has been proposed for juvenile haddock *Melanogrammus aeglefinus* (Marshall and Frank 1995) and North Sea cod (Myers and Stokes 1989), distinguishing among density-dependent and density-independent factors at multiple spatial scales is difficult. Furthermore, without a priori information about the suitability of different habitats, DDHS arguments frequently become tautological (Shepherd and Litvak 2004).

For mature female blue crabs in Chesapeake Bay, the most heavily utilized overwintering habitat appears to be the deep waters of the lower bay main stem (Schaffner and Diaz 1988; Jensen et al. 2005). Habitat preferences of males and immature blue crabs are less well defined but appear to include deep water in tributaries and the main stem (Abbe and Stagg 1996). If the lower bay main stem represents ideal overwintering habitat, and density-dependent pressures force crabs to seek more marginal habitat at higher abundances, then the distribution of blue crabs would be expected to move northward as abundance increases, as seen in Figure 7b.

Although the correlation between blue crab distribution and abundance is consistent with DDHS, the limiting resource and the behavioral mechanism for maintaining DDHS are not apparent. Space is the most obvious potentially limiting resource because blue crabs do not feed during their dormant winter stage. The highest density of crabs observed in the trawl data was 5.6 crabs/m², and in this case, space might well be limiting. Such densities appear to be very rare, however, 99.4% of samples having densities less than 1 crab/m². At these lower densities, it is not clear how space could be a purely physically limiting resource (i.e., that additional crabs would be forced to move elsewhere for lack of a place to bury). Although aggressive interactions are common among blue crabs and density-dependent agonism, interference, and cannibalism are important factors regulating the use of habitat and food resources in the summer (Mansour and Lipcius 1991; Hines and Ruiz 1995; Clark et al. 1999a, 1999b), a behavioral explanation for space limitation in the winter seems unlikely, given that crabs are believed to be buried in the sediment in a dormant state and are probably unable to defend their space. A strong

test of the DDHS hypothesis would also require knowledge of how fitness (or some proxy of fitness) varies spatially (Shepherd and Litvak 2004)—information that may now be available from a study of spatial variation in winter blue crab mortality rates in Chesapeake Bay (Rome et al. 2005).

Environmental changes offer an alternative explanation for the observed changes in winter distribution patterns. Winter densities of mature female blue crabs have been shown to vary with bottom type, geomorphology (basin or channel), salinity, and temperature (Schaffner and Diaz 1988; Jensen et al. 2005). Hypoxia, although common in deeper bay waters in the summer, is apparently not severe enough in the winter (Wang et al. 2001) to be lethal to blue crabs. Changes in bottom type and geomorphology are likely to have occurred in Chesapeake Bay because of dams on tributaries and dredging of channels. Such potential changes have not yet been sufficiently quantified, however, for them to be tested as possible causal factors in the shift in blue crab winter distribution. The influence of both temperature and salinity on blue crab growth, respiration, and mortality is well documented from laboratory studies (Tagatz 1969; Engel and Eggert 1974; Guerin and Stickle 1992; Smith 1997, Brylawski and Miller 2003). Because blue crabs do not feed during their winter dormant period, they must balance energy budgets by reducing costs, rather than increasing consumption. Combined, these laboratory studies suggest that within the range of temperatures and salinities found in Chesapeake Bay, respiratory costs are minimized at lower temperatures and higher salinities, although mortality rates rise when temperatures drop below about 5°C. Other analyses of the WDS data show that low February temperatures are associated with high winter mortality rates (Bauer 2005; Rome et al. 2005), but that salinity appears to be more consistently important than temperature in explaining winter distributions of mature female blue crabs (Jensen et al. 2005).

The weak but statistically significant relationship between the latitude of the centroid and fall flow of the Susquehanna River may be related to either temperature or salinity because river water is both colder and less saline than water within the bay. Rome et al. 2005 found that blue crab winter mortality rates were highest in the cold, low salinity waters of the upper bay main stem and tributaries. Higher Susquehanna River flow would be expected to decrease temperatures and salinities

overall; however, due to gravitational circulation, increased Susquehanna flow may push the salt wedge northward, increasing the bottom salinity in upper bay waters (North et al. 2004). This northward movement of the salt wedge in high-flow years would be consistent with the northward movement of the centroid observed here.

Regardless of the mechanism, changes in winter distribution may have an impact on the population dynamics of blue crabs. The de facto winter refuge in the upper bay, where no winter crab fisheries exist, protects a decreasing proportion of the population as stock size declines and the distribution shifts to the south. This increase in the proportion of crabs vulnerable to the winter dredge fishery holds whether or not DDHS is the causal mechanism. The relationship between the fishery catchability coefficient and the latitude of the centroid, together with the observed declines in density in main-stem waters of the lower bay (open to the dredge fishery) but not in lower bay tributaries (closed to the dredge fishery), are cause for concern. Combined, these two patterns suggest that blue crabs have become more vulnerable as their distribution has shifted southward and are being depleted in the lower bay main stem at a greater rate than elsewhere in the bay. This potential compensatory mechanism could be offset by stricter controls on the winter dredge fishery.

The results of this study show significant declines in winter abundance and concurrent changes in the distribution of blue crabs in Chesapeake Bay. The distributional changes are consistent with the predictions of DDHS models and also appear to be related to interannual differences in freshwater flow; however, alternative explanations exist that cannot be rejected based on the available data. Whether the observed distributional changes are due to DDHS, freshwater flow, or other unidentified factors, they may interact with exploitation patterns to hasten the decline of the blue crab stock in Chesapeake Bay. The distributional maps provide a potentially useful tool for designing spatial management strategies that could avoid such declines.

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