ABSTRACT

Title of Thesis:	**SPATIAL ECOLOGY OF BLUE CRAB (*CALLINECTES SAPIDUS*) IN CHESAPEAKE BAY**
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Spatial heterogeneity is a striking feature of the blue crab life history and fisheries in Chesapeake Bay. However, a quantitative assessment of their spatial distribution and the factors controlling it has been lacking. Based on 13 years of data from a baywide winter dredge survey, geostatistical and two-stage generalized additive models (GAMs) are used to characterize blue crab distributions and investigate environmental factors responsible for the distribution of mature females, respectively. A landscape-based distance metric, the "Lowest-Cost Path" (LCP) distance, is developed as an alternative to Euclidean distance for kriging in estuaries. Estimates of variogram parameters differed significantly between the two metrics but kriging accuracy did not. Geostatistical abundance estimates show significant declines from 1990 to 2002. The observed relationship between changes in distribution and changes in abundance is suggestive of density-dependent habitat selection. Depth and distance from the Bay mouth were the most important predictors of mature female abundance.

SPATIAL ECOLOGY OF BLUE CRAB (*CALLINECTES SAPIDUS*) IN
CHESAPEAKE BAY

By

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stage I models (b). Values in (a) represent the area under the ROC curve (AUC), the critical p-values: $p_{optimum}$ (p_{opt}) and p_{fair}, and their sensitivity (Sens.), specificity (Spec.), and percent correct predictions (% Corr.). Values in (b) represent the AUC where models developed with data from one year (columns) are applied to data from another (rows). Values on the diagonal represent intra-annual cross-validation where models developed using a training data subset are applied to the test data subset for the same year. AUC values greater than 0.7 are highlighted in black.

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Chapter 1: Introduction

Introduction

Blue crab (*Callinectes sapidus*) is an important component of the Chesapeake Bay ecosystem and supports one of the largest and most valuable fisheries in the Bay. A detailed knowledge of its distribution patterns within the Bay can provide valuable insights into its ecological relationships and increase the efficacy of spatial management strategies such as protected areas and time-area closures. The goal of this thesis is to describe the winter distribution of blue crab in Chesapeake Bay and to examine the factors responsible for the observed patterns. The development and validation of statistical tools to accomplish this goal are additional objectives.

The blue crab life history in Chesapeake Bay is marked by distinct differences in habitat use at different developmental stages and between males and females (Figure 1). Blue crab spawns in the high-salinity waters of the lower Bay and zoeae are advected offshore where they develop through several stages in continental shelf waters before returning to settle in the Bay (see Epifanio (2003) for an overview of spawning and larval transport and development). Newly settled crabs are found in highest densities in the lower Bay in summer and early fall (Lipcius & Van Engel 1990; Metcalf *et al*. 1995) and are thought to settle preferentially in submerged aquatic vegetation (SAV) (van Montfrans *et al*. 2003) where mortality rates from predation are lower (Orth and van Montfrans 2002). Later stage juveniles and adult males are widely distributed throughout the Bay in the summer and overwinter in the tributaries and the mainstem, undergoing limited migrations (T. Miller, unpubl. data).

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Mature females undergo much longer migrations in the late summer and early fall to deep high-salinity waters in the lower Bay (Hines *et al*. 1995; McConaugha 1995) where they release zoeae and overwinter.

Winter is an important time in the blue crab life history. In southern populations, blue crabs continue to feed, grow, and molt throughout the year (Smith and Chang *In press*). In northern populations, including Chesapeake Bay, winter temperatures drop below a physiological threshold forcing blue crabs to enter a dormant period (Tagatz 1969). During this time, crabs bury into the sediment and growth ceases. Natural mortality during the dormant winter period is thought to be an important factor in blue crab population dynamics with higher mortality in cold winters (Sharov *et al*. 2003). Although overall fishing mortality rates are lower in the winter, the winter dredge fishery in the lower Bay may have a disproportionate impact on the population because it targets mature females with high reproductive value (Miller 2003). Spatial management strategies such as the Lower Bay Spawning Sanctuary (LBSS) have been implemented in an attempt to control fishing mortality on this vulnerable portion of the population (Lipcius *et al*. 2003).

Winter is an ideal time to conduct baywide sampling of blue crabs since they are dormant, and consequently there is no risk of bias due to movement (Vølstad *et al*. 2000). Since the winter of 1989-1990, a Bay-wide Winter Dredge Survey (WDS) has been conducted using a consistent protocol every year between December and March (Sharov *et al*. 2003). This survey employs a stratified random design with approximately 1,500 stations per year. In each year, depletion experiments are conducted at several locations throughout the survey domain (Zhang *et al*. 1993;

Vølstad *et al.* 2000). From these studies, vessel and year specific correction factors (catchability coefficients, q) have been developed to standardize effort and to translate catch into an estimate of density based on the area swept (Sharov *et al.* 2003). The WDS survey has provided important insights into the abundance and exploitation of blue crab in Chesapeake Bay (Zhang and Ault 1995; Vølstad *et al.* 2000; Sharov *et al.* 2003) and the effectiveness of the LBSS (Seitz *et al.* 2001) and migration corridor (Lipcius *et al.* 2001). Moreover, because of its geographic and temporal scope, the WDS is an ideal dataset for investigating the effects of spatial distribution on blue crab population dynamics (Miller 2003).

Changes in distribution are interesting from an ecological perspective. Identification of the factors that regulate the distribution of a species has been a fundamental question in ecology since Hutchinson's classic paper defining fundamental and realized niches (Hutchinson 1957). A niche is the "n-dimensional hyperspace" defined by the range of biotic and abiotic factors that limit the species distribution. Often, physical environmental factors form the primary or fundamental definition of niche as they represent physiological limits to the distribution. Abiotic parameters are easily measured in the laboratory and in the field, and studies that relate the distribution of focal species to the abiotic environment may reveal aspects of the species fundamental niche (Peterson and Vieglais 2001). Within the physiological limits that define the fundamental niche, the distribution of a species may be further restricted by biotic interactions (Connell 1961). This smaller subset of the fundamental niche is termed the "realized" niche. Extensive research on blue crab has revealed insights into both its fundamental and realized niches. Research has

identified estimates of limiting salinity and temperature levels for survival of blue

crab (Tagatz 1969), and the presence of a physiological temperature limit for growth

of approximately 10º C below which growth ceases (Brylawski and Miller 2003).

Other studies have suggested a role for SAV in limiting vulnerability to predation of

juveniles (e.g., Orth and van Montfrans 2002).

Intra-specific interactions can also influence species distributions. The

suitability of a particular habitat may decrease as the density of a species using that

habitat increases. This idea is central to Parker and Sutherland's (1986) Ideal Free

Distribution concept. Individuals that distribute themselves according to an IFD all

experience the same growth potential. The IFD concept underlies MacCall's (1990)

basin model. This model predicts that at low population density, most individuals of

a species will concentrate in optimal habitat, whereas as density increases, individuals

move toward increasingly less optimal habitat, which becomes equally suitable

because of its lower density of conspecifics. The degree to which such mechanisms

operate with regard to blue crab in Chesapeake Bay is currently unknown.

A thorough understanding of a stock's distribution and the ability to detect

changes in the distribution can be an important asset for management also. One

explanation for the unexpected collapse of some fished populations involves

undetected changes in distribution (Hutchings 1996). Most stock assessment models

assume that landings are directly proportional to stock abundance (Quinn and Deriso

1999). The coefficient of proportionality is termed the catchability coefficient, q.

When this proportionality fails, stocks are said to be hyper or hypo-dispersed. This is

often the case in a spatially-structured (i.e., non-randomly distributed) populations

(Walters 2003), such as schooling fish, that may be caught very efficiently even as the total number of aggregations declines. 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).

The WDS, an intensive point sampling (the one-minute tows can be considered a single point within the context of the entire Bay) of a continuous process, lends itself to analysis using geostatistical methods. The fundamental techniques of geostatistics, variogram modeling and kriging, were developed to describe the distribution of valuable ore based on a collection of bore-hole samples, but have since become widely used in ecology (Legendre 1993; Rossi *et al*. 1992) and fisheries science (Sullivan 1991; Petitgas 1993; Rivoirard *et al*. 2000). The variogram describes the spatial autocorrelation structure of the data, i.e., the decrease in relatedness between pairs of points as the distance between them increases. Spatial autocorrelation is a necessary prerequisite to accurate spatial interpolation using kriging. Preliminary variogram analysis of the WDS data showed strong spatial autocorrelation, indicating that kriging could be an effective technique for mapping the distribution of blue crab.

While the WDS data are well suited to analysis using geostatistics, the Chesapeake Bay, a highly invaginated estuary, is not. Variogram modeling and kriging, like most spatial analysis techniques, traditionally use a Euclidean or straight-line distance metric to quantify the degree of physical separation between points. Such a metric is intuitive and useful in open areas whose boundaries can be

thought of as forming a convex polygon. In such cases, there are no barriers

separating pairs of points, and Euclidean distance is a suitable metric. Few estuaries

match this ideal. In the Chesapeake Bay, for example, two points in adjacent

tributaries may be close by Euclidean distance yet quite separate from the point of

view of an aquatic organism or a water-dispersed contaminant. A more appropriate

metric is necessary for spatial modeling in irregularly shaped regions with barriers.

Such metrics have been developed, but they either rely on a GIS-based network

approach (Little *et al.* 1997; Gardner *et al.* 2003) which works well in narrow

tributaries, but is unsuitable for wide open areas, or a FORTRAN program that is not

easily applied to other geographic areas (Rathbun 1998). These methods have

demonstrated the potential increase in prediction accuracy to be gained by utilizing a

more appropriate distance metric. The conditions under which such a metric is

necessary remain undefined, however, and a need exists for an efficient and

transferable solution to this problem.

Kriging is a useful tool for providing an accurate, quantitative description of

the distribution of blue crabs. It provides little information, however, about the

environmental parameters that define suitable winter habitat (but see Sullivan 1991

for an example of combining a habitat variable i.e., depth, and kriging). Blue crabs

are clearly not randomly distributed throughout the Chesapeake Bay. In the spring

and summer, juveniles and molting individuals of both sexes are strongly associated

with SAV. In the fall, mature females migrate from summer habitat toward spawning

and overwintering habitat in the lower Bay. Males and immature females undertake

more limited migrations toward deep water in the tributaries and main stem.

Temperature and salinity are dominant factors in the bioenergetics of the blue crab (Brylawski and Miller 2003), which is likely to take on increased importance during the winter dormant stage when bioenergetic costs cannot be balanced by increased feeding. Winter distributions of mature females likely reflect an attempt to maximize survival and reproductive success since both spawning and overwintering occur in the deep water of the lower Bay.

Given the broad suite of environmental variables that may be influencing blue crab distributions, a statistical method for habitat suitability modeling must be able to test and integrate a large number of variables individually and in interaction. The approach must also be flexible enough to fit non-linear responses and accommodate the large number of zero catches that result from short tows and the patchy distribution of blue crab. Two-stage generalized additive models (GAMs) provide such a method. GAMs allow for fitting flexible regression splines to each habitat variable individually (Hastie and Tibshirani 1990) and are more effective than polynomial regression at modeling threshold responses. The two-stage approach addresses the zero-inflated distribution of the data by modeling presence-absence (binomial distribution) independently of density given presence (lognormal distribution). Given enough data, habitat models can be developed for each year and compared to see whether the relationships described by the model are general and stable.

Objectives

This thesis addresses fundamental questions about the distribution and abundance of blue crab in Chesapeake Bay during winter. The winter dredge survey provides an extensive, spatially-referenced data base of the distribution and abundance of blue crab in Chesapeake Bay. However, to date these data have been analyzed using design-based approaches only. I will apply geostatistical methods to estimate the winter abundance and distribution of blue crab in Chesapeake Bay. There are three specific objectives:

OBJECTIVE 1. Develop and evaluate an alternative to Euclidean distance for use in geostatistical models.

I will develop and test an approach that uses a "Lowest Cost Path" (LCP) distance metric (the shortest distance between two points that is constrained to remain within the body of water) as the basis for variogram modeling and kriging. The approach to this question involves substantially modifying a set of geostatistical methods (variogram modeling and kriging) so that they are suitable for use in estuaries or other non-convex regions with barriers. I will compare the precision and bias of the LCP distance-based and Euclidean distance-based approaches. Results of this work are presented in Chapter 2.

OBJECTIVE 2. Quantify the abundance and winter distribution of blue crab in Chesapeake Bay and determine the extent to which density-dependent factors control their distribution.

The application of geostatistical methods to the winter dredge database permits predictions of the abundance of crabs at unsampled locations. Maps of predicted distributions can be further analyzed to estimate abundance and the moments of the distribution. These secondary results will be quantified to (1) provide a comparison with design-based estimates of crab abundance and (2) to address questions about blue crab population dynamics and density-dependent changes in their distributions. The results of these analyses are presented in Chapter 3.

OBJECTIVE 3. Describe the relationship between abiotic variables and the winter distribution of mature female blue crab in Chesapeake Bay.

The environmental factors that influence the winter distribution of mature females are investigated using a two-stage GAM, which models presence /absence and abundance at individual stations separately. The temporal breadth of the WDS data also allows for a cross-validation of this method in which the predictive power of environmental variables important in one year is assessed in other years. The results of these analyses are presented in Chapter 4.

Chapter 2: Landscape-based geostatistics: a case study of the distribution of blue crab in Chesapeake Bay

Abstract

Geostatistical techniques have gained widespread use in ecology and the environmental sciences. Variograms are commonly used to describe and examine spatial autocorrelation, and kriging has become the method of choice for interpolating many spatially-autocorrelated variables. Most applications of geostatistics to date have defined the separation between sample points using simple Euclidean distance. In heterogeneous environments, however, certain landscape features may act as absolute or semi-permeable barriers. The effective separation in this case may be more accurately described by a measure of distance that accounts for the presence of barriers. Here I present an approach to geostatistics based on a lowest-cost-path (LCP) function, where the cost of a path is a function of both the distance and the type of terrain crossed. The modified technique is applied to 13 years of survey data on blue crab abundance in Chesapeake Bay. Use of this landscape-based distance metric significantly changed all three variogram parameters but did not result in consistent improvements in the accuracy of predictions of abundance at unsampled locations.

Introduction

A trend of increasing spatial realism has been evident throughout the history of ecological modeling. Hufaker's (1958) experiments demonstrated the importance of space in a predator-prey system and encouraged modelers to seek out appropriate ways of incorporating a spatial component into their work. Early work by Hassell and May (1973) showed that the addition of a spatial component to models of predator-prey interactions enhanced the stability of the resulting equilibrium. Space in this model was implicit, but models taking into account the explicit spatial arrangement of the model components soon followed (e.g., Pulliam _et al_. 1992). More recently, ecologists have started to use spatially-realistic models where interactions take place within a specific landscape (e.g., Wahlberg _et al_. 1996).

Space has also been increasingly recognized as an important component of statistical models in ecology. Legendre (1993) and Rossi _et al_. (1992) document a shift from assumptions of spatial independence and homogeneity, to an understanding of spatial autocorrelation as a source of useful information, provided that the appropriate statistical tools are used. Geostatistical modeling is a common approach to developing spatially-explicit statistical models. Accurate incorporation of spatial autocorrelation is important in geostatistical models that test hypotheses (Legendre and Troussellier 1988) or predict the distribution of species and their interactions in space (Bez 2002). In both cases, incorrect specification of the spatial covariation can introduce spurious patterns in the analyzed data that can lead to erroneous rejection of null hypotheses or inaccurate predictions of distributions.

Geostatistics is increasingly used for analytical rather than descriptive purposes, e.g., to estimate abundance (Sullivan 1991; Bez 2002) or parameterize other models (Fuchs and Deutz 2002). Consequently, the importance of accuracy in geostatistical applications is growing. Traditionally, geostatistical approaches have specified spatial covariance based on the Euclidean distance between sampled points. Implicit in the use of Euclidean distance is the assumption that the process or feature of interest is continuously distributed between any two points. However, in many instances, the space separating two sampled points may present a biological or physical barrier that limits the distribution of the process or feature.

The Importance of Barriers in Ecological Modeling

Spatial heterogeneity at several scales is a common feature of nearly all landscapes and can have important consequences for the way organisms move and interact. One of the simplest but most important impacts of spatial heterogeneity occurs when one landscape type serves as a barrier to movement and dispersal. Barriers are important in determining biogeographic, ecological, and evolutionary patterns (Grinnell 1914; MacArthur and Wilson 1967; Gilpin and Hanski 1991; Brown and Lomolino 1998). The recognition of barriers, however, has generally been restricted to a few high-profile models (e.g. island biogeography and metapopulation dynamics) that explicitly describe their effects. However, as habitat fragmentation and isolation continue to increase, barriers are an increasingly important component of many landscapes.

Several recent studies have applied a diversity of approaches to quantitatively account for the effects of barriers. Rupp and Chapin (2001) used a spatially realistic simulation model to predict the impact of the Brooks Range in northern Alaska as a barrier to shifts in forest cover induced by global warming. In this case, the presence of barriers resulted in a 2000-year lag in the expansion of forests to the North Slope. A recent spatially-explicit simulation of a Lotka-Volterra predator-prey system (Nakagiri *et al*. 2001) showed that even when barriers are present at a fairly low density and directly affect only the prey species their presence can lead to extinction of both species. In a study of within population genetic variation of field mice, Landry and Lapointe (2001) concluded that a composite isolation index, which takes into account landscape barriers, was a better predictor of variation than simple geographic distance alone. Taken together these studies indicate a growing interest in the impacts of underlying landscape barriers on many ecological processes.

Streams and estuaries are systems where barriers are a prominent feature of the landscape. It has long been recognized by stream ecologists that Euclidean distance is an inappropriate metric, and distance measured along the thalweg is commonly used. This metric recognizes that most processes in a stream are only continuous within the aquatic habitat. Many estuaries are characterized by highly invaginated shorelines where converging tributaries are separated by narrow peninsulas of land. Conditions on opposite sides of a peninsula can show much greater variation than their geographic proximity suggests. In some cases, adjacent tributaries, because of differences in the geology or land use of their watersheds, show remarkable differences in their chemical and biological characteristics (Pringle

and Triska 1991). Not surprisingly then, the first attempts to incorporate the effects of barriers into geostatistical modeling occurred in estuaries (Little *et al*. 1997; Rathbun 1998).

Geostatistics and Ecological Landscapes

Increased interest in modeling the spatial component of many ecological phenomena has paralleled improvements in geostatistics as an analytical tool and geographic information systems (GIS) as a modeling environment. Geostatistical tools have gained widespread acceptance not only in the field of ecology, but also in other areas such as epidemiology, geology, hydrology, and population genetics. In ecology, the most common uses of geostatistics have been to describe the spatial autocorrelation structure using the variogram, and to interpolate and map data using kriging (Aubry and Debouzie 2000). Variations on ordinary kriging have been used to model presence/absence data (indicator kriging), interpolate one variable based on its relationship to a second variable (co-kriging), and to incorporate a trend surface (universal kriging). Geostatistical techniques, including block kriging, have also become a standard tool for abundance estimation based on spatially autocorrelated survey data, especially for fisheries acoustic surveys (Sullivan 1991; Petitgas 1993; Rivoirard *et al*. 2000; Bez 2002). A model-based geostatistical approach can be preferable to traditional design-based methodology when autocorrelation is present because many design-based methods fail to take advantage of the additional knowledge present in the spatial autocorrelation structure (Aubry and Debouzie 2000, 2001).

Heterogeneous landscapes can impose patterns that violate the assumptions of geostatistics. For example, second order stationarity (i.e., spatially constant mean and variance) and isotropy of the variogram in space are the strongest assumptions of the geostatistical model. These assumptions are also likely to be violated in the presence of any ecologically important gradients in the landscape. For instance, a resource gradient in a meadow may result in a trend in mean plant density parallel to the gradient (violation of the constant mean assumption). Spatial autocorrelation is likely to be stronger and extend further when measured perpendicular to the resource gradient (i.e., at similar resource levels), and consequently the variograms will exhibit anisotropy. A similar effect is often seen in data from coastal systems in which autocorrelation extends further when measured parallel to the shoreline, i.e., along rather than across depth contours. Checking for and correcting these landscape-induced violations of the assumptions has become an integral step to geostatistical modeling through the introduction of easily applied corrections such as detrending, universal kriging, and variogram models that incorporate geometric anisotropy.

Efficient and easily implemented solutions to landscape barriers, however, have not been available. Consequently, their impacts are largely ignored. A commonly used approach to interpolation in the presence of barriers, which is implemented in many GIS programs, is to simply reject points that are separated by a barrier. This approach effectively divides the prediction area into many convex regions in which only points contained within a given region are used for prediction. In complex landscapes with many barriers, the result of this approach is that relatively

few points are used for prediction in some areas, and therefore greater sample sizes are needed to achieve the same degree of accuracy.

While a simple test for the presence of influential barriers is not available, we can define pre-conditions for the importance of barriers. Barriers are only likely to have a substantial impact on geostatistical interpolation when the following two general conditions apply:

1) The extent of the survey and the prediction area is larger than the scale at which barriers intervene. For example, peninsulas may be effective barriers to the dispersal of marine organisms among adjacent bays. They would have little impact on predictions, however, if a survey and the prediction area were limited to a single bay.

2) The range of spatial autocorrelation is larger than the scale at which barriers intervene. In an estuary, we would expect little impact if the Euclidean distance between sample or prediction points in adjacent bays was greater than the range parameter from the variogram. This is because points separated by a distance greater than the range are essentially uncorrelated and receive very little weight when predictions are made.

Visual inspection of the sample and prediction points on a map of the underlying landscape can indicate quickly whether condition one applies. It is more difficult, however, to determine *a priori* whether the range is greater than the scale at which barriers intervene since barriers may influence the empirical variogram and consequently affect the estimate of the range.

A Landscape-Based Distance Metric

What are appropriate alternatives to Euclidean distance when barriers exist and the spatial scale of the modeling effort and the range of spatial autocorrelation indicate that they may have an impact on geostatistical analysis? Sampson and Guttorp (1992) suggest an empirical non-parametric approach to determining the appropriate distance metric in cases where a time series of observations for each sample site is available. Such a data rich environment, however, is likely to be the exception for most ecologists. Rathbun (1998) divided the study region into a series of adjacent convex polygons based on a digitized shoreline of the estuary. This approach splits the estuary into increasingly smaller polygons until the shortest through water distance between all sample points is achieved. Little *et al*. (1997) recognized the suitability of a GIS as an efficient environment for conducting this type of spatial calculation. They defined a network of line segments connecting points in an estuary. While computationally efficient for narrow regions where movement is only possible along one path, this approach is difficult to apply in the more open portions of an estuary where distance both along and across the principal axis of the estuary must be considered.

Here I develop a distance metric that is equally applicable to nearly linear networks and open areas, terrestrial or aquatic, and accounts for the presence of barriers in the landscape. It is calculated using the cost-weighted distance function common to many GIS programs. This raster function calculates the lowest-cost distance from any pixel in a digitized map to any other. Cost is defined by a cost raster where the pixel values represent the relative ease of movement through the

associated habitat type. Diagonal movements are allowed and their cost is estimated

from the length of the diagonal rather than the cell size. The total cost of a given path

is the sum of the individual cost pixels encountered along that path multiplied by the

pixel size. When the landscape is defined in terms of absolute barriers, the binary

case, passable habitat is given a cost of 1 while barrier habitat is given an infinite cost

(e.g. a "no data" value). The resulting distance is simply the length of the shortest

path between two points that does not cross a barrier. For each point in the survey

data set, a distance raster map is produced whose cell values represent the lowest-cost

distance from the cell to the sample point.

The landscape-based approach was tested using data from the winter dredge

survey (WDS) of blue crabs (*Callinectes sapidus* Rathbun: Portunidae) in Chesapeake

Bay conducted yearly by the Maryland Department of Natural Resources and the

Virginia Institute of Marine Science. These data have been used to quantify crab

abundance (Zhang and Ault 1995) and fishery exploitation (Sharov *et al*. 2003) in

Chesapeake Bay. Like many estuaries, the Chesapeake Bay has several tributaries

separated by long, narrow peninsulas of land that present a barrier to the distribution

of many aquatic variables at a scale that makes them potentially influential for

baywide modeling efforts. The tributaries differ widely in the land-use characteristics

of their watersheds with some, such as the Potomac River, draining large urban areas,

and others, such as the Susquehanna River and many eastern shore tributaries,

draining primarily agricultural land. Thus, sample points in adjacent tributaries,

although quite close in Euclidean distance, can differ substantially in their chemical

and biological characteristics.

The WDS takes place during the crabs' dormant period limiting potential bias due to movement. It has been conducted annually since 1990 with an average of 1,413 stations per year, providing a comprehensive sample of the blue crab population in the Bay. Preliminary variogram analysis showed that blue crab catches exhibit distinct spatial autocorrelation at a range greater than the separation of some sample points in adjacent tributaries. This indicates that Euclidean distance-based kriging techniques may rely on samples from adjacent tributaries, and that a landscape-based approach may increase prediction accuracy.

Methods

Data

All data utilized were from the winter dredge survey (WDS) of the blue crab population in Chesapeake Bay. Full details of the survey design and application are provided in Vølstad *et al*. (2000) and Sharov *et al*. (2003). Briefly, the survey consisted of a one-minute tow of a 1.83 m wide crab dredge at each station. Stations were chosen randomly each year within three strata. Sample size ranged from approximately 900-1,500 stations per year. Depletion experiments were conducted yearly to determine catchability coefficients that could be used to transform catch into an estimate of absolute abundance (Zhang *et al*. 1993; Vølstad *et al*. 2000). The variable studied was the density of blue crabs (including all age and size classes) per 1000 m^2, calculated by dividing the absolute abundance estimate by the dredge area swept.

Sample coordinates were based on the starting location of each tow, and the tow distance was calculated from the start and end coordinates determined by Loran-C in early years and differential GPS more recently. Tows shorter than 15 m and longer than 500 m (1.4% of the total data) were not used in this analysis. All coordinates were projected to Universal Transverse Mercator (UTM) zone 18 before analysis. Annual density estimates were detrended to meet the geostatistical assumption of stationarity. For detrending, a second order two-dimensional polynomial of spatial trend with interactions was fit to each year. The model was simplified using backward elimination with a significance level to stay equal to 0.01. This relatively stringent criterion was used to avoid overfitting the trend. Variogram analysis, kriging, and cross-validation were conducted on the residuals.

Incorporation of Landscape-based Distance into Geostatistical Algorithms

The detrended residuals were used to estimate variograms for both the Euclidean and the LCP distance metrics. Euclidean distances were calculated using standard algorithms programmed within Matlab (The Mathworks, Cambridge, MA). Intersample lowest-cost path (LCP) distances for every pair of sample locations were calculated using a cost-distance algorithm programmed in the Visual Basic macro language within ArcView v8.3 (ESRI, Redlands, CA) where LCP distance was calculated along the path that minimized the distance function:

$$\sum (C_i \cdot X)$$

where C_i is the cost coefficient of the ith habitat type (here C_i is equal to one for cells in the water and is effectively infinite for cells on land) and X is the distance across

an individual cell. X is equal to the cell size for cells that are crossed in the north-

south or east-west direction or $\sqrt{(2 \cdot cellsize^2)}$ for cells that are crossed diagonally.

The resulting distances are written to the intersample distance matrix. This matrix is

used for calculating the variogram. A second matrix containing the LCP distances

from each sample point to each prediction point is calculated and used for prediction

and mapping.

Robust variograms were calculated according to Cressie (1993), with a Matlab

program that used distances from the Euclidean and landscape-based distance

matrices. A 250 m bin size was used to calculate the empirical variogram to a

distance of 40 km. Exponential and Gaussian variogram models were fit to the

empirical variograms using nonlinear least squares (SAS system, NLIN procedure)

where starting parameter values were chosen by eye.   The best fitting variogram

model, i.e., the model with the lowest mean squared error, was used for kriging and

variogram comparison. The variogram parameters for the Euclidean and landscape-

based distance metrics were compared using the sign rank test.

Following variogram selection, kriging was conducted in a Matlab program

modified to use Euclidean and landscape-based distances from a user-defined

distance matrix and a neighborhood of the 10 nearest points. Blue crab density in

each 1 km grid cell was predicted by adding the kriged prediction to the trend at the

center of every cell in the landscape. Prediction accuracy for both Euclidean and

landscape-based methods was assessed using the prediction error sum of squares

(PRESS) statistic. The PRESS statistic is a cross-validation measure calculated by

leaving one observation out of the data set and using the remaining points to predict

the value at that site. The PRESS statistic is simply the sum of the squared difference

between the predicted and observed values at each site. Predicted abundances were

then mapped in ArcView v8.3 for visual comparison.

Differences between the two distance metrics are likely to be accentuated as

distances increase between neighboring sample points. Within a given landscape,

increased distance between sample points increases the likelihood that a barrier will

intervene at some point along the straight line connecting any two points. Increasing

the average distance between pairs of sample points without changing the underlying

spatial structure can be achieved by taking a random subset of the data. The potential

impact of increased intersample distance was examined by taking 50 random subsets

of 200 sample points each and calculating the average difference in PRESS.

Similarly, differences between the Euclidean and LCP based kriging

predictions are likely to be greater in regions of the Bay where more barriers are

present. In the mainstem of the Bay, few barriers exist and the Euclidean and LCP

distances are likely to be similar. In the tributaries and in areas of the Bay with

islands and complex shorelines, the Euclidean and LCP distances, and consequently

the kriging predictions, are more likely to show differences. To examine these

potential regional differences, predictions were made and the PRESS was compared

for a subset of the data from Tangier Sound, a region with many islands and inlets.

Results

Spatial trends in abundance were found in all years. In most cases, the

underlying trend in the data was described best by a model of the form:

Density = $\beta_0 + \beta_1 x + \beta_2 y + \beta_3 xy$

where x refers to the easting value and y the northing value. The trend model for 1998

also included an x^2 term, and that for 2000 included an x^2 and a y^2 term.

Gaussian variogram models were chosen for all years, except 1990 and 1992,

where an exponential model provided a better fit (Table 1). In many cases, the

exponential model provided a marginally better fit, but was rejected because it

resulted in unrealistic variogram parameters (e.g., negative nugget or unrealistically

high range). In all years, choice of variogram model was the same for both distance

metrics.

Comparison of the variograms calculated under a Euclidean distance metric

with those from the LCP distance metric revealed systematic differences in the

variogram parameters. Inter-sample distances calculated using the LCP algorithm

were on average 11-17 km (14-23%) greater than the equivalent Euclidean distances

(Table 1). The variogram parameters, the nugget (Figure 3), sill (Figure 4), and range

(Figure 5), were all significantly lower on average for the LCP distance variograms.

Compared to the Euclidean distance variograms, the LCP distance variograms had a

lower nugget in eight out of the ten years compared, with an average difference of

236 (sign rank test, p = 0.049); a lower sill in nine out of ten years, with an average

difference of 1,038 (sign rank test, p = 0.049); and a lower range in eight out of ten

years, with an average difference of 3.32 km (sign rank test, p = 0.049). The equal

significance values for these three tests are coincidental. The effect of this pattern of

differences was to reduce the inter-station variability at any given distance.

Representative variograms are shown for 1996 (Figures 6 and 7), a year of relatively

small (0.01%) difference in prediction accuracy and for 2001 (Figures 8 and 9), the year of greatest difference (3.46%) in prediction accuracy. The variograms for 2001 are an example of a case where the exponential variogram provided a somewhat better fit than the Gaussian model, but was rejected because it resulted in an unrealistically high estimate of the range. In both years, the estimated nugget, partial sill, and range are lower for the LCP distance metric.

Despite this difference in the distances and in the variogram parameters, the PRESS statistic comparison shows only small differences in prediction accuracy between the two distance metrics (Table 2). Differences in PRESS range from 0.01 – 3.46% with a mean increase in PRESS of 0.2% when LCP distance is used. Of the 13 years of survey data tested, only 7 showed greater prediction accuracy when LCP distance is used.

Results were similar for the random subsample and the Tangier Sound subset (Table 3). For the random subsample, the difference in PRESS ranged from 0.07 – 1.47% with a mean increase in PRESS of 0.25% when LCP distance is used. In Tangier Sound, the difference in PRESS ranged from 0.15 –7.29% with a mean increase in PRESS of 0.94% when LCP distance is used. The direction of the difference in PRESS was not consistent with 4 out of 13 years for the random subset and 7 out of 13 years for Tangier Sound showing greater prediction accuracy when LCP distance is used.

Consistent with the small differences in PRESS, maps of predicted blue crab density show broadly similar patterns. Baywide patterns of blue crab distribution appear similar between the two methods in both 1996 (Figure 10) and 2001 (Figure

11). Smaller scale differences are apparent, however, especially in the unsampled

upper reaches of some tributaries. In the upper Potomac River, for example, the

Euclidean-based map for 1996 (Figure 10a) shows high predicted density because the

nearest samples (by Euclidean distance) are high values in the adjacent Patuxent

River. The LCP-based map for the same year (Figure 10b) predicts low abundance in

the upper Potomac River based on the nearest samples downstream.

Discussion

Differences in prediction accuracy were expected to result from the

impact of the landscape-based distance metric at two distinct stages of the

geostatistical modeling process: variogram estimation and kriging. Use of an LCP

distance metric changed estimates of the underlying spatial structure as summarized

in the variogram. Estimates of all three variogram parameters were significantly

lower under the landscape-based distance metric, indicating lower variation and a

shorter estimated distance of spatial autocorrelation (range). The landscape-based

distance metric also changed the sample points (and their weights) used in kriging,

reducing the importance of points separated by barriers from the prediction site.

However, differences in variogram estimates did not yield a consistent effect on the

accuracy of the kriging predictions. No consistent improvements in kriging accuracy

were seen even when distances among points were increased (the random subsample

analysis) or the analysis was restricted to areas of the Bay with many barriers (the

Tangier Sound analysis).

Although many factors interact to influence prediction accuracy, the unique shape of Chesapeake Bay may have played a role in reducing the increase in accuracy that was expected from the LCP distance metric. Many of the Bay tributaries, particularly on the west side, run parallel to one another. Because of this parallel orientation, the nearest point in an adjacent tributary is often at approximately the same distance from the tributary mouth. Such a point, while in a different tributary, may well show similar blue crab density because of its similar location relative to the tributary mouth. In this case, predictions using points in adjacent tributaries may in fact be more accurate.

This study is not the first to attempt landscape distance based prediction in estuaries, and the results of other approaches to kriging with a landscape-based distance metric have been equally equivocal. Both Little *et al*. (1997) and Rathbun (1998) found improvements in the prediction of some variables but not others. Little *et al.* (1997) found improvements in prediction accuracy (on the order of 10-30% reduction in PRESS) for only four out of eight variables when they applied a linear network-based distance metric. For the other four variables, use of the network-based distance metric increased the PRESS by 5-10%. Rathbun (1998) found slight improvements in cross-validation accuracy using a water distance metric for predicting dissolved oxygen but slightly worse accuracy when predicting salinity. Although variogram parameters differed between the two distance metrics in the Rathbun (1998) study, with the water distance metric resulting in higher variance and a longer range, no systematic comparisons were possible in that study since only one sample was analyzed.

Two recent studies in stream systems (Torgersen *et al*. In press; Gardner *et al*. 2003) apply geostatistical tools based on the distance between sample sites along a stream network. Torgersen *et al*. (In press) used a network-based distance metric to quantify spatial structure in cutthroat trout abundance in an Oregon stream system. Although the distance metric used provided clear variogram patterns, no explicit comparison was made with a Euclidean distance metric. Gardner *et al*. (2003) found improvements (lower prediction standard errors and predictions that better met expectations) in the prediction of stream temperature when a network-based metric was used, but did not report cross-validation statistics. Variogram parameters were also found to change in this study with the network-based metric resulting in smaller nugget but longer range.

The effect of alternative distance metrics on variogram parameters is difficult to predict since opposing influences may interact. For example, increasing the distance between points is likely to result in a longer estimated range, as seen in the Rathbun (1998) and Gardner *et al*. (2003) studies. Since a landscape-based metric reduces the influence of points separated by a barrier, which are expected to differ more than their Euclidean separation would suggest, it also seems likely to reduce the sill parameter (as seen in this study), a measure of overall variability. Because the range and the sill parameters are often highly correlated, however, the overall effect is unpredictable.

Concurrently and independently of this study, Krivoruchko and Gribov (2002) applied a similar technique for calculating LCP distance and used it to model air quality in California. They used a digital elevation model (DEM) to define a cost

map representing the relative impedance of the environment to the spread of air

pollution. Regions with steep changes in elevation were given a higher cost than flat

land in order to account for the preferential spread of air masses along rather than

across elevation contours. Interpolation was conducted using the inverse distance

weighted method. Visual inspection of interpolated maps based on Euclidean

distance and those produced using the landscape-based distance supported the use of

the latter technique; however, no formal comparison was presented.

One of the currently unresolved problems with using a landscape-based

distance metric for kriging is assuring the validity of the covariance matrix (Rathbun

1998). There is no guarantee that the covariance function for a given combination of

variogram model and non-Euclidean distance metric will be non-negative definite.

That is:

$$\sum_{i=1}^{m}\sum_{j=1}^{m} a_i a_j C(\mathbf{s}_i - \mathbf{s}_j) \geq 0$$

where s_i and a_i represents all finite collections of spatial location $\{s_i: i = 1,\ldots,m\}$ and

real numbers $\{a_i: i = 1,\ldots,m\}$ and $C(x)$ is the covariance function (Cressie 1993).

Consistently valid combinations of variogram model and distance metric are yet to be

determined. Candidate covariance functions can be tested, however, and alternative

approaches used if they fail to meet the non-negative definiteness criterion. Although

all of the covariance matrices in this analysis met this criterion, there is no guarantee

that this would hold true for the set of all possible sample locations. Krivoruchko and

Gribov (2002) suggest a moving average approach to estimating the covariance

model that is not subject to the same criterion. It should be noted that variograms,

spatial autocorrelation statistics, and deterministic interpolation methods are not affected by this problem.

While the simple binary (passable or barrier) case is presented in this example, the LCP approach can incorporate varying degrees of impedance to the continuity of the process or population under study. For example, one type of habitat may represent an insurmountable barrier while another may only slow the spread of the process. Parameters used to define the degree of impedance or 'cost' of different landscape types could come from many sources depending on the type of variable studied. For mobile organisms, costs could be based on studies of animal movement such as Dyer *et al*. (2002) or the translocation experiments by Bélisle (2001) although the extent to which different habitat types present a barrier to movement may not be static (Thomas *et al*. 2001). For temporary barriers the cost might simply be the inverse of the fraction of time that the barrier is passable. For spatial modeling of chemical contaminants, cost parameters might come from laboratory experiments of diffusion and transport in different media.

Landscape ecologists have long recognized that Euclidean distance is rarely the most appropriate metric when considering the ecological relatedness among points in a landscape (Forman and Godron 1986). When flows between points are of interest "time-distance", i.e., the quickest route, may be preferable. However, time-distance requires detailed knowledge of how an organism disperses through various habitat types. Time-distance has an added complication in that it may be asymmetric, where the time-distance from A to B is not necessarily the same as that from B to A. This is likely to be the case in stream systems, hilly terrain, and other environments

that impose directionality on animal movement. Nevertheless, the idea that the distance metric should reflect the relative ease or speed of moving along a particular path remains valid.

The LCP approach to variogram estimation and kriging presented here represents an easily incorporated modification to commonly used geostatistical techniques. The benefits of using this approach depend on the study environment (e.g. scale and extent of barriers), the spatial distribution of the variable being studied, and the study objectives (e.g. variogram estimation, mapping, or quantitative prediction). Although the expected increases in prediction accuracy did not materialize in this study, the relatively unique configuration of parallel tributaries within the Bay may have been partly responsible. This approach, however, is a general one and can be applied to other locations or data sets for which greater differences in accuracy may be found. The potential also exists for the LCP distance metric to be incorporated into other types of spatial analyses such as home range estimation, habitat modeling, and deterministic interpolation methods.

Chapter 3: Geostatistical Analysis of Blue Crab (*Callinectes sapidus*) Abundance and Winter Distribution Patterns in Chesapeake Bay

Abstract

Spatial heterogeneity is a striking feature of the blue crab life history and fisheries in Chesapeake Bay. Patterns of sex- and age-specific habitat use have long been documented. However, a quantitative assessment of the spatial distribution of blue crabs has been lacking. Here, I apply geostatistical techniques (variogram modeling and kriging) to 13 years of data from a winter dredge survey (WDS) to describe the pattern of spatial autocorrelation in blue crab density and map patterns of blue crab winter abundance. These maps are then used to derive a time-series of baywide abundance and to examine changing patterns of habitat use and aggregation. Geostatistical-based abundance estimates are higher on average than those calculated from design-based methods, although both time series show a large and significant decline in abundance from 1990 - 2002. The latitude of the weighted centroid of blue crab density in Chesapeake Bay exhibited a significant positive relationship with Baywide abundance, suggesting density-dependent changes in distribution. The range parameter of the variogram was not found to be significantly related to abundance, suggesting that blue crab patch size may be unrelated to population density. Such quantitative and spatially-explicit information provides a potentially useful base for constructing population models and evaluating alternative management options.

Introduction

There is an increasing recognition of the importance of space and spatially-explicit information for understanding the ecology, population dynamics, and management of marine resources (Nishida and Booth 2001). This trend is a result of a growing awareness of the risks of not accounting for the spatial dynamics of exploited populations (Hutchings 1996; Walters 2003) coupled with new methods for incorporating space into single species models (Caddy 1975) as well as mixed fishery models (Pelletier *et al*. 2001) and multi-species trophic models (Walters *et al*. 1999). These spatial models and spatially-explicit management strategies such as time-area closures and marine protected areas are being used increasingly to manage fisheries. While 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.

Blue crab is an important benthic predator and scavenger (Eggleston *et al*. 1992; Mansour and Lipcius 1993) that provides 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. Blue crab spawns in mid to late summer in the high salinity waters of the lower Bay (Van Engel 1958; Jones *et al*. 1990). The larvae are advected offshore where they develop through several immature stages before returning to the Bay and settling, often in sea grass beds, in the lower Bay (Lipcius & Van Engel 1990; Metcalf *et al*. 1995). Seagrass beds and other structurally complex habitats continue

to provide important nursery and molting habitat for juvenile and adult stages (Orth and van Montfrans 1987; Orth *et al.* 1996). In late fall, blue crab in Chesapeake Bay undertake a migration to deeper water where they overwinter in the sediment. Winter habitat use and migration patterns are sex- 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 lower Bay spawning habitat (Hines *et al.* 1995; McConaugha 1995; Turner *et al.* 2003).

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 spring "peeler runs" of molting crabs, and pots and trot lines are used to catch crabs of both sexes from spring through fall. Management efforts have responded to this 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 mainstem of the Bay in Maryland whereas trot-lines 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 to 2,400 km^2. This sanctuary, however, protects crabs only during the summer (June 1 – 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 likely be improved using maps of blue crab winter distribution.

Time series of blue crab relative abundance are available from several fishery-independent surveys including the Maryland and Virginia trawl surveys (Lipcius *et al*. 2003), the Calvert Cliffs pot survey (Abbe and Stagg 1996), and the baywide winter dredge survey (Sharov *et al*. 2003). However, the spatial analysis of these surveys has been conducted at a very coarse scale only, with information generally divided into two geographic categories, usually either upper bay/lower bay or Maryland/Virginia (e.g., Miller 2003). Geostatistical methods are one approach to analyzing fine-scale patterns of distribution (Rivoirard *et al*. 2000).

Geostatistical modeling techniques 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 and kriging. 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). Although variogram modeling is often simply an intermediate step before kriging, the range parameter can be used to parameterize other models (Fuchs and Deutz 2002) or to determine sampling intervals (Maravelias 1999; Kendall *et al. In press*). Kriging is an interpolation method that makes use of the spatial structure defined in the variogram to predict values of a variable at unsampled sites. Kriging can be used for descriptive purposes such as mapping (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).

Do geostatistical approaches have advantages over classical design-based approaches for estimating the abundance of marine resources? Ignoring spatial autocorrelation can result in biased estimates of the variance. Aubry and Debouzie (2000, 2001) demonstrated the superiority of model-based geostatistical techniques for hypothesis testing in the presence of spatial autocorrelation. The presence of positive autocorrelation (where values for neighboring pairs of points are more similar to one another than are distant ones), if not dealt with appropriately, can result in an effective overestimation of sample size since samples are not entirely independent. Rossi *et al*. (1992) and Legendre (1993) showed that while 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.

Improvements in abundance estimation are not the only rationale for applying spatial modeling techniques to data on blue crab winter distributions. 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 biology-based criterion for setting reserve boundaries. Such maps would 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. Finally, quantitative maps allow researchers to develop and test hypotheses about habitat use and ecological relationships.

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 for blue crab in the Chesapeake Bay), they also permit the examination of density-dependent changes in distribution. Theoretical models of density-dependent habitat selection (DDHS), including the discrete space "ideal despotic distribution" (Fretwell 1972) and the continuous space "basin model" (MacCall 1990), suggest 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 these models have most often been used to describe foraging behavior (Krebs and Inman 1992), i.e., habitat selection to maximize consumption, they can also be applied to habitat selection to balance consumption and predation risk (Utne *et al*. 1993; Grand and Dill 1997), or minimize energetic costs and maximize survival based on abiotic environmental factors (Kemp *et al*. 2003).   Blue crab winter habitat selection is most likely to correspond to this last situation since blue crab does not

forage during its winter dormant period and its energetic costs (Brylawski and Miller 2003) and winter mortality rates (Sharov *et al*. 2003) are known to vary with temperature and salinity.

To the extent that theoretical habitat selection models provide an accurate description of blue crab behavior, changes in the variogram parameters and distribution maps can be expected as population density changes. The range parameter of the variogram indicates the maximum distance at which spatial autocorrelation is present between pairs of points, and has been used as a proxy for patch size (e.g., Biondi et al. 1994, Maravelias & Haralabous 1995, and Dent & Grimm 1999). If suitable blue crab winter habitat is patchily distributed, with highest suitability occurring toward the center of the patch, then blue crab patches are likely to increase in size as the population density increases. Such increases in patch size would result in increases in the estimated ranges. Changes in blue crab density may also manifest themselves as broad-scale changes in crab distribution within the Bay. Blue crabs are known to undergo migration toward deeper water in the fall with mature females moving to the deep waters of the lower Bay and males and immature females moving to deep water of the tributaries and mainstem of the Chesapeake Bay. Since deep water represents preferred habitat, and more deep water (though not the deepest point in the Bay) is found in the lower Bay, DDHS models predict that the distribution of blue crabs is likely to move northward into less favorable habitat as density increases. I examine the extent to which blue crab winter distributions fit the predictions of DDHS models by testing the following hypotheses:

H1 - The centroid of the blue crab distribution moves northward as baywide blue crab abundance increases.

H2 - The range parameter of the variograms increases as baywide blue crab abundance increases.

Methods

Data

All data analyzed in this study were from the winter dredge survey (WDS) of the blue crab population in Chesapeake Bay that has been conducted annually since 1990. 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 one-minute 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 two years of the survey, however, twenty-two and twenty-five strata were used, with each of the major tributaries and embayments forming a separate stratum. Sample size ranged from approximately 900-1500 stations per year. Depletion experiments, in which the same area was dredged repeatedly, were conducted yearly to determine the fraction of blue crabs sampled by a single dredge tow, the catchability coefficient (q). Based on these experiments, Vølstad *et al*. (2000) used an exponential model to estimate vessel and year specific catchability coefficients and transform catch at each station into an estimate of absolute abundance. The variable analyzed here is the density of blue

crabs (number per 1000 m^2), calculated by dividing the absolute abundance estimate by the dredge area swept.

The spatial analyses employed here are based on sample coordinates defined by the starting location of each tow, and the tow distance was calculated from the start and end coordinates as determined by Loran-C in early years and differential GPS 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 (UTM) zone 18 before analysis, although 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, results of these studies have not shown a consistent improvement in prediction accuracy compared to traditional kriging methods based on Euclidean distance. Preliminary investigation suggests that improvements in prediction accuracy of blue crab density in Chesapeake Bay from a landscape-based distance metric are small and inconsistent with a small decrease in accuracy observed on average (see Chapter 2). Consequently, the Euclidean distance metric is used in this analysis.

In order 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, and variogram modeling and kriging were conducted on the residuals. For detrending, a second order two-dimensional spatial trend with interactions was fit

for each year. The model was simplified using backward elimination with a significance level to stay equal to 0.01. This relatively stringent criterion was used to avoid overfitting the trend.

Robust empirical variograms (Cressie 1993) were calculated in SAS (VARIOGRAM procedure, SAS Corporation, Cary, NC). Variogram estimation was limited to stations separated by up to 40 km with a lag size of 250 m. Spherical, exponential, and Gaussian variogram models were fit to the empirical variogram (SAS NLIN procedure, SAS Corporation, Cary, NC), and the best fitting model was chosen except in cases where one variogram model resulted in unrealistic variogram parameters (such as a negative nugget) or failed to converge.

Following variogram selection, ordinary kriging was conducted in SAS (KRIGE2D procedure, SAS Corporation, Cary, NC) with a kriging neighborhood of the 10 nearest sample points. Blue crab density was mapped at a 1 km grid scale by adding the kriged predictions (residuals) to the trend at the centroid of every mapped grid cell. 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 of unsuitable winter habitat for blue crabs due to low salinity. Kriging variance maps were also created. Mapping was conducted in ArcView v8.3 (ESRI Corp, Redlands, CA). 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.

In order 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, a linear regression of abundance against time was fit. The values for the slope of the regression were then mapped in order to visually evaluate patterns of change in density. Although the large number of regressions (11,189) and the presence of spatial autocorrelation prevent rigorous significance testing, a probability cut-off of 0.05 is used to limit the possibility of displaying spurious trends. Cells meeting the $p < 0.05$ were classified as increasing (positive trend), moderate decline (negative trend < 0.1 crabs per 1000 m^2 per year), and strong decline (negative trend > 0.1 crabs per 1000 m^2 per year)

The relationship between winter abundance and catch per unit of effort (CPUE) from the winter dredge fishery was assessed by linear regression of CPUE against geostatistical and design-based abundance estimates. Detailed trip-level effort data for this fishery is only available from 1994 to the present. Information on dredge fishery license sales, however, is available for the entire 1990-2002 time period. Consequently, CPUE is calculated here as landings per license. A strong correlation ($r = 0.96$) exists between landings per dredge day and landings per license, indicating that landings per license is a reasonable proxy for CPUE calculated based on more detailed effort data.

Density-dependent Habitat Selection

A centroid was calculated from the distribution maps for each year. The centroid is simply a mean latitude and longitude of all grid cells weighted by the estimated density in each cell. Although calculation of a centroid is possible from the

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raw data, values calculated in this manner reflect the distribution of samples, as well as 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 test the predictions of DDHS models, the effective range of spatial autocorrelation and the latitude of the centroid were regressed against baywide blue crab abundance. The effective range of spatial autocorrelation is equal to the range parameter of the variogram for spherical models, but by convention is considered to be the distance at which the semivariance is equal to 95% of the sill for exponential and Gaussian models which approach the sill asymptotically. Two alternative explanations for changes in distribution patterns were examined in the same manner. Changes in freshwater flow (and therefore the location of the salt front) due to interannual differences in precipitation were tested as a possible explanation by regressing the latitude of the centroid against the mean flow rate of the Susquehanna River measured at Conowingo, MD (USGS 2004) for the preceding fall (October-December). Conversely, changes in the relative number of mature females may explain the observed pattern. To test this alternative, the latitude of the centroid was regressed against the percentage of mature females in the population. Since geostatistical estimates of mature female abundance are not feasible due to 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 mature female and total blue crab abundance (G. Davis unpubl. data).

Results

Spatial trends in abundance were found in all years. Trend models are summarized in Table 4. Gaussian variogram models were chosen in most years, except in 1992 and 1997, where a spherical model provided a better fit and 2000 where the best fitting model was exponential (Table 4).

Spatial patterns of blue crab density in Chesapeake Bay (Figures 12-24 a) showed a great deal of interannual variability, but areas of consistently high or low density are also evident. Predicted densities in the upper reaches of many tributaries and in the northernmost part of the mainstem should be viewed with caution since few samples exist in these areas and consequently the uncertainty there is high (Figures 12 - 24 b). The map of average blue crab density over the 13-year study period (Figure 25a) shows complex patterns with high density in many lower Bay tributaries and eastern shore embayments. However, some clear patterns emerged. Crab abundance in the deeper channels north of the Patuxent River, and south of the Potomac River in the main stem is consistently below average. Similarly, Tangier and Pocomoke Sounds always exhibit above average abundances. Temporal trends in blue crab density over the 13-year study period (Figure 25b) differ in different parts of the Bay with much of the lower Bay mainstem and the eastern shore showing declines and some indication of an increase in crab density in the upper Potomac. The upper Potomac, however, falls in an area of consistently high variance indicating that the significance of the trend in this area is highly uncertain.

Trends in the time-series of baywide blue crab abundance (all individuals larger than 15 mm of both sexes) estimated using geostatistical methods (Figure 26) generally agree well with design-based estimates of abundance (G. Davis unpubl. data), although the geostatistical estimates are higher in most years. Notable exceptions to this general agreement are apparent, however, in the first two years (1990 and 1991) where the geostatistical estimates are 38% and 73% higher respectively. Both geostatistical and design-based abundance estimates show significant negative trends (geostatistical: $R^2 = 0.53$, $p = 0.005$; design-based: $R^2 = 0.55$, $p = 0.004$) with a decrease in baywide abundance of 80% and 66%, respectively from 1990 to 2002. Winter dredge fishery CPUE is 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 27).

The centroid of blue crab density in Chesapeake Bay exhibits substantial interannual variability. Consistent with the North-South orientation of the Bay, the variability in the location of the centroid is more pronounced in the North-South than in the East-West direction. Generally, the centroids for earlier years fall to the north of those from later years. This temporal trend in the latitude of the centroid (Figure 28) is statistically significant ($R^2 = 0.43$, $p = 0.01$). An even stronger relationship exists between the latitude of the centroid and the estimated Baywide blue crab abundance (Figure 29, $R^2 = 0.78$, $p < 0.001$). There is no apparent relationship between the latitude of the centroid and the percentage of mature females in the Chesapeake Bay blue crab population (Figure 30, $R^2 = 0.05$, $p = 0.484$). A weak but significant positive relationship exists between fall flow of the Susquehanna River

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and the latitude of the centroid (Figure 31, $R^2 = 0.33$, p = 0.041). There is no apparent relationship between the effective range of spatial autocorrelation and estimated Baywide blue crab abundance (Figure 32, $R^2 = 0.05$, p = 0.447).

Discussion

For the time series over which the WDS has been conducted, the Chesapeake Bay blue crab stock has undergone substantial and significant decline. Over this same time period, the winter distribution of crabs has exhibited marked interannual variability. Some regions have shown consistently high abundance e.g., Tangier Sound and the lower portions of the three major lower Bay tributaries (Rappahannock, York, and James Rivers). Additionally some areas exhibit high abundance, but not consistently so e.g., the uppermost mapped portion of the Bay and the uppermost portions of many tributaries, particularly the Potomac River. Estimates 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 likely to be made up largely of mature females, shows substantial interannual variation.

Consistent with the overall declines in blue crab abundance, more areas of the Chesapeake Bay exhibit a pattern of decreasing density than exhibit increasing density. Decreases in density are apparent in some of the most consistently high-density regions of the Bay including the eastern shore area from the Choptank River south through Tangier Sound. The major western shore tributaries generally 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 lower Bay mainstem. 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.

Two statistical approaches to estimating crab abundance, design-based and

geostatistical, both showed a pattern of declining abundances over the 13-year period

from 1990-2002. Geostatistical estimates of Baywide blue crab abundance were

generally higher than estimates derived from design-based methods, especially in the

first two years of the time-series. Differences in the estimates between design-based

methods and model-based methods are not unexpected as the accuracy of either

estimate will be influenced by the degree to which the assumptions of the analysis 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. Variogram model fits were more problematic with several years

showing spikes at short distances or increases that failed to level off within the 40 km

range over which the variograms were plotted. Other studies, however, have found

that kriging is fairly robust to misspecification of the variogram parameters (Diamond

and Armstrong 1984; Stein and Handcock 1989). Although the variogram fits were

problematic, all variograms showed strong evidence of spatial autocorrelation – a source of information that design-based methods fail to utilize.

A further important reason for differences in the two estimates is their assumptions about unsampled areas. The design-based approach effectively assigns a density equal to the mean stratum density to all areas of a stratum and then multiplies this mean by the area of the stratum. Unsampled areas are also assigned this mean stratum density, with the assumption that all areas of the stratum are proportionally reflected in the mean given large enough sample sizes. The geostatistical approach explicitly assigns values to unsampled areas based on the values of the nearest sampled locations. The likely reason for the observed differences in abundance estimates between these two methods relates to sparsely sampled regions of a stratum. Design-based approaches implicitly assign values for unsampled locations based on the sample mean, whereas geostatistical approaches extrapolate from the nearest sample points. Accordingly, sample points in sparsely sampled regions are given disproportional weight in the geostatistical method. Consequently, 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 mainstem.

In this specific comparison, the area over which blue crab distributions are calculated also differs. This is another potential cause of the difference between the two abundance estimates. The geostatistical abundance estimates presented here

were calculated over an area of 11,189 km^2 while the design-based approach

presented by Sharov *et al*. (2003) used an area of 9,812 km^2, a 12.3% smaller

estimate. Although both areas were estimated in a GIS, different shoreline files or

map projections may result in different area estimates. A more important source of

differences may be the definition of what constitutes Bay waters. For this study,

abundance was estimated for all grid cells falling to the south of the northernmost

sample point (out of all years) and inshore of a line approximately connecting Cape

Henry and Cape Charles. The 1 km grid size limited the extent to which the narrow

upper reaches of tributataries were represented in abundance calculations. Rescaling

the design-based abundance estimates by the ratio of the two areas slightly reduces

the magnitude of the discrepancy between design-based and geostatistical estimates,

but does not change the overall patterns.

It is not possible to determine which abundance estimation method more

accurately estimates the size of the blue crab stock in Chesapeake Bay. However, the

significant correlations between winter dredge fishery landings and the two

abundance estimates provides support for both methods. The stronger correlation

between landings and the geostatistical abundance estimate suggests that this method

may do a better job of capturing inter-annual fluctuations in abundance. Interestingly,

the 1990 and 1991 (the years for which the two methods differed most dramatically)

geostatistical abundance estimates fall close to the regression line indicating that

these unusually high estimates may be an accurate reflection of higher abundance in

the first two years of the survey. This correlation only addresses pattern, however,

not the scale of the estimates. A strong correlation between landings and abundance

estimates could be found even if the estimates were consistently higher or lower than true abundance.

One of the most striking patterns that emerged from analysis of the density maps was the positive relationship between the latitude of the centroid of blue crab density and the abundance of blue crabs in the Bay. While it is notoriously dangerous to infer process from pattern, several alternative explanations for this pattern were examined, and DDHS remains the most convincing. Two of the most plausible alternative explanations, the percentage of mature females and fall Susquehanna River flow rate, were examined and neither displayed a strong relationship with the latitude of the centroid. The weak positive relationship between fall flow and the latitude of the centroid is most plausibly explained by gravitational circulation shifting the salt front northward in bottom waters. Despite the lack of convincing alternative explanations, the observed pattern can only be seen as suggestive of DDHS since other untested factors may be influencing the distribution of blue crab. The shift in centroid over the time series of the WDS may reflect several physical and biological variables that also exhibited trends over the same time period and could be implicated in the observed changes in the centroid.

Although the relationship between the location of the centroid and blue crab abundance strongly implicates DDHS, the limiting resource and the behavioral mechanism for maintaining DDHS are not apparent. Space is the most obvious potentially limiting resource since blue crabs do not feed during their dormant winter stage. The highest density of crabs observed in the trawl data was 5,614 crabs per 1,000 m^2. At this density, more than five crabs would be found in an average 1 m^2

quadrat, and space might well be limiting. Such densities appear to be very rare, however, with 99.4% of samples having densities less than 1,000 crabs per 1,000 m^2. 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 is thought to influence habitat selection by juveniles (van Montfrans *et al*. 2003), a behavioral explanation for space limitation in the winter seems unlikely given that crabs already buried in the sediment are in a dormant state and are probably unable to defend their space.

Another possible factor affecting the distribution of crabs is the winter dredge fishery. The WDS takes place over a four-month period from December to March. During this time, an active winter dredge fishery with landings during the period 1990 - 2002 of 4 - 31 million crabs per year (S. Iverson unpubl. data) – representing 1 - 5% of the total overwintering population) – takes place in the lower Bay. As the season progresses, samples from the WDS increasingly reflect the impact of the winter dredge fishery on winter distributions. The effect of the winter dredge fishery on the latitude of the centroid depends on how catch varies in relation to abundance. If catch is a constant proportion of abundance, the winter dredge fishery would have no effect on the centroid. Alternatively, if catch is a constant which does not vary with abundance, the winter dredge fishery would cause the latitude of the centroid to be inversely related to abundance since the fishery would remove a smaller and smaller fraction of the lower Bay population as abundance increased. Only if the winter dredge fishery removed a greater fraction of the lower Bay population as

abundance increased could the winter dredge fishery cause the observed positive

relationship between abundance and the latitude of the centroid. The apparently

linear relationship between landings and abundance suggests that the first relationship

(catch is a constant proportion of abundance) is the most likely, indicating that the

winter dredge fishery is unlikely to be a significant cause of the changes in the

location of the centroid.

The lack of any apparent relationship between the effective range of spatial

autocorrelation and blue crab abundance suggests that either: 1) the range is not a

suitable proxy for patch size; or 2) patch size is not related to baywide abundance.

Although several studies have used the range parameter from variograms as an

estimate of patch size (e.g., Biondi et al. 1994, Maravelias & Haralabous 1995, and

Dent & Grimm 1999), none appear to have tested this relationship. The range is

likely influenced not only by patch size, but also by other characteristics of a spatial

distribution such as distance between patches and patch shape. The ranges observed

in this study were typically on the order of tens of kilometers. While patchiness at

this scale may also have biological meaning – for example, patches of the deep lower-

Bay habitat used by mature females may be of this size – smaller scale patchiness on

the order of tens to hundreds of meters may be more relevant, particularly in many of

the tributaries and embayments. This smaller scale patchiness is probably not well

sampled by the survey and contributes to the nugget, which incorporates

measurement error and variability below the sampling resolution (Cressie 1993).

Alternatively, the assumption that DDHS would result in larger patches may be

wrong. Suboptimal habitat patches may become suitable as densities increase within optimum patches, resulting in more, but not necessarily larger, patches of blue crabs.

What do density dependent changes in winter distributions mean for the population dynamics of blue crab? If DDHS does play a role in determining distributions, and lower densities result in more crabs overwintering in optimum habitat, then natural overwintering mortality rates may decline. Such a compensatory mechanism has not previously been documented in blue crab populations and understanding its potential effects will require more research on overwintering mortality. Potential gains due to decreased overwintering mortality may be offset, however, by increased fishing mortality rates in the lower Bay as the distribution shifts southward. 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 potential depensatory 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 distribution. The distributional changes are consistent with the predictions of DDHS models, however, alternative explanations exist which cannot be rejected based on the available data. Whether the observed distributional changes are due to DDHS or not, 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.

Chapter 4: Winter Distribution of Blue Crab (Callinectes sapidus) in Chesapeake Bay: Application and Cross-validation of a Two-stage Generalized Additive Model (GAM)

Abstract

I present a two-stage generalized additive model (GAM) of the distribution of mature female blue crab (*Callinectes sapidus*) in Chesapeake Bay based on data from a fishery-independent winter dredge survey. The distribution and abundance of blue crabs was modeled as a flexible function of depth, salinity, water temperature, distance from the Bay mouth, distance from submerged aquatic vegetation (SAV), and bottom slope for each of the 13 years of available data. Depth, salinity, temperature and distance from the Bay mouth were found to be the most important environmental determinants of mature female blue crab distributions. The response curves for these variables displayed patterns that are consistent with laboratory and field studies of blue crab/habitat relationships. The generality of the habitat models was assessed using intra- and inter-annual cross-validation. Although the models generally performed well in cross-validation, some years showed unique habitat relationships that were not well predicted by models from other years. Such variability may be overlooked in habitat suitability models derived from data collected over short time periods.

Introduction

Blue crab (*Callinectes sapidus*) ranges along the Atlantic coast of the American continent from Brazil to Canada. Evidence does not support the existence of distinct genetic populations, but functional sub-populations are recognized with only limited exchange between them (McMillen-Jackson et al. 1994). Over the species' wide latitudinal range, individual sub-populations can experience markedly different environments. Temperature is likely the key environmental parameter causing the variation observed in life history schedules (Smith 1997). Central to temperature's role is the existence of a physiological minimum temperature (T_{min}), close to 10° C, below which molting, and hence growth, ceases (Brylawski and Miller 2003). As temperatures increase above T_{min}, the period between molts shortens, and thus, overall rates of growth increase. In particular, the proportion of the year during which temperatures are above T_{min} is an important determinant of the life history pattern expressed. In the Gulf of Mexico, average bottom water temperature is above T_{min} throughout the year, and crabs grow sufficiently fast so that they can mature, reproduce and enter the commercial fishery in a single year. In contrast, water temperatures in mid-latitudes are unfavorable between late November and late April. During this period, crabs enter a dormant phase during which they bury into the sediments. Thus in mid-latitude populations, growth and maturation occur in different years so that individuals take a minimum of 18-24 months to complete their life cycle.

Because overwintering blue crabs in Chesapeake Bay do not feed and are unlikely to experience significant predation, bioenergetic costs are likely to play a

dominant role in determining overwintering survival. Laboratory studies (Tagatz

1969, McKenzie 1970) have shown that salinity and temperature interact with thermal

tolerances dependant on both salinity and acclimation temperature. These results

suggest that salinity and temperature, as well as factors such as depth, which might

serve to limit temperature fluctuations, may be important in determining choice of

overwintering habitat; however no studies to date have examined the extent to which

winter distributions of blue crab reflect differences in these variables.

The blue crab population in the Chesapeake Bay supports the single largest

blue crab fishery in North America. Assessments of this stock indicate recent

declines in both abundance and landings (Chesapeake Bay Stock Assessment

Committee 2003) despite efforts to reduce fishing mortality (Chesapeake Bay

Commission 2001). Winter distributions in the Bay have been an emphasis of recent

research for several reasons. Most directly, estimates of abundance and rates of

exploitation of blue crab in Chesapeake Bay, on which stock assessments have been

based, have been derived from a baywide, fishery-independent winter dredge survey

(WDS) conducted between December and March (Sharov et al. 2003). Also making

the winter distribution of crabs important is concern over the vulnerability of

spawning females in a winter dredge fishery (Miller 2003) and the efficacy of a

dispersal corridor (Lipcius et al. 2001) and a combined marine protected area and

dispersal corridor (Lipcius et al. 2003) that has recently been established in the

Virginia (southern) portion of Chesapeake Bay. Thus, the ability to predict blue crab

winter distribution has become desirable.

Generalized additive models (GAMs) provide a flexible non-parametric or semi-parametric framework to model the relationship between a response and one or more predictor variables (Hastie & Tibshirani 1990). GAMs do not require the distributional assumptions of traditional parametric approaches and provide the ability to fit flexible non-linear response curves to individual predictor variables. In GAMs, the response variable is assumed to be the sum of separate individual functions of each of the predictor variables with a link function appropriate to the distribution of the response variable (e.g., a Poisson link function is often specified for count data). In the more familiar generalized linear models (GLMs), these individual functions of the predictor variables are linear. In GAMs, the individual functions may be linear or may be non-parametric smoothers such as regression splines, which are better suited to modeling many common biological response curves such as threshold functions. Different functions may be specified for each predictor variable, allowing for response curves that are specific to the individual predictors.

The use of GAMs to model organism/habitat relationships increased following publication of Hastie and Tibshirani's (1990) book and Swartzman et al.'s (1992) application of this technique to model groundfish in the Bering Sea. GAMs have since become widely used in marine sciences to predict abundance and identify important habitats (e.g., Swartzman et al. 1994,1995, Maravelias et al. 2000a, Reid & Maravelias 2001) and to model stock-recruitment relationships (Cardinale & Arrhenius 2000).

Two-stage GAMs are an extension of the basic structure in which the response variable is modeled first as a binomial variable (presence/absence or yes/no) and

secondly the non-zero observations (presence or yes) are modeled as a continuous or count variable, usually with a Gaussian or Poisson distribution respectively. The two stages may then be combined multiplicatively to yield an overall prediction (Barry & Welsh 2002). This approach is particularly useful in modeling aquatic organisms, for which, because of their patchy distributions, survey catches are often zero-inflated, (Maravelias 1999). Two-stage GAMs have been used in fisheries to improve estimates of various stock assessment indices (e.g. Borchers et al. 1997, Piet 2002) and to model salmon feeding and growth (Rand 2002).

However, despite the widespread use of GAMs, studies have yet to examine their ability to find general relationships that are valid beyond the particular data set or year modeled. A risk of using highly flexible, non-parametric methods is that the resulting predictive models may fit the modeled data so specifically that they may have little predictive power when applied to other data sets. The underlying goal of most habitat modeling studies is not simply description of the trends in the modeled data, but also to produce predictions valid in other years/locations. Ideally, GAMs should produce an understanding of the functional relationship between an organism and various components of its environment. Cross-validation, by testing the ability of models based on one data set to accurately predict values in another, is a useful means of assessing the generality of a model.

Here I fit two-stage GAMs for each of thirteen years of data from the WDS to determine the environmental variables that regulate winter distribution of mature female blue crab in Chesapeake Bay. Subsequently, cross-validation is used to assess

the ability of models developed to predict distributions in one year to predict the distribution of crabs in other years.

Methods

I modeled the distribution of mature female blue crab in Chesapeake Bay. Mature females were chosen as the focus of this study because of their greater per capita contribution to future generations and because current management strategies, including the lower bay spawning sanctuary, are focused specifically on their protection.

Data

The WDS has been conducted annually between December and March since the winter of 1989-1990. Full details of the survey design are provided in Sharov et al. (2003), and are only summarized here. Survey years will henceforth be referred to by the year in which the survey was completed, e.g. the first survey is the 1990 survey. Stratification and sample size in the first three years of the survey were different than in the remaining years, but except for this change the survey has been conducted consistently throughout the period of record. From 1993 – present, 1255 – 1599 stratified random stations were sampled within three region-based strata. During the period 1990 – 1992, there were more strata and generally fewer (867 – 1395) samples. A typical distribution of station locations and densities of mature female blue crabs is shown in Figure 2. One-minute tows of a 1.83m-wide crab dredge were made at each station. The length of each tow was determined by either

Loran-C or a differential global positioning system (DGPS). All crabs greater than 15

mm carapace width were measured, sexed and enumerated. Additionally,

environmental parameters were measured at each station. Depletion experiments

(Zhang *et al*. 1993; Vølstad *et al*. 2000), in which the same area was dredged

repeatedly, were conducted yearly since 1992 to determine the fraction of blue crabs

sampled by a single dredge tow, i.e., the catchability coefficient (q). Based on these

experiments, an exponential model was used to estimate vessel and year specific

catchability coefficients that were used to transform catch at each station into an

estimate of absolute abundance.

Environmental Variables

Six environmental variables were chosen for consideration in the GAMs based

on availability and known or plausible roles in influencing blue crab distributions.

Depth was measured at each WDS site. The five remaining variables, salinity, water

temperature, distance from the Bay mouth, distance from the nearest submerged

aquatic vegetation (SAV), and bottom slope, were derived using data from other

sources and a geographic information system (GIS).

Although surface salinity and temperature were measured at each WDS site,

the more relevant measurements for describing blue crab winter habitat choice are the

bottom salinity and temperature at the time when they bury into the sediment. For

this reason, temperature and salinity used in this analysis were interpolated from

Chesapeake Bay Water Quality Monitoring Program data (Chesapeake Bay Program

1993). December bottom temperature and salinity maps were produced for each year

using data collected at 99-123 sites per year. The data were first spatially detrended

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in order to satisfy the assumption of first-order stationarity (Cressie 1993).

Detrending was conducted using linear regression and northing, easting, and northing

x easting interaction terms. Variogram modeling and ordinary kriging were

conducted on the residuals before adding the trend back to the kriged predictions.

Gaussian, spherical, and exponential variogram models were fit to empirical

variograms using non-linear least squares (SAS, NLIN procedure) and the best fitting

model (lowest mean squared error) was used for kriging (SAS, KRIGE2D procedure).

Interpolated bottom temperature and salinity were mapped in ArcView v3.2 and maps

from the previous December were used to assign values to each WDS site.

Distance from the Bay mouth was calculated along the shortest through-water

path between the dredge start point and a point in the mouth of the Bay midway

between Cape Henry and Cape Charles. This distance was calculated in ArcView

v3.2 using a customized script based on the lowest-cost path function and a raster

map of the Bay with a resolution of 250 m (see Chapter 2). This variable was chosen

based on a preference by mature females for higher salinity water in the lower Bay

waters where their offspring may be more easily advected off-shore (Johnson 1995).

Distance from SAV was chosen as a potentially important environmental variable

because of known affinities by blue crabs for SAV (Orth et al. 1996) during the

spring and summer and the hypothesis that mature females may choose the nearest

suitable winter habitat. In accord with this hypothesis, SAV distributions from the

previous summer were used, e.g., 1989 SAV distributions were used to predict 1990

(i.e., winter 1989-1990) crab distributions. Distance from the nearest SAV beds was

calculated using maps of annual Chesapeake Bay SAV distributions derived from

aerial photography (Orth et al. 2001). Distance from SAV was calculated as the straight-line distance and was log transformed in order to conform to a normal distribution.

Maps of Chesapeake Bay bottom type are not of sufficient spatial and temporal resolution to allow us to incorporate bottom type directly into our analyses. Accordingly, I used bottom slope as a proxy for benthic habitat type. This approach assumes areas of high slope are likely to be unstable and hence inappropriate overwintering habitat. Bottom slope was calculated from a high-resolution (30m) bathymetric digital elevation layer (National Oceanic and Atmospheric Administration 1998) in ArcView v3.2. Bottom slope was log transformed and multiplied by a factor of 10 in order to conform to a normal distribution on a similar scale as the other environmental variables.

Two-stage Generalized Additive Models

Two-stage GAMs were used to describe the relationship between mature female blue crab density and the six environmental variables. Models were developed independently for each year of data using a randomly selected training subset representing 75% of the data in an individual year (650-1199 stations). The remaining 25% of the data were reserved for cross-validation. In the first stage of the analysis, presence or absence of mature female crabs was modeled using a logistic model with a binomial error distribution and a logit link function. In this stage, the probability of crab occurrence at any site was modeled as an additive function of the six environmental variables (D = water depth (m), M = distance to the Bay mouth

(km), V = distance (km) to SAV beds, S = salinity (ppt), B = bottom slope, and T = water temperature (°C)), given by:

$$\hat{p} = s(D) + s(M) + s(V) + s(S) + s(B) + s(T) \tag{1}$$

where I is the binary response indicating presence or absence in a sample, $\hat{p}$ is the estimated probability that I = 1 (presence), the s's are unique regression spline functions for each environmental variable. Penalized regression splines (Wood & Augustin 2002) were fit using the mgcv (v1.0-9) package for R v1.9.1.

In the second stage of the model, log transformed mature female blue crab density (# $1000m^{-2}$) of only those stations at which at least one mature female crab was caught was modeled as a function of environmental covariates with the assumption of a Gaussian error distribution. The model equation was:

$$\ln(\hat{m}) = s(D) + s(M) + s(V) + s(S) + s(B) + s(T) \tag{2}$$

where $\hat{m}$ is the predicted density of mature female blue crabs given occurrence, and the other variables are as given above. Subsequently, the predicted log abundance, $\ln(\hat{y})$, at a given location was calculated as the product of Stage I and Stage II:

$$\ln(\hat{y}) = \hat{p}\ln(\hat{m}) \tag{3}$$

(Barry & Welsh 2002).

The flexibility of the response curves was optimized using an iterative method that rewards model fit and penalizes degrees of freedom (Wood 2000). This approach avoids the subjectivity inherent in choosing degrees of freedom *a priori* and ensures that the models provide the best fit with the fewest degrees of freedom. An initial full model containing all six variables was simplified by removing insignificant variables (backward elimination) until all remaining variables were significant (a = 0.05). All

possible two-variable interactions using the remaining variables were then added to the model, and the model was again pared down to only significant terms. Non-significant main effect terms (a single response variable with no interaction) were retained, however, if they were also part of a significant interaction. In two instances, the model-fitting algorithm would not converge when the degrees of freedom for an interaction term were not fixed. In these cases, a range of plausible degrees of freedom were given, and the model with the highest adjusted R^2 was selected.

Model fit, Cross-validation, and Mapping

Receiver operating characteristic (ROC) curves were used to assess the fit and generality of stage I (presence/absence) models. Although ROC curves are commonly used to assess logistic regression models (Hosmer and Lemeshow 2000) and have been used to assess habitat models developed through logistic regression (e.g., Bonn & Schroder 2001, Scholten et. al. 2003, Gibson et al. 2004), they can also be applied to any model that produces estimates of p (the probability of presence) for a binomially distributed response variable. ROC curves are simply a plot of sensitivity (the fraction of correctly predicted presences) against specificity (the fraction of correctly predicted absences) with changing critical values of p (p_{crit}, the probability above which presence is predicted). An ROC curve for a model with no discriminatory power is simply a straight line with a slope of one, i.e., as p_{crit} changes, any increase in sensitivity is offset by an equivalent loss of specificity. ROC curves are used here to calculate the area under the ROC curve (AUC, a measure of discriminatory power), p_{opt} (the value of p which results in the highest percentage of correct predictions), and p_{fair} (the value of p for which sensitivity and specificity are

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equal). AUC is a threshold-independent (i.e., it does not depend on a specified p_{crit})
summary statistic that ranges from 0 (no discriminatory power) to 1 (perfect
discriminatory power) and has been previously used to assess the generality of
logistic regression-based habitat models (Bonn & Schroder 2001). Although criteria
for evaluating AUC values are to some extent arbitrary, Hosmer and Lemeshow
(2000) suggest the following cut-offs: 0.7-0.8 acceptable, 0.8-0.9 excellent, >0.9
outstanding.

Cross-validation was also used to assess the transferability of the combined
models (the product of stage I and stage II) fit to training datasets to a separate test
data set from the same year (i.e., intra-annual cross-validation) or to data from
another year (i.e., inter-annual cross-validation). The predictive ability of each
combined model was assessed by regressing predicted values on the observed values.
The resulting least-squares correlation coefficient was used as an index of model
performance. Two hypotheses were tested:

1) Models fit to a training data set perform better (i.e. higher r) on the training data
than on independent test data from the same year.

2) Models perform better in intra-annual cross-validation than when applied to data
from other years (inter-annual cross validation).

To test these hypotheses, the Fisher (1915) transformation was used to
normalize the cross-validation correlation coefficients (r). The first hypothesis was
tested using a paired t-test of the transformed correlation coefficients and the second
was tested using a t-test for two samples with equal variance. To aid interpretation of
the results of the cross-validation analyses all individual models were compared to the

grand mean (including inter- and intra-annual) cross-validation r. I calculated standardized normal deviates:

$$z = \frac{\left(r_{i,j} - \bar{r}\right)}{s}$$

where $r_{i,j}$ is the Fisher (1915) transformed coefficient of determination for predictions from the model year i, applied to observed year j, $\bar{r}$ is the grand mean, and s the sample standard deviation of $\bar{r}$

In order to visualize predicted mature female blue crab distributions, predictions from the most general model (i.e., the model with the highest mean cross-validation r-squared value), were mapped for stage I, stage II, and the combined model. Predictions were made for 1 km by 1 km grid cells based on the values of the predictor variables for each cell. Values of the dynamic predictor variables (temperature, salinity, and distance from SAV) used in mapping were the values within each grid cell for the summer (distance from SAV) or December (temperature and salinity) preceding the most general model.

Results

Model Development

Significant correlations were present between many pairs of explanatory variables (Table 5). Most notably, there was a strong and negative correlation (r = -0.64) between salinity and distance from the Bay mouth. Moderately strong correlations occurred between salinity and temperature (r = 0.34), and between depth and bottom slope (r = 0.28). Although the correlations among the explanatory

variables were often statistically significant, even the two most strongly correlated variables (salinity and distance from the Bay mouth) do not overlap entirely as salinity patterns are strongly influenced by freshwater flow from the western shore tributaries, which, combined with the Coriolis effect, results in a pattern of lower salinities in the eastern Bay. Colinearity among the explanatory variables was not deemed sufficient to drop variables from the full models, but will be considered in the interpretation of model selection results.

All six explanatory variables were included as either significant main effects or in interaction terms in at least three of the final models, however, no variable occurred in all models (Table 6). Distance from Bay mouth and depth were the most commonly included variables. In stage I, distance from the Bay mouth was significant in 9 out of 13 years and depth was significant in all years. Distance from Bay mouth appeared in 10 out of 13 years for stage II models, while depth was included in 5 stage II models. Water temperature also appeared commonly in stage I, occurring in 9 out of 13 years, but was only found to be significant in 2 of the stage II models. Salinity was included in 8 years for stage I and in 2 years for stage II. Importantly, salinity was often included in stage I models when distance from the Bay mouth was not. The remaining two variables, bottom slope and distance from SAV, were not often found to be significant in either model stage.

Penalized regression spline fits of individual environmental factors to blue crab density varied from simple linear functions to highly complex curves. Response curves are presented for the most commonly included variables, distance from the Bay mouth (Figure 33), salinity (Figure 34), depth (Figure 35), and temperature

(Figure 36), for all years in which they were included as significant main effect terms only, i.e., not in interaction.

Relationships between crab distribution and abundance and distance from the Bay mouth showed two dominant patterns. A linear decline in crab density with increasing distance from the Bay mouth was seen in four of the seven Stage II models examined (Figure 33, panels d, e, j, and l). The second pattern, a maximum at approximately 25-50 km, was observed in two Stage I (Figure 33, panels b and c) and two Stage II models (Figure 33, panels j and h). The shape of these response curves at greater distances from the Bay mouth was highly variable, reflecting the relatively rare catch of mature female blue crabs in the upper Bay, and some curves (Figure 33, panels c, f, g, and k) suggest that the decline in crab density may level off beyond 100 km from the Bay mouth.

Response curves for salinities below 15-20 ppt were characterized by lower probabilities of presence and lower abundance given presence as well as extreme variability due to the smaller number of samples at low salinity. Some curves (Figure 34, panels a, e, and f) showed a maximum or a leveling off at approximately 25 ppt.

The relationship between crab abundance and depth showed a general increase in both probability of crab presence and in density given presence as depth increases. Within this generally positive trend, a maximum (Figure 35, panels a and e) or a leveling off of the curve (Figure 35, panels c, d, and h) was frequently observed at approximately 15-20 m.

Differences were apparent between the Stage I and Stage II response curves for temperature. Stage I curves (Figure 36, panels a - f) showed a generally negative

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relationship between temperature and the probability of crab presence while Stage II curves (Figure 36, panels g and h) both indicate a positive relationship between temperature and crab density given presence. Substantial interannual differences in December bottom temperatures, however, make it difficult to compare models for which, in some cases, the temperature ranges do not overlap.

Model Fit, Cross-validation, and Mapping

I used the models developed on the training data in a single year to predict crab abundance for the test data for that year, and for the entire datasets for alternative years (Table 7). Two-stage GAMs developed using the six habitat variables included in this study explained between 13% and 36% (mean $R^2 = 0.277$) of the variability in blue crab winter densities in the training data set (Table 7a). WDS samples were characterized by a large percentage (80-90%) of observations containing no mature female blue crabs, as well as a small number of very high-density samples. The two-stage models generally predicted realistic densities but underestimated the observed variability. For example, predicted log densities from the 1998 two-stage model showed a similar mean as the survey observations, with the linear regression of observed vs. predicted falling nearly coincident with the one-to-one line, but showed lower variability, i.e., fewer low- or zero-density predictions and a lower range of predicted values (Figure 37). Observed densities show a notable gap between tows with zero catches and the lowest predicted densities.

The mean R^2 for the intra-annual comparison was 0.192. Results for the intra-annual cross-validation showed that there was a significant difference in model

performance between test data and training data (paired t-test, p = 0.002). The inter-annual cross-validation displayed substantial variation among years and was significantly less accurate than the intra-annual cross-validation (t-test, p < 0.001).

The cross-validation table (Table 7b) represents the ability of a model developed with data from one year (columns) to predict data from other years (rows), and it displays two different but related pieces of information. Examining the patterns within a column evaluates the characteristics of one model. Patterns within a row relate to the characteristics of a particular data set.

The column patterns show that apart from 1990 and 2001 all models yielded above average r values for at least four other years of data. This suggests that the models, though they differ in their individual parameters, do capture some general features of the blue crab habitat preference. The 1998 model displayed above average cross-validation r values for all years except 1990, 1995, and 2002. The other striking feature of the column patterns is that the 1990 and 2001 models yield below average r values for nearly all data sets except test data from the same year.

The row patterns offer further information about inter-annual differences. The year 1990 is well predicted (i.e. above average r) only by the model from the same year. The data for 1995 is simply difficult to predict with any model. The 1994 data are well predicted by models from any year other than 1990, 1997, or 2001.

Stage I (presence/absence) models were evaluated using ROC curves to assess model fit (Table 8a) and generality (Table 8b). The percent of correct predictions for models applied to the training data varied from 82-93% at p_{opt} and from 74-85% at p_{fair}. The AUC for the training data varied from 0.81 to 0.91. These levels are

equivalent to Hosmer and Lemeshow's (2000) excellent rating. AUC values were generally lower for the cross-validation where models developed with data from one year were applied to data from another year; however, all models displayed acceptable discriminatory power (AUC > 0.7) for at least four other years. The stage I models from 1997 and 1998 were the most general with AUC > 0.7 for all years other than 1995. The 1995 data were well predicted only by stage I models from 1994 and 1995.

Predictions from the stage I (Figure 38a), stage II (Figure 38b), and combined (Figure 38c) models were mapped for the 1998 model since this year exhibited the greatest generality for both stage I and the combined model. Critical p-values used for classifying the stage I map were $p_{fair} = 0.15$ and $p_{opt} = 0.455$. Of the samples in the 1998 training data that contained one or more mature female blue crabs, 77% occurred within the shaded areas of Figure 38a, and 40% occurred within the dark shaded area. Much of the mainstem Bay south of the Rappahannock River is shaded indicating higher probability of blue crab presence. North of the Rappahannock River, shaded areas are generally restricted to the deeper mainstem channels and the channel in Tangier Sound.

Patterns of predicted density given presence (conditional density) shown in Figure 38b are broadly similar to patterns in probability of occurrence. Higher conditional densities are predicted in the lower Bay mainstem and in deeper channels throughout the Bay. The higher conditional densities predicted in the upper reaches of western shore tributaries are not found in the stage I model and are apparently extrapolations of the salinity effect beyond the range of sampled salinities.

The combined model (Figure 38c) is derived from raster multiplication of Figures 38a and 38b and reflects the influence of both model stages. Highest predicted densities are found in the lower Bay mainstem and deep channels. The high conditional densities predicted in stage II for the upper reaches of western shore tributaries are largely nullified by the low probability of crab presence predicted for these areas in stage I.

Discussion

The spatial pattern of winter distribution and abundance of mature female blue crabs in Chesapeake Bay were significantly related to several environmental factors over thirteen years. Depth and distance from the Bay mouth (and their interaction) were the dominant variables for predicting both presence/absence and abundance of mature female blue crab. Increased depth was associated with increased probability of finding crabs and increased crab abundance where they were present. Although greater depths are generally associated with lower Bay waters, depth may also have a direct effect on habitat suitability by providing some protection against rapid temperature changes due to changing air temperature.

Probability of crab presence and crab abundance generally decreased with distance from Bay mouth, although in some years a maximum was discernible at 25-50km from the Bay mouth. The correlation between distance from the Bay mouth and other environmental variables, salinity in particular, makes it difficult to determine what, if any, direct influence distance from the Bay mouth could have on blue crabs. However, mature female blue crabs both spawn and overwinter in the lower Bay, and it is likely that effective offshore transport of newly hatched crab

larvae is dependent on their release location within the Bay. The role of distance

from the Bay mouth in explaining abundance of mature female blue crab may be

related to selection for optimum larval transport conditions or a balance between

conditions favoring higher survival and those favoring reproductive success.

Salinity and temperature were also frequently found to be significant factors

in determining crab distributions, although perhaps not as often as might be expected

given the demonstrated effects of salinity and temperature on the bioenergetics

(Guerin & Stickle 1992, Brylawski & Miller 2003), growth (Tagatz 1968, Smith

1997), and survival (Tagatz 1969) of blue crabs in the laboratory. Higher salinities

were associated with higher probability of blue crab presence and higher density

given presence, with a maximum of 25 ppt observed in some years. Females

migrating from the upper Chesapeake Bay likely do not spawn until the season after

mating (Turner et al. 2003), however there are potential advantages to overwintering

in the lower Bay. Although adult females tolerate a wide range of salinities, they may

be less efficient osmoregulators at lower salinity (Tan and Van Engel 1966), and may

be less tolerant of extreme temperatures at low salinity (Tagatz 1969). Laboratory

studies have demonstrated that blue crab respiration increases at decreasing salinity

(Engel and Eggert 1974, Guerin and Stickle 1992), thus overwintering in high salinity

waters may allow females to conserve energy.

Higher temperatures were associated with a lower probability of crab

presence, but higher density given presence. Blue crabs may be expected to have

conflicting demands regarding temperature. Mortality rates increase sharply below

5°C (L. Bauer, pers. obs.), but respiration and metabolic costs begin to increase

rapidly above approximately 15°C (Brylawski & Miller 2003). Still, it is unclear why the direction of the temperature response should vary between stage I and stage II models.

Response curves of the two remaining variables are complex and do not coincide with simple biological explanations. Bottom slope and distance from SAV showed little ability to explain crab distributions or abundance. Even when these variables were determined to be significant, the response curves were highly variable and no support was provided for the hypothesis that lower slope and shorter distance from SAV represent preferred winter habitat. Such year-to-year variability in response curves may indicate that relationships to some habitat parameters are complex and dynamic or may change with changes in population size. It is also likely that some spurious relationships may be found to be significant when fitting 26 separate models.

Although correlation among environmental parameters is likely the norm rather than the exception, such dependencies must be considered when evaluating model selection results. For example, a strong correlation exists between salinity and distance from the Bay mouth. As a result, although both variables were common in the final models, it was relatively unusual for both to be included in the same model. Although efforts were made to make all variables equally likely to enter into the model (e.g., by transforming non-normally distributed variables and rescaling some variables so that all were of the same magnitude), inherent differences in variability and measurement error are still likely to influence model selection. As Håkanson and Peters (1995) have pointed out, if two environmental parameters are equally related to

a response, it is the parameter with lower variability and lower measurement error that is most likely to be selected. In this case, the static variables, depth and distance from the Bay mouth have an advantage in that they can be measured with little error and they do not change over time. Even if individual crabs are selecting an overwintering location based on temperature and salinity at the time of burying, depth and distance from the Bay mouth may be more powerful predictors of distributions, despite not being the proximate cue, to the extent that they integrate information about salinity and temperature over the period during which crabs are selecting an overwinter location. Such questions cannot be resolved through an empirical habitat modeling approach.

Despite the highly flexible modeling process and the inclusion of interactions among parameters, the full two-stage GAMs explained only a fraction (13-36% when applied to the training data) of the variability in crab abundance. In addition, the two most important variables, depth and distance from the Bay mouth, are spatially static and thus cannot explain interannual changes in distribution patterns. Either there exist other important environmental determinants of crab distributions than those explored here or, although habitat affinities clearly exist, as evidenced by the consistent significance of some of the environmental parameters, much of the observed variability in distribution patterns is not the result of habitat selection. If other environmental factors are guiding habitat selection, it is unclear what those factors may be. Although hypoxia is prevalent in deeper Bay waters in the summer, winter dissolved oxygen levels are sufficient for blue crabs in even the deepest Bay waters (Wang et al. 2001). Better benthic habitat maps would allow us to fully test for the

influence of bottom type; however, I suggest that the inclusion of different environmental indices would lead to only incremental rather than wholesale improvements in model fit. I conclude that variability in the winter distribution of mature female blue crab is primarily due to factors other than habitat such as the timing of the onset of cold weather and density-dependent habitat selection (discussed below).

Although blue crab density was difficult to predict, the broader question of determining whether a given habitat is likely to contain blue crabs or not proved more tractable. Stage I (presence/absence) models showed considerable ability to discriminate between suitable and unsuitable habitat with approximately 75-80% correct predictions at p_{fair}. The discriminatory power of the stage I models was also maintained when applied to other years with an average AUC of 0.71. Indeed, the most general stage I model, the 1998 model, yielded an AUC greater than 0.7 for all but one of the other years indicating that it provides broadly applicable predictions which could be useful for management purposes. Furthermore, the probability map for the 1998 stage I model confirms observations that mature female blue crab catch per unit effort (CPUE) is higher in deep water (Lipcius et al. 2001) and in the lower Bay but also predicts relatively high probabilities of occurrence in some of the deeper channels of the middle and upper Bay and Tangier Sound. Mature females are found in WDS samples at these middle and upper Bay locations, but it is unclear whether these individuals represent crabs that failed to complete their migration to the lower Bay, as suggested by Turner et al. (2003), or if these deep middle and upper Bay channels also represent preferred overwintering habitat. One of the component

variables of the 1998 stage I model is the dynamic variable, temperature. To the extent that temperature patterns vary from year to year, the predictions of the model are also likely to shift giving the model the ability to adapt its predictions to changing environmental conditions.

The use of a GIS in combination with habitat suitability models has become widespread as a method of visualizing and mapping the results of habitat modeling (Stoner et al. 2001), as a qualitative test of habitat model output (Zheng et al. 2002), and as a tool for measuring variables that were not or could not be measured in the field (Brown et al. 2000, Clark et al. 2003). Variables such as slope, bathymetric variance, and distance from a particular point or habitat type may provide important information about habitat suitability, but cannot be easily measured in the field. In this study, three of the GIS-derived variables (through-water distance from the Bay mouth, salinity and temperature) were found to be important factors for predicting distributions while the other two (bottom slope and distance from SAV) were not. The ease with which such GIS-derived variables can be calculated and tested for predictive ability makes this an appealing method for exploring potential habitat suitability factors. Maps derived from such GIS-based habitat models may be useful for locating marine protected areas and dispersal corridors, which, for blue crab in Chesapeake Bay, are currently based simply on observations of higher concentrations of adult females at greater depths (Lipcius et al. 2001) as well as non-biological concerns such as enforceability.

The cross-validation confirmed the ability of GAMs to describe general patterns, but provides a warning against naïve application of models to predict

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distributions in other years. Although the mean inter-annual cross-validation R^2 value (0.101) was significantly lower than that for the intra-annual comparison (0.192), most models provided above average fits to several other data sets, and the best model provided above average predictions for 10 out of 13 other years. The failures of model generality were confined primarily to two or three years. The data for 1990 are a good example. Despite the fact that the 1990 model showed a slightly above average fit to the training data ($R^2 = 0.299$), the 1990 data were poorly predicted in inter-annual cross-validation with R^2 values below average for all comparisons. The intra-annual cross-validation R^2, however, was approximately average. Similarly, the 2001 model showed the best fit of any model to the training data ($R^2 = 0.360$) and well above average intra-annual cross-validation, yet displayed poor generality with below average inter-annual cross-validation R^2 values for all comparisons. This indicates that although the strength of the response to habitat variables in 1990 and 2001 was normal, the details of that response were different than those observed in most other years. The explanation appears to lie in the unusually early and severe winters of 1989-1990 and 2000-2001, which had the two lowest average December temperatures observed over the 13 years of the survey. Thus, hypotheses or management actions developed from habitat-models based on 1990 or 2001 data would likely not be applicable to other years. However, there was no reason *a priori* to anticipate this lack of generality from the model fits or intra-annual cross-validations. Accordingly, I caution against the application of habitat models based on a single year of data without adequate inter-annual cross-validation.

Although models were generally transferable, some years consistently defied prediction by models developed from other years' data. The data from 1995, for example, were poorly predicted by all models and had the poorest observed fit to the training data. The relationships between blue crabs and their habitat in 1995 appear to be weak or highly variable as all models fit poorly to data from this year. Despite this high variability in 1995, the mean response to environmental variables in this year appears to have been fairly typical as the 1995 model displayed above average prediction accuracy when applied to 4 other years of data.

Some of the interannual variation in the models and their cross-validation performance is likely related to the date of onset of cold weather and the severity of the winter. As ectotherms, blue crabs are restricted in their level of activity by ambient temperatures. Early onset of cold weather is thought to result in an arrested migration that may strand individual blue crabs in sub-optimal habitat. Consequently, the earlier the onset of cold weather, the less likely observed distributions reflect true habitat preference. Prolonged periods of cold weather also appear to increase the amount of winter mortality (Sharov et al. 2003). To the extent that crabs concentrate in areas where overwinter survival is higher, severe winters may highlight the expression of existing habitat affinities by preferentially removing individuals that stray from optimal habitat. Conversely, severe winters are likely to obscure the consequences of habitat choice based on factors other than survival, for example, spawning success.

Density dependent changes in habitat use offer an intriguing alternative explanation for inter-annual differences. MacCall's (1990) basin model predicts that

at low population density all individuals will concentrate in the preferred habitats. As population density increases, the preferred habitats become full and individuals are forced to seek out alternative sub-optimal sites. Over the 13 years of the winter dredge survey, estimates of bay-wide mature female abundance show a more than four-fold variation from a high of 182 million in 1991 to a low of 41 million in 2001. These observed changes in abundance are significantly correlated with changes in the location of the center of mass of blue crab distributions (see Chapter 3).

Despite inter-annual variation and the existence of non-habitat related influences, a GAM approach offers unique insights into the factors determining winter distributions of mature female blue crabs. Environmental factors were considered not in isolation, but simultaneously and in interaction. The value of the GAM approach is that, from this collection of intercorrelated variables, it was possible to discern general patterns that persisted from year to year and to identify depth and the distance from the Bay mouth as the two most important environmental determinants of winter habitat. The details of these relationships and formal hypothesis tests for individual factors are more appropriately the domain of other methods.

GAMs have become widely recognized as an important tool for understanding species distributions (reviewed in Guisan et al. (2002)) because they effectively address many of the statistical challenges (e.g. non-linear responses, complex interactions, and counts that are zero-inflated or otherwise problematic in their distribution) associated with field survey data. One of the concerns with using such a flexible approach is that better model fit might come at the expense of generality.

Although some applications of GAMs have successfully addressed concerns

regarding generality by dividing large data sets into different years and analyzing

them separately (e.g. Begg & Marteinsdottir 2002) or including a year term (e.g.

Maravelias et al. 2000b) in the model, and one has used inter-annual cross-validation

to compare two separate model years (Forney 2000), this is the first systematic test of

GAM habitat model generality. Interannual differences in the structure of models,

together with their performance in cross-validation trials, underscore the importance

of having more than a single year "snapshot." Although most models performed well

in cross-validation, a few years were different enough from the general pattern that

they resulted in models with little ability to predict distributions in other years. Such

aberrant years can provide unique insights (in this case, suggesting the importance of

the timing of cold weather) and, with multiple years of data, they can be identified

and effectively dealt with. In the absence of sufficient temporal scope to the data,

however, habitat suitability models may be misleading.

Chapter 5: Conclusion

<u>Introduction</u>

The goal of this thesis is to describe the winter distribution of blue crab in Chesapeake Bay and to examine the factors responsible for the observed patterns. Three objectives (corresponding to the three central chapters of this thesis) were identified and met:

1) Develop and evaluate an alternative to Euclidean distance for use in geostatistical models.

2) Quantify the abundance and winter distribution of blue crab in Chesapeake Bay and determine the extent to which density-dependent factors control its distribution.

3) Describe the relationship between abiotic variables and the winter distribution of mature female blue crab in Chesapeake Bay.

<u>Objective 1</u>

The first objective of this thesis (Chapter 2) involved the development of an appropriate distance metric for blue crab in Chesapeake Bay, the incorporation of this metric into an algorithm for variogram calculation and kriging, and the comparison of the predictions from this method to those of standard geostatistical methods. Though ultimately unsuccessful in consistently improving prediction accuracy for blue crab in Chesapeake Bay, the Lowest Cost Path (LCP) distance metric represents a simple and

general solution to applying geostatistical methods in the presence of landscape barriers and may yield improvements in prediction accuracy when applied to other variables or other geographic settings. The reasons for the failure of this method to improve prediction accuracy are unclear, but likely involve the particular geography of Chesapeake Bay – strong gradients along parallel tributaries. The significant differences in variogram parameters between the LCP metric and the standard Euclidean metric are reason enough to use this approach when an accurate description of the spatial autocorrelation structure in the presence of barriers is all that is desired. This paradox - the fact that variograms changed significantly but prediction accuracy did not - further suggests that Euclidean distance provides some useful information despite the fact that it is intuitively the "wrong" metric to use when barriers are present. Defining the circumstances under which a landscape-based distance metric such as LCP is appropriate will require further investigation in different settings and in the same setting with different variables. The extent to which the LCP metric can improve other spatial analytical techniques such as home range estimation and habitat modeling remains an open and interesting question.

Other attempts to use landscape-based distance metrics for kriging in estuaries have met with similarly mixed results. Little *et al*. (1997) used a linear network approach to calculating shortest paths through the water in Murrells Inlet, SC in order to predict concentrations of contaminants in the water and in oyster tissues. They found improvements in prediction accuracy when "in-water" distance was used for four of the eight variables, but small decreases in prediction accuracy for the other four. There was no attempt to explain the characteristics that might determine

whether a variable would show improved accuracy with the alternative metric. The

linear network approach used by Little *et al*. (1997) is computationally efficient for

geographic areas that resemble linear networks, i.e. where the width of traversable

habitat is negligible compared to the length, and has been used successfully by other

researchers (Gardner *et al*. 2003; Torgersen *et al. In press*). It becomes increasingly

awkward and inefficient in open areas where connectivity is possible in all directions.

In geographic areas containing open areas as well as barriers, an alternative

approach to calculating distances is required. Rathbun (1998) offers one such

approach and applied it to model salinity and dissolved oxygen (DO) in Charleston

Harbor, SC. The landscape-based distance metric resulted in small improvements in

prediction accuracy for DO but slight decreases in accuracy for salinity. Although

this landscape-based metric is applicable in open regions as well as narrow linear

areas, it relies on a FORTRAN program that is not as easily transferred to other

geographic areas as the GIS-based approach used here. Rathbun's (1998) method is

also unable to account for variable permeability of different types of barriers, an

advantage of the LCP metric that must be explored further.

Objective 2

The second objective of this thesis involved quantifying patterns of blue crab

winter distribution in Chesapeake Bay and examining the internal population factors

that may be responsible for changes in these patterns. Although the baywide

abundance estimates calculated using a geostatistical approach differ substantially

from design-based estimates in the first two years of the winter dredge survey (WDS),

similar downward trends in abundance are apparent in both time-series over the 13 years of the survey. The traditional design-based analysis of the WDS fails to incorporate valuable information on spatial autocorrelation structure and may not be the most accurate method of estimating baywide abundance from this survey. The accuracy of geostatistical methods could be enhanced by simple changes to the station allocation methods. For example, one source of uncertainty in the abundance estimates is the lack of stations in some years at the extremes of the blue crab's winter distribution in the northernmost part of the mainstem and the upper part of the Potomac River. Geostatistical estimates could be improved without compromising the historical continuity of the survey by adding a few non-random stations at the edges of the distribution. Both estimation methods would be improved by reducing the zero-inflation in the data. Longer tows would reduce the number of tows with no crabs, but would require re-evaluation of the catchability coefficients. Accurate calculation of tow length is critical for calculating densities based on the area-swept method, and the survey would benefit from adopting the most precise and accurate georeferencing methods available. This is particularly important given the extremely short tows where small absolute errors in position can have a large proportional impact on the estimated tow length and consequently the estimated density.

The sharp declines in blue crab abundance coupled with high fishing mortality rates (Sharov *et al*. 2003; Rugolo *et al*. 1998) suggest that overfishing is occurring and management action is needed to reverse the decline. Sharov *et al*. (2003) calculated fishing mortality rates for the period 1990 – 1999 that were generally higher than $F_{max} = 0.64$ (Rugolo *et al*. 1998) but, except in 1999, lower than

the threshold fishing mortality rate adopted by the Bi-state Blue Crab Advisory

Committee (Anonymous 2001) of $F_{10\%} = 1.08$ year^{-1} (Miller and Houde 1998).

Spatial management strategies such as marine protected areas and time-area closures

are increasingly being used to increase biodiversity and reduce fishing mortality rates

on vulnerable segments of the population (Halpern 2003). The lower bay spawning

sanctuary is one such spatial strategy currently used with some success in the

Chesapeake Bay blue crab fishery (Lipcius *et al.* 2003) but it offers protection to blue

crabs only during the summer months.

The distributional maps developed in Chapter 3 of this thesis could be used to

designate specific winter closed areas that are small (making them easier to enforce

and more politically feasible) but effective at protecting the spawning stock during its

winter aggregations. These maps may also be useful for limiting the impact of

management actions that may have an adverse effect on blue crab winter habitat. For

example, these distribution maps have already been incorporated into the Chesapeake

Bay dredged material disposal and beneficial use management process. Finally, the

maps may be useful as an input to other modeling efforts. For example, spatial multi-

species trophic models such as EcoPath with EcoSpace (Walters *et al.* 1999) require

detailed information on the distribution (or at least habitat preferences) of component

species.

From an ecological point of view, the distributional maps are more interesting

not as static snapshots, but for the insights they provide into the dynamic processes

that may drive blue crab distributions over a nearly four-fold change in density. The

evidence for an intra-specific explanation (density-dependent habitat selection

(DDHS)) for the observed changes in distribution was examined. One line of evidence implicates DDHS, and another suggests that the relationship between density and patch size may be more complicated than hypothesized. The fact that changes in the location of the centroid of blue crab density are highly correlated with baywide abundance suggests that DDHS may exist in blue crabs. Changes in the range of spatial autocorrelation, however, were not positively correlated with baywide abundance. For mature females, and to a lesser extent for males and immature females, the deep waters of the lower Bay mainstem provide ideal overwintering habitat. A southward trend in the centroid as baywide abundance decreases can be interpreted as a density-dependent contraction of the overwintering distribution toward the most favorable habitat. The trend map supports this interpretation since relatively little of the lower Bay shows a negative trend in density.

The lack of any apparent relationship between the effective range of spatial autocorrelation and blue crab abundance suggests that either: 1) the range is not a suitable proxy for patch size; or 2) patch size is not related to baywide abundance. There is evidence for both of these alternative explanations. Although the range parameter of variograms is frequently assumed to be an estimate of patch size, this relationship has yet to be rigorously tested. The range is likely influenced not only by patch size, but also by other characteristics of a spatial distribution such as distance between patches and patch shape. The survey design may also have precluded accurate estimation of patch size. Smaller scale patchiness – on the order of tens to hundreds of meters – is likely to be missed since the distance between adjacent samples is generally too great to accurately represent small patches. Alternatively,

the assumption that DDHS would result in larger patches may be wrong. Suboptimal habitat patches may become suitable as densities increase within optimum patches, resulting in more, but not necessarily larger, patches of blue crabs.

Comparison with winter dredge fishery CPUE suggests that geostatistical methods may provide a more accurate description of fluctuations in abundance and, consequently, that declines in blue crab abundance may be greater than previously believed. Maps of blue crab density provide a guide to spatial management strategies and a method of evaluating their potential impacts. Observed relationships between abundance and distribution patterns are consistent with DDHS. Alternative explanations for these patterns exist, however, and only controlled experiments could show conclusively whether blue crabs exhibit DDHS.

Objective 3

External abiotic variables such as salinity, temperature, and depth are also likely to play a part in determining the winter distribution of blue crab in Chesapeake Bay. Their influence on mature females was the subject of Chapter 4. Mature females have long been known to differ from males and immature females in many aspects of their life history (Van Engel 1958). They are also thought to have the most specific winter habitat preferences, as they undergo long migrations from their summer habitat throughout the Bay to their spawning and overwintering habitat in the deep high-salinity waters of the lower Bay (Hines *et al*. 1995; McConaugha 1995). How strong a role does habitat play in determining where mature females overwinter?

What constitutes ideal winter habitat for mature females? And does this definition of ideal habitat vary from year to year?

The answer to the first question is that although some habitat variables (most notably depth and distance from the Bay mouth) are consistent and statistically significant predictors of mature female abundance, combined, they explain only 13-36% of the observed variation in abundance in the training data set. Although the possibility remains that other unknown habitat variables could improve the predictions, the results of this thesis suggest that habitat is an important but not decisive determinant of where mature females overwinter. Other non-habitat related factors that may influence distributions include DDHS (discussed in Chapter 3), and the time at which water temperatures drop below the critical threshold for dormancy. This latter explanation is discussed in Chapter 4 in relation to the failure of the 1990 and 2001 models to accurately predict abundances in other years. It may be that mature female blue crabs set off on their winter migrations in response to an unknown environmental cue. Some of them reach ideal habitat while others are arrested in their migration by a drop in temperature forcing them to overwinter in less than ideal habitat. This hypothesis is consistent with the fact that the winters of 1989-1990 and 2000-2001 saw the two lowest December temperatures on record over the 13-year history of the WDS.

Ideal overwintering habitat for mature female blue crabs in Chesapeake Bay appears to be defined by a combination of depth, distance from the Bay mouth, and to a lesser extent, salinity and temperature. The first two factors, both individually and in interaction, were found to be significant predictors of blue crab presence or

absence in all years and of abundance given presence in many years. Crabs were more likely to be found and were more numerous when they were found as depth increased. In some years, there was evidence of a peak at around 15-20 m, but in others the relationship appeared linear. Probabilities of crab presence and abundance given presence were highest near the Bay mouth, though in some years the maximum occurred at approximately 25-50 km from the mouth.

Although prediction accuracy was significantly lower when models developed on data from one year were used to predict abundance in another, the failures (i.e., comparisons showing below average cross-validation R^2) were confined to a couple of non-representative years (such as 1990 and 2001 mentioned above). This pattern is consistent with the hypothesis that habitat preferences are stable but in some years the early onset of cold weather prevents many crabs from reaching ideal habitat. It also highlights the potential to be misled by single-year snapshots of the distribution of any mobile organism.

The results of Chapter 4 confirm the ability of two-stage GAMs to describe general habitat relationships that are valid beyond the particular data set on which they were developed. Because of their flexibility, GAMs are fast becoming the method of choice for empirical modeling of the relationship between the distribution of organisms and the distribution of habitat variables (Guisan *et al*. 2002). Their flexibility, however, has raised concerns that they may fit the input data so specifically that their generality and transferability are compromised. Few previous habitat modeling studies have had sufficient data to test this concern (but see Forney 2000). Here the transferability of GAMs (both intra- and inter-annually) was

confirmed with the caveat that the models are only as general as their input data is representative.

Conclusion

Blue crab winter distributions in Chesapeake Bay are dynamic and are likely driven by a complex interaction of intrinsic (i.e., density-dependent) and environmental factors coupled with a good deal of chance (e.g., the timing of the onset of cold weather).   Despite this complexity, strong relationships are apparent. The bulk of the blue crab distribution has clearly moved southward over the 13 years of the WDS concurrently with a significant decline in baywide abundance. Environmental variables, most notably depth and distance from the Bay mouth, have a significant effect on mature female blue crab distributions in all years.

These findings have implications for the management and ecology of blue crab. The significant decline in abundance suggests that stronger management actions should be taken to ensure the long-term stability of the fishery. The distribution maps developed here provide a useful tool for guiding these management actions. Theories of DDHS are intuitively appealing, but little evidence exists to show whether they apply to natural populations. The correlation between the latitude of the centroid of blue crab density and abundance suggests that DDHS may apply to blue crab.

In addition to insights on blue crab ecology, this thesis also advances the use of two statistical techniques: geostatistics and generalized additive models. Although landscape-based distance metrics have been used in geostatistics before, the methods

used previously to calculate such metrics have not been as flexible, efficient or transferable as the GIS-based LCP metric presented here. The long-term utility of this approach will depend on a better understanding of the conditions under which a landscape-based distance metric can improve prediction accuracy. Likewise, two-stage GAMs have been used to model organism/habitat relationships before, but they have not been rigorously cross-validated to insure that their predictions are general and transferable.

The results of this thesis suggest three lines of future work. First, modest changes to the WDS could improve the prediction accuracy of geostatistical methods without compromising the historical continuity of the data. Second, further investigation into the density-dependence of blue crab distributions may confirm the applicability of DDHS models. Third, analysis of other variables in Chesapeake Bay or other regions with many barriers using the LCP-distance based geostatistical tools developed here could determine the conditions under which the use of such techniques is warranted.

Appendix I – Matlab Functions

1) – PRESSkrige, used to calculate the Prediction Error Sum of Squares (PRESS) statistic

```
function [Result]=PRESSkrige(ID,var,krig_para,model,model_para,dist1_1)
% function [Result]=PRESSkrige(ID,var,krig_para,model,model_para,dist1_1)
% Calculates the Prediction Error Sum of Squares (PRESS) statistic
% Input Parameters:
% ID - A unique identifier for each sample
% var - the measured value of the sample
% neighborhood parameters:
% krig_para(1,1) - maximum search radius for kriging
% krig_para(1,2) - minimum number of neighboring data points used for kriging
% krig_para(1,3) - maximum number of neighboring data points used for kriging
% variogram parameters:
% model - variogram model type: 1=spherical, 2=exponential, 3=Gaussian, 4=linear
% model_para(1,1) - nugget
% model_para(1,2) - sill, i.e. nugget + partial sill
% model_para(1,3) - range
% model_para(1,4) - power for exponential (if applicable, otherwise set to 1)
% model_para(1,5) - length scale for hole effect (if applicable, otherwise set to 1)
%
% Other functions called:
%
% variogrammodel - calculates semivariance for given lag distances
% Author: D. Marcotte
%
% sum_nan - sums a vector or matrix ignoring NaN values
% Author: Jim Ledwell, 10/97 Woods Hole Oceanographic Institution
%
% By Olaf Jensen, University of Maryland Center for Environmental Science,
% Chesapeake Biological Laboratory
% Last modification  June 17, 2004
% Based on original code by Dezhang Chu, Woods Hole Oceanographic Institution

range=krig_para(1);
kmin=krig_para(2);
kmax=krig_para(3);
EPS=2^(-52);

n=length(var);          % n = number of data points
kn=length(krig_para);
var=reshape(var,n,1);   % ensure var is a column vector
model_type=2; % variogram
```

```matlab
tp=ones(n,1); %pre-allocate prediction vector

% Kriging

for j=1:n

  r=dist1_1(j,:);

  if kmin >= n
    indx_sort=1:n;
    k=1:n;nk=n;
  else
    [r_sort, indx_sort]=sort(r);
    ind=find(r_sort <= range);
    nd=length(ind);
    if isempty(ind)
      k=2:min(kmin+1,n);
    elseif ind(nd) >= kmin & ind(nd)-1 < kmax
      k = 2:ind(nd);
    elseif ind(nd) >= kmax
      k = 2:kmax+1;
    elseif ind(nd) < kmin
      k = 2:min(kmin+1,n);
    end
    nk=length(k);
  end


  M20=variogrammodel(model,r(indx_sort(k)),model_para);
  M2=[M20 1 ]';

if  j == 1 | kmin < n
    rs=dist1_1(indx_sort(k),indx_sort(k));
    K0=variogrammodel(model,rs,model_para);

    K0(1:nk+1:nk^2)=zeros(nk,1);
    K=[K0 ones(nk,1);ones(1,nk) 0];

    K_inv=inv(K);
end

  lambda=K_inv*M2;

  tp(j)=sum_nan(lambda(1:nk).*var(indx_sort(k)));
```

end

% Results

Pre_result(:,1)=var;
Pre_result(:,2)=tp;
Pre_result(:,3)=(var-tp)^2;

Result=sum(Pre_result(:,3));

2) – Variogrammodel, returns the semivariance for given lag distances

Author: D. Marcotte

```
 function y = variogrammodel(type, r, model_para)
% function y = variogrammodel(type, r, model_para)
%    computes the theoretical semi-variogram.
%    |type| = model index for semivariogram/correlogram
%    type > 0: semi-variogram
%         < 0: correlogram
%      r = vector lag distances
%  model_para = [ p1 p2 p3 p4 p5];
%
%      p1: Nugt = nugget effect
%      p2: Sill = sill
%      p3: L = length scale for the main lobe
%      p4: p = power for the expenential
%      p5: b = length scale for hole effect
%
%      model type:
%          01 = spherical
%          02 = exponential
%          03 = gaussian
%          04 = linear
%
%      models including hole effects
%          05 = C * [ 1 - (sin b*r) / r ] + Nugt
%          06 = C * [ 1 - (exp(-r/L))     * cos(br) ] + Nugt
%          07 = C * [ 1 + (exp(-r/L))     * cos(br) ] + Nugt
%          08 = C * [ 1 - (exp(-(r/L)^2)) * cos(br) ] + Nugt
%          09 = C * [ 1 -              Jo (br) ] + Nugt
%          10 = C * [ 1 -  exp(-r/L)      * Jo (br) ] + Nugt
%          11 = C * [ 1 -  exp(-(r/L)^2)  * Jo (br) ] + Nugt
%              12 = C * [ 1 -  exp(-(r/L)^2)  * (1 - br)] + Nugt
%          13 = C * [ 1 -  exp(-(r/L)^p)  * Jo (br) ] + Nugt
```

```
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% Author: D. Marcotte
% Version 2.1  97/aug/18
% Revised by Dezhang Chu,   10-29-98

Nugt=model_para(1);
Sill=model_para(2);
L=model_para(3);
p=model_para(4);
b=model_para(5);
C=Sill-Nugt;
n = length(r);
rL = r ./ L;

switch abs(type)
case 1
   indx1=find(rL < 1);
   indx2=find(rL >= 1);
   rL1=rL(indx1);
   rL2=rL(indx2);
   y1 = C * ( 1.5 .* rL1  -  0.5 .* rL1.^3)+Nugt;
   y2 = Sill * ones(size(rL2));
   y(indx1)=y1;
   y(indx2)=y2;
   y=reshape(y,size(r,1),size(r,2));
 case 2
   y = C * ( 1 - exp(-(r/L)))+Nugt;
 case 3
  y = C * ( 1 - exp(-(r/L).^2))+Nugt;
 case 4
  y = C .* r+Nugt;
 case 5
   y = C .* ( 1 - sin(b.*(r+eps))./(r+eps) )+Nugt;
 case 6
  y = C * ( 1 - exp(-r/L) .* cos(b*r) )+Nugt;
 case 7
  y = C * ( 1 + exp(-r/L) .* cos(b*r) )+Nugt;
 case 8
  y = C * (1 - exp(-(r/L).^2) .* cos(b*r) )+Nugt;
 case 9
  y = C * ( 1 - bessel(0, b*r) )+Nugt;
 case 10
  y = C * ( 1 - bessel(0, b*r) .* exp(-r/L) )+Nugt;
 case 11
```

```
  y = C * ( 1 - exp(-(r/L).^2) .* bessel(0, b*r) )+Nugt;
 case 12
   y = C * ( 1 - exp(-(r/L).^2) .* (1 - b*r.^2) )+Nugt;
 case 13                                      % generalized exponetial-Bessel
   y= C* (1 - exp(- (r/L).^p).* bessel(0, b*r))+Nugt;
end
```

3) – Sum_nan, sums a vector or matrix ignoring NaN values

   Author: Jim Ledwell, 10/97 Woods Hole Oceanographic Institution

```
function    psum=sum_nan(A,k)
%% function    psum=sum_nan(A,k)
%% computes the summation which ignores all nan's
%% if A is an 1D array, k is not necessary, if A is a matrix
%% k is optional. Without k or k = 1, A is summed over column,
%% and k = 2, summation is over rows
%%
% Author: Jim Ledwell, 10/97 Woods Hole Oceanographic Institution


D=size(A);
if D(1) == 1 | D(2) == 1                              % 1-D array
  [indx]=find(~isnan(A));
  psum=sum(A(indx));
else
  if nargin == 1
   k=1;                          % default direction: sum over each column
  end
  if k == 1
   for i=1:D(2)
     [indx]=find(~isnan(A(:,i)));
     if length(indx) > 0
       psum(i)=sum(A(indx,i));
     else
       psum(i)=nan;
     end
   end
  else
   for i=1:D(1)
     [indx]=find(~isnan(A(i,:)));
     if length(indx) > 0
       psum(i)=sum(A(i,indx));
     else
       psum(i)=nan;
     end
```

```
        end
    psum=psum(:);
  end
end
```

Tables

Table 1. Summary of variogram model parameters. Numbers in italics denote parameters that were fit by eye and were not used in variogram comparisons.

Year	Sample size	Distance Metric	Variogram Model	Nugget	Partial Sill	Range(km)
1990	863	Euclidean	Exponential	18,173	22,455	54
		LCP	Exponential	16,448	25,042	55
1991	964	Euclidean	Gaussian	9,736	30,484	55
		LCP	Gaussian	*8,000*	*12,000*	*30*
1992	1392	Euclidean	Exponential	792	1,408	25
		LCP	Exponential	763	997	16
1993	1253	Euclidean	Gaussian	6,963	20,254	50
		LCP	Gaussian	*6,000*	*6,000*	*35*
1994	1427	Euclidean	Gaussian	7,108	885	35
		LCP	Gaussian	*7,000*	*900*	*30*
1995	1598	Euclidean	Gaussian	1,324	10,165	49
		LCP	Gaussian	1,178	5,436	41
1996	1580	Euclidean	Gaussian	3,877	11,461	34
		LCP	Gaussian	3,444	7,453	28
1997	1587	Euclidean	Gaussian	2,848	6,075	29
		LCP	Gaussian	2,860	4,446	29
1998	1573	Euclidean	Gaussian	1,160	1,580	33
		LCP	Gaussian	1,195	1,222	38
1999	1519	Euclidean	Gaussian	581	2,042	33
		LCP	Gaussian	564	1,181	27
2000	1511	Euclidean	Gaussian	592	1,220	24
		LCP	Gaussian	587	1,075	23
2001	1556	Euclidean	Gaussian	281	1,114	25
		LCP	Gaussian	263	830	22
2002	1530	Euclidean	Gaussian	416	1,409	35
		LCP	Gaussian	377	867	30

Table 2. Baywide. Prediction Error Sum of Squares (PRESS) for kriging predictions based on Euclidean and Lowest-Cost Path (LCP) distance metrics, the percent difference in PRESS between the two metrics (positive numbers indicate greater prediction accuracy for the LCP metric), the average increase in intersample distance for the LCP metric, and the mean percent difference over 13 years.

Year	Euclidean PRESS $(*10^3)$	LCP PRESS $(*10^3)$	Percent Difference	Average Absolute Increase in Intersample Distance (km)	Average Percent Increase in Intersample Distance
1990	65.64	65.09	0.84	16.84	23.12
1991	61.08	61.53	-0.73	12.13	15.27
1992	6.46	6.49	-0.47	12.77	16.53
1993	38.00	38.21	-0.54	14.60	20.11
1994	29.57	29.48	0.28	16.19	21.10
1995	19.80	19.63	0.87	14.13	18.99
1996	50.00	49.99	0.01	12.87	16.83
1997	16.12	16.19	-0.41	11.10	14.52
1998	9.58	9.68	-1.04	11.86	15.65
1999	10.23	10.14	0.95	11.87	15.44
2000	5.24	5.23	0.11	11.34	14.50
2001	4.49	4.65	-3.46	11.06	14.09
2002	6.10	6.04	0.94	11.68	15.30
		mean:	-0.20	12.96	17.03

Table 3. Tangier Sound and Baywide random subsample. Prediction Error Sum of Squares (PRESS) for kriging predictions based on Euclidean and Lowest-Cost Path (LCP) distance metrics, the percent difference in PRESS between the two metrics (positive numbers indicate greater prediction accuracy for the LCP metric), and the mean percent difference over 13 years. Only the mean percent difference in PRESS is given for the random subsample.

Year	Tangier Euclidean PRESS $(*10^3)$	Tangier LCP PRESS $(*10^3)$	Tangier Percent Difference	Random Subsample Percent Difference
1990	31.60	31.28	1.02	-0.36
1991	5.78	5.91	-2.22	0.55
1992	1.30	1.31	-0.92	-0.74
1993	0.30	0.33	-8.45	-0.84
1994	10.93	10.89	0.38	0.67
1995	3.55	3.41	3.98	-0.05
1996	5.38	5.33	0.87	-1.29
1997	1.72	1.70	0.70	0.07
1998	1.29	1.29	0.15	-0.86
1999	0.51	0.51	1.15	1.47
2000	1.22	1.23	-1.15	-0.86
2001	0.80	0.86	-7.29	-0.46
2002	0.44	0.44	-0.41	-0.58
		mean:	-0.94	-0.25

Table 4. Summary of sample size (N), variogram parameters, variogram models, and spatial trend models based on northing (X) and easting (Y).

Year	N	Nugget	Partial Sill	Range (km)	Model	X	Y	XY	X^2	Y^2	XY^2	YX^2	X^2Y^2
1990	919	12,749	12,502	13,710	Gaussian	x	x		x		x		x
1991	947	11,272	25,144	45,037	Gaussian		x		x	x			x
1992	1,340	731	1,008	52,532	Spherical		x						
1993	1,194	5,000	8,000	25,000	Gaussian	x	x	x					
1994	1,382	2,631	6,168	26,409	Gaussian		x			x	x	x	x
1995	1,523	908	4,950	43,144	Gaussian	x		x	x			x	
1996	1,523	3,304	8,557	32,278	Gaussian	x		x	x				x
1997	1,506	1,664	15,467	196,671	Spherical		x		x	x			x
1998	1,510	754	1,424	31,194	Gaussian	x	x				x	x	
1999	1,457	407	1,383	34,206	Gaussian	x					x	x	x
2000	1,421	260	3,754	147,284	Exponential		x	x	x	x			x
2001	1,464	192	797	28,676	Gaussian	x	x	x	x	x			
2002	1,457	254	866	33,048	Gaussian	x	x	x					

Table 5. Pearson correlation coefficients between all pairs of environmental variables. Significant correlations (p<0.05) are shown in bold. All other correlations are insignificant (p>0.05).

	Distance (M)	Salinity (S)	Depth (D)	Temp. (T)	Slope (B)	SAV (V)
Distance (M)	1					
Salinity (S)	**-0.637**	1				
Depth (D)	**-0.038**	**0.192**	1			
Temp. (T)	**-0.091**	**0.341**	**0.118**	1		
Slope (B)	**0.107**	**-0.073**	**0.284**	-0.002	1	
SAV (V)	-0.010	**-0.133**	**0.139**	**0.079**	**-0.055**	1

Table 6. Model selection results for (a) stage I (i.e. presence/absence) and (b) stage II (abundance) GAMs. Significance test p-values are given for the explanatory variables distance from Bay mouth, salinity, depth, temperature, bottom slope, distance from SAV, and interaction terms. Terms that were not significant (ns, $p > 0.05$) were dropped from the model unless they were involved in a significant interaction. Degrees of freedom were fixed for terms in bold. The adjusted r-squared and percent of deviance explained are also given for each model.

Year	N	Distance (M)	Salinity (S)	Depth (D)	Temp. (T)	Slope (B)	SAV (V)	Interaction I	Interaction II	R^2 adj	Dev. Explained
1990	650	ns	<0.001	0.579	0.005	ns	ns	D/T 0.027	ns	0.274	31.5
1991	723	0.728	ns	0.003	ns	0.048	ns	M/D <0.001	ns	0.246	26.1
1992	1046	ns	<0.001	<0.001	ns	ns	ns	ns	ns	0.221	22
1993	941	ns	0.229	0.702	<0.001	ns	0.044	S/D <0.001	ns	0.255	27.1
1994	1071	0.992	0.003	<0.001	ns	ns	0.036	M/S 0.036	M/V 0.030	0.225	28.1
1995	1199	ns	0.047	<0.001	0.906	ns	ns	**S/T 0.005**	ns	0.097	17.7
1996	1187	<0.001	0.081	0.368	<0.001	ns	0.52	S/V 0.001	S/D <0.001	0.255	27.6
1997	1193	0.1	<0.001	<0.001	<0.001	ns	ns	M/D <0.001	ns	0.189	23.1
1998	1181	0.933	ns	<0.001	<0.001	ns	ns	M/D <0.001	ns	0.267	28.3
1999	1139	<0.001	ns	0.468	0.181	ns	ns	D/T 0.014	ns	0.197	27.2
2000	1133	<0.001	ns	<0.001	<0.001	ns	ns	ns	ns	0.27	28.6
2001	1167	0.002	ns	<0.001	<0.001	ns	ns	**M/D 0.002**	ns	0.328	38.4
2002	1148	0.011	0.012	<0.001	ns	ns	0.018	M/D 0.002	ns	0.215	29.8

a

Year	N	Distance (M)	Salinity (S)	Depth (D)	Temp. (T)	Slope (B)	SAV (V)	Interaction I	Interaction II	R^2 adj	Dev. Explained
1990	91	ns	ns	ns	0.004	ns	0.007	ns	ns	0.136	16.5
1991	161	<0.001	ns	0.002	ns	0.002	0.047	ns	ns	0.31	34.9
1992	197	<0.001	ns	0.003	ns	ns	ns	ns	ns	0.116	12.5
1993	166	<0.001	ns	ns	ns	ns	ns	ns	ns	0.145	15.6
1994	150	<0.001	ns	ns	ns	ns	ns	ns	ns	0.265	29.6
1995	88	0.002	ns	ns	ns	0.047	ns	ns	ns	0.219	31.8
1996	204	<0.001	ns	<0.001	ns	ns	ns	ns	ns	0.359	39.3
1997	149	0.024	ns	<0.001	ns	ns	0.037	M/D 0.002	ns	0.457	50.1
1998	185	0.022	<0.001	0.007	ns	ns	ns	ns	ns	0.393	41.9
1999	102	<0.001	ns	ns	0.002	ns	ns	ns	ns	0.318	35.1
2000	193	ns	<0.001	ns	ns	ns	ns	ns	ns	0.182	19.3
2001	116	<0.001	ns	ns	ns	ns	ns	ns	ns	0.136	14.4
2002	100	ns	ns	ns	ns	ns	0.024	ns	ns	0.077	9.8

b

Table 7. *Callinectes sapidus* . Cross-validation where models developed with data from one year (columns) are applied to data from another (rows). Values in (a) represent the cross-validation r-squared. Values on the diagonal (in bold for (a)) represent intra-annual cross-validation where models developed using a training data subset are applied to the test data subset for the same year. The first row of (a) represents the model fit to the training data. Values in (b) represent the z-score, i.e., the number of standard deviations above or below the grand mean Fisher (1915) transformed cross-validation correlation coefficient.

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
training	0.299	0.315	0.255	0.296	0.270	0.130	0.314	0.241	0.346	0.232	0.305	0.360	0.239
1990	**0.099**	0.064	0.016	0.069	0.059	0.091	0.014	0.060	0.081	0.001	0.015	0.069	0.013
1991	0.028	**0.219**	0.048	0.135	0.174	0.071	0.128	0.071	0.195	0.043	0.148	0.009	0.086
1992	0.003	0.257	**0.291**	0.191	0.265	0.210	0.146	0.099	0.271	0.235	0.273	0.069	0.221
1993	0.129	0.188	0.128	**0.238**	0.113	0.089	0.113	0.090	0.165	0.022	0.047	0.031	0.125
1994	0.000	0.194	0.200	0.232	**0.244**	0.237	0.117	0.056	0.194	0.176	0.222	0.041	0.124
1995	0.010	0.032	0.040	0.063	0.095	**0.086**	0.016	0.008	0.040	0.023	0.048	0.010	0.014
1996	0.043	0.111	0.088	0.077	0.098	0.042	**0.168**	0.110	0.152	0.017	0.005	0.062	0.081
1997	0.087	0.165	0.095	0.171	0.097	0.055	0.129	**0.197**	0.172	0.024	0.097	0.054	0.110
1998	0.035	0.105	0.085	0.109	0.079	0.066	0.084	0.099	**0.129**	0.008	0.049	0.005	0.044
1999	0.000	0.155	0.236	0.157	0.139	0.174	0.108	0.088	0.176	**0.196**	0.205	0.080	0.184
2000	0.042	0.206	0.222	0.202	0.183	0.191	0.092	0.077	0.243	0.255	**0.311**	0.069	0.165
2001	0.078	0.184	0.108	0.080	0.121	0.009	0.129	0.078	0.166	0.036	0.054	**0.228**	0.087
2002	0.001	0.083	0.075	0.016	0.084	0.021	0.019	0.056	0.084	0.062	0.128	0.061	**0.089**

a

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
1990	**0.04**	-0.43	-1.38	-0.36	-0.52	-0.06	-1.44	-0.50	-0.20	-2.10	-1.41	-0.37	-1.46
1991	-1.08	**1.35**	-0.69	**0.48**	**0.89**	-0.33	**0.39**	-0.33	**1.11**	-0.79	**0.62**	-1.61	-0.12
1992	-1.91	**1.72**	**2.04**	**1.07**	**1.79**	**1.26**	**0.60**	**0.05**	**1.85**	**1.51**	**1.87**	-0.37	**1.37**
1993	**0.40**	**1.04**	**0.39**	**1.53**	**0.21**	-0.08	**0.22**	-0.07	**0.80**	-1.22	-0.71	-1.03	**0.36**
1994	-2.16	**1.10**	**1.16**	**1.47**	**1.59**	**1.53**	**0.26**	-0.57	**1.10**	**0.92**	**1.38**	-0.82	**0.35**
1995	-1.58	-0.99	-0.84	-0.45	-0.01	-0.13	-1.37	-1.66	-0.84	-1.20	-0.70	-1.58	-1.43
1996	-0.78	**0.20**	-0.09	-0.25	**0.03**	-0.80	**0.83**	**0.18**	**0.67**	-1.36	-1.78	-0.47	-0.19
1997	-0.11	**0.80**	0.00	**0.86**	**0.02**	-0.58	**0.41**	**1.13**	**0.87**	-1.18	**0.02**	-0.59	**0.18**
1998	-0.93	**0.12**	-0.13	**0.17**	-0.22	-0.41	-0.15	**0.04**	**0.40**	-1.66	-0.68	-1.80	-0.77
1999	-2.28	**0.69**	**1.52**	**0.71**	**0.52**	**0.89**	**0.15**	-0.10	**0.92**	**1.12**	**1.21**	-0.21	**1.00**
2000	-0.80	**1.22**	**1.38**	**1.18**	**0.99**	**1.07**	-0.04	-0.25	**1.59**	**1.70**	**2.22**	-0.36	**0.80**
2001	-0.24	**0.99**	**0.15**	-0.21	**0.32**	-1.61	**0.40**	-0.23	**0.81**	-0.91	-0.60	**1.43**	-0.11
2002	-2.07	-0.17	-0.28	-1.39	-0.16	-1.25	-1.31	-0.56	-0.15	-0.46	**0.39**	-0.48	-0.08

b

Table 8. Evaluation of stage I (presence/absence) model fits to the training data (a) using receiver operating characteristic (ROC) curves and cross-validation of stage I models (b). Values in (a) represent the area under the ROC curve (AUC), the critical p-values: p-optimum (p_{opt}) and p_{fair}, and their sensitivity (Sens.), specificity (Spec.), and percent correct predictions (% Corr.). Values in (b) represent the AUC where models developed with data from one year (columns) are applied to data from another (rows). Values on the diagonal represent intra-annual cross-validation where models developed using a training data subset are applied to the test data subset for the same year. AUC values greater than 0.7 are highlighted in black.

Year	AUC	p_{opt} Value	Sens.	Spec.	% Corr.	p_{fair} Value	Sens.	Spec.	% Corr.
1990	0.870	0.470	0.396	0.975	89.4	0.155	0.780	0.785	78.5
1991	0.839	0.453	0.460	0.927	82.3	0.235	0.752	0.749	75.0
1992	0.809	0.575	0.284	0.973	84.3	0.180	0.746	0.740	74.1
1993	0.845	0.580	0.277	0.983	85.9	0.180	0.765	0.767	76.6
1994	0.862	0.405	0.393	0.951	87.3	0.175	0.793	0.793	79.3
1995	0.824	0.325	0.046	0.997	92.7	0.085	0.773	0.762	76.3
1996	0.851	0.470	0.373	0.966	86.4	0.195	0.770	0.770	77.3
1997	0.837	0.410	0.302	0.974	89.0	0.125	0.752	0.748	74.9
1998	0.849	0.455	0.400	0.960	87.2	0.150	0.768	0.770	77.0
1999	0.869	0.380	0.294	0.981	91.9	0.110	0.784	0.786	78.6
2000	0.859	0.533	0.290	0.972	85.6	0.200	0.777	0.783	78.2
2001	0.905	0.540	0.302	0.983	91.5	0.110	0.845	0.847	84.7
2002	0.884	0.400	0.310	0.979	92.1	0.105	0.810	0.819	81.8

a

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
1990	0.74	0.69	0.65	0.74	0.73	0.76	0.64	0.73	0.72	0.44	0.57	0.68	0.71
1991	0.71	0.78	0.65	0.79	0.75	0.74	0.78	0.75	0.81	0.65	0.69	0.63	0.70
1992	0.58	0.76	0.77	0.72	0.78	0.74	0.74	0.71	0.79	0.79	0.79	0.72	0.78
1993	0.73	0.78	0.73	0.79	0.74	0.74	0.72	0.72	0.76	0.60	0.67	0.54	0.73
1994	0.58	0.80	0.78	0.77	0.82	0.81	0.82	0.76	0.79	0.78	0.78	0.73	0.75
1995	0.63	0.64	0.62	0.67	0.72	0.70	0.65	0.63	0.66	0.64	0.67	0.50	0.65
1996	0.66	0.69	0.64	0.65	0.67	0.62	0.72	0.70	0.71	0.57	0.62	0.69	0.69
1997	0.67	0.72	0.64	0.70	0.66	0.66	0.68	0.76	0.73	0.59	0.65	0.65	0.67
1998	0.64	0.73	0.69	0.72	0.67	0.71	0.70	0.76	0.77	0.56	0.60	0.57	0.64
1999	0.64	0.80	0.81	0.77	0.82	0.81	0.82	0.81	0.85	0.85	0.86	0.68	0.86
2000	0.73	0.77	0.79	0.74	0.80	0.76	0.74	0.77	0.79	0.83	0.84	0.71	0.79
2001	0.74	0.75	0.72	0.71	0.74	0.57	0.76	0.71	0.77	0.63	0.78	0.80	0.80
2002	0.52	0.71	0.73	0.59	0.70	0.62	0.65	0.74	0.75	0.70	0.76	0.52	0.75

b

Figures

Figure 1.

Zoea

Megalopae

High Salinity Waters

Low Salinity Waters

Egg Bearing Female

♀

♂

Juveniles

Coupling Adults

Figure courtesy of C. Chenery
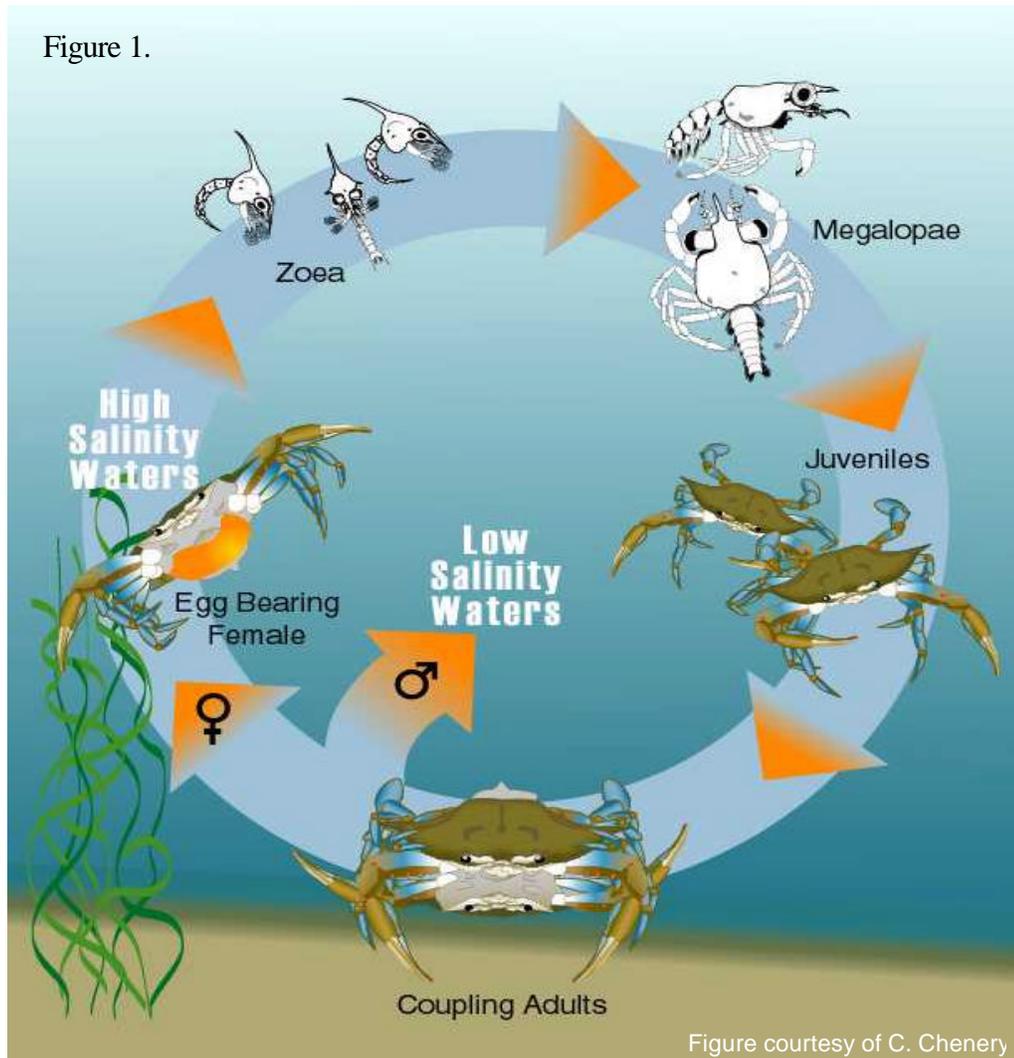
1998 Density of mature females

log (#/1000 m sq.)

- ·   0.00
- ○   0.01 - 4.00
- ●   4.01 - 7.44

Susquehanna River

Choptank River

Potomac River

Patuxent River

Tangier Sound

Rappahannock River

Pocomoke Sound

York River

James River

N

Figure 2.

Kilometers

0   25   50   100

Figure 3. The value of the nugget parameter from variograms based on a Euclidean and a Lowest Cost Path (LCP) distance metric. The black line represents equality.

Figure 4. The value of the range parameter from variograms based on a Euclidean and a Lowest Cost Path (LCP) distance metric. The black line represents equality.

Figure 5. The value of the sill parameter from variograms based on a Euclidean and a Lowest Cost Path (LCP) distance metric. The black line represents equality.

Figure 6. Euclidean distance based variogram for 1996

Figure 7. Lowest-cost path (LCP) distance based variogram for 1996

Figure 8. Euclidean distance based variogram for 2001

Figure 9. Lowest-cost path (LCP) distance based variogram for 2001

Blue crab density
(#/1000 m sq.)

- negative
- 1 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- 251 - 1,318

Figure 10.
a. Euclidean distance metric

b. LCP distance metric

Blue crab density
(#/1000 m sq.)

negative
1 - 10
11 - 50
51 - 100
101 - 250
251 - 1,318
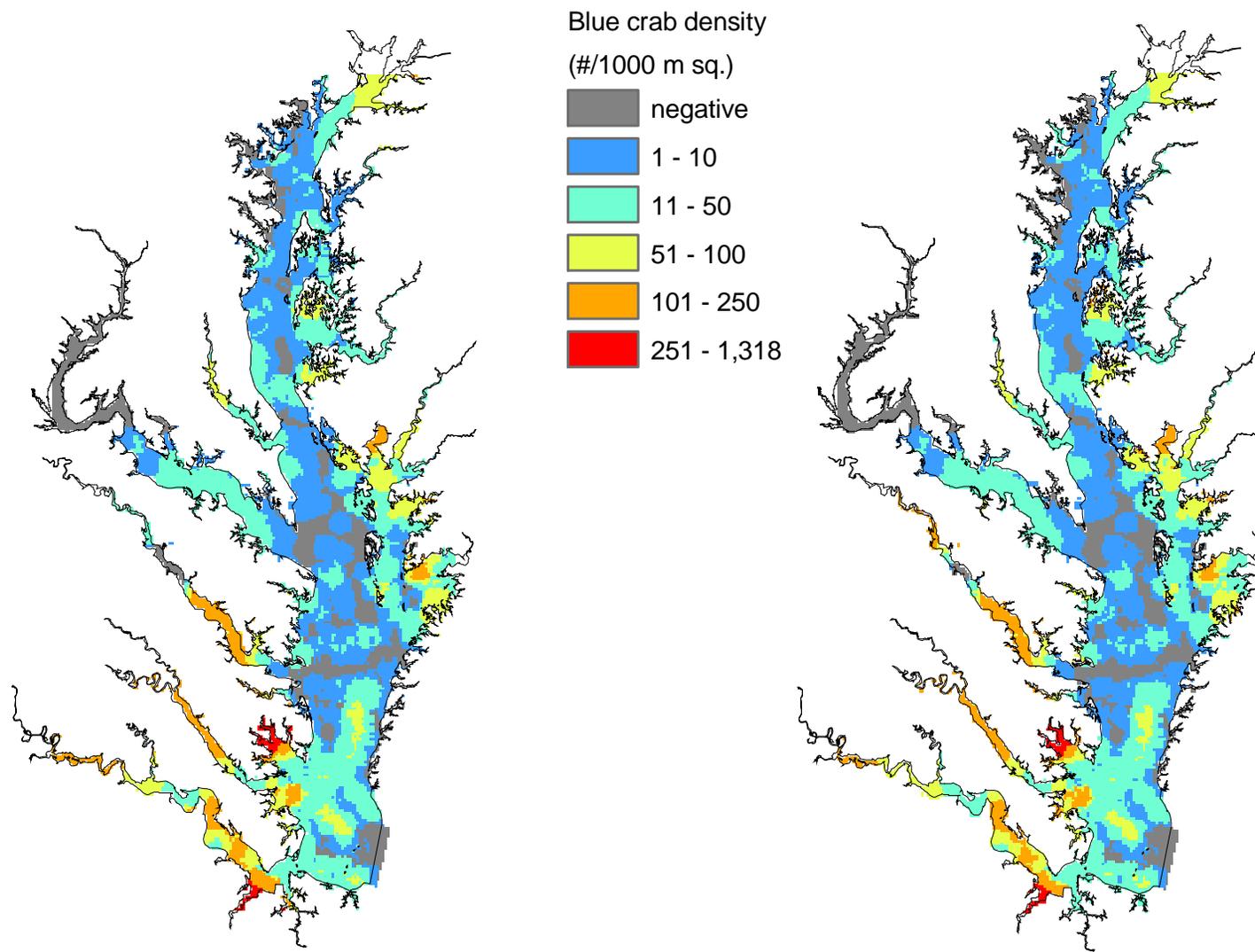
Figure 11.
a. Euclidean distance metric

b. LCP distance metric

Blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 200

Low : 115
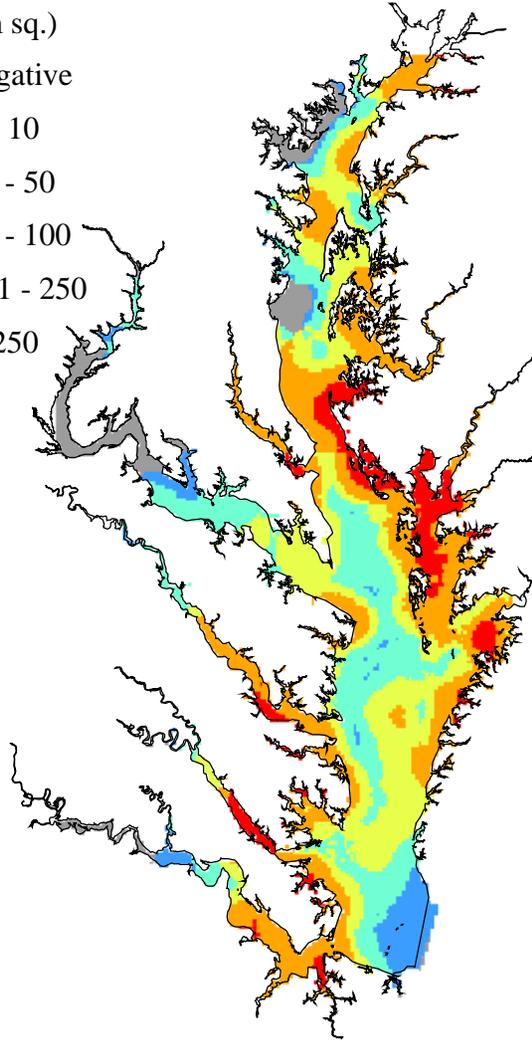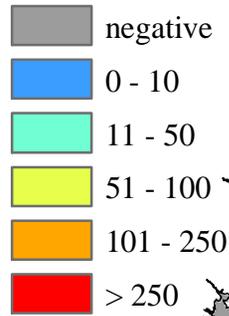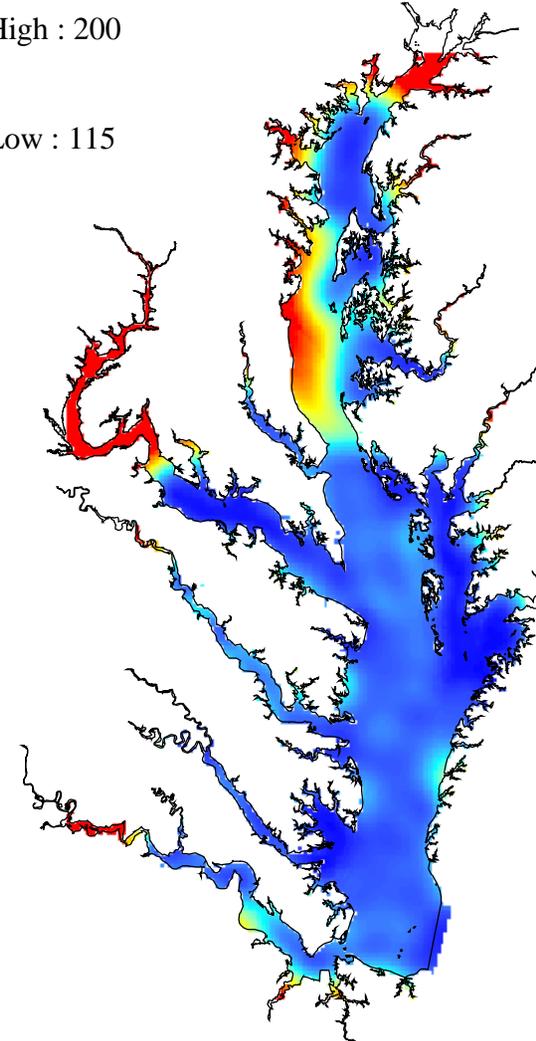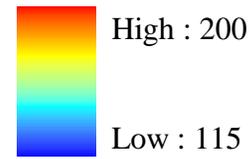
Figure 12.
a. 1990 Blue crab density

b. Standard error of blue crab density

Blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 232

Low : 108
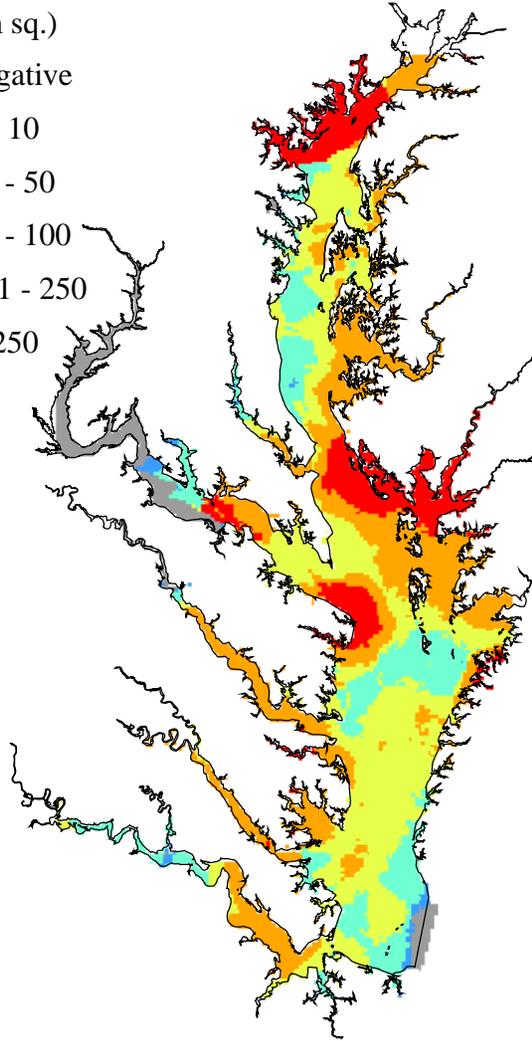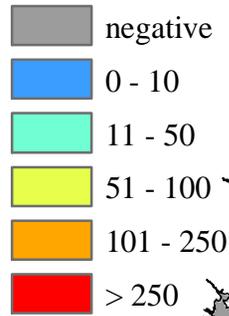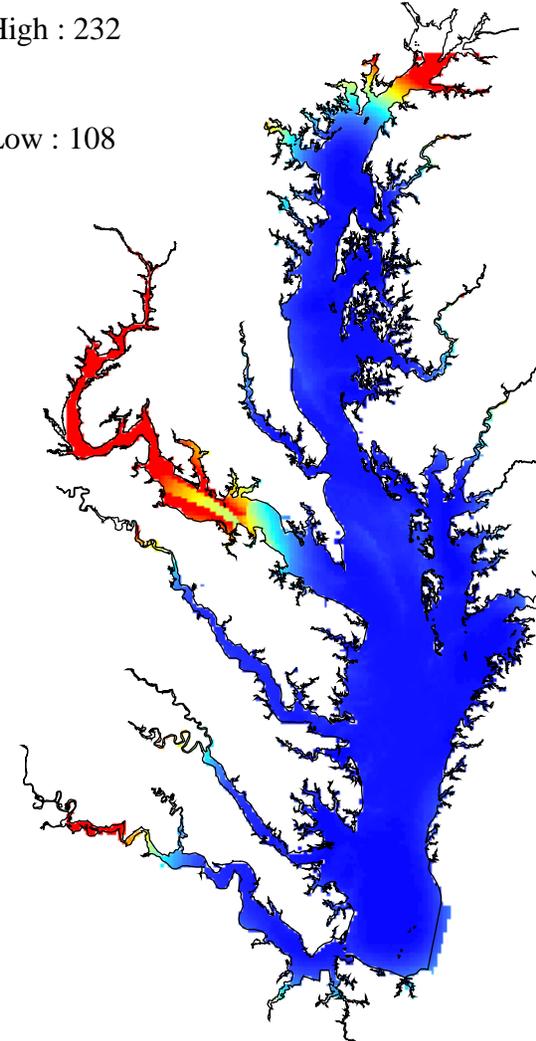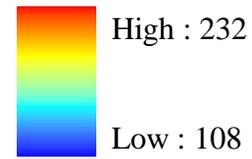
Figure 13.
a. 1991 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 211
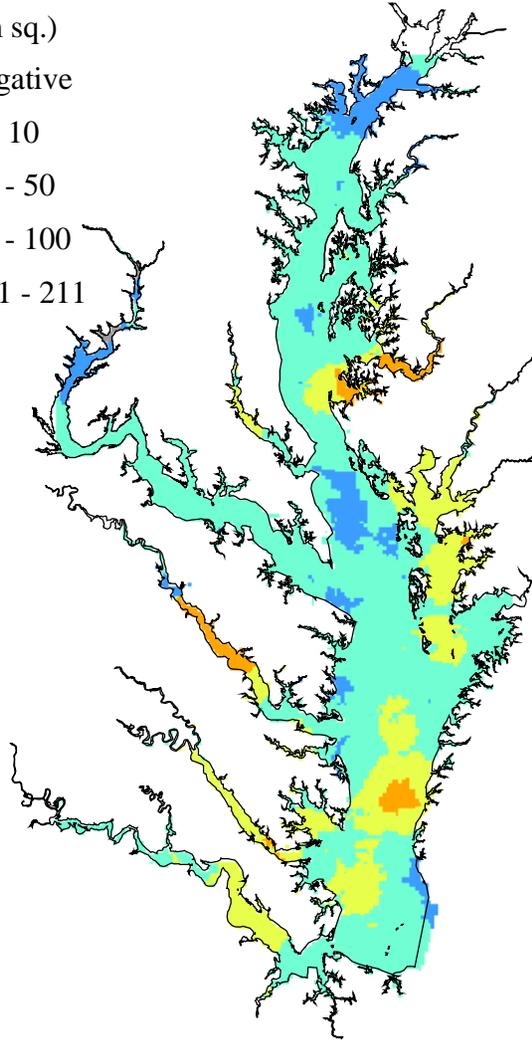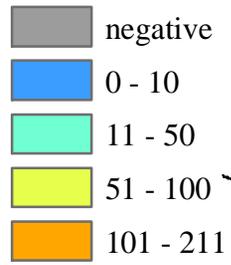
Standard Error
High : 46
Low : 28
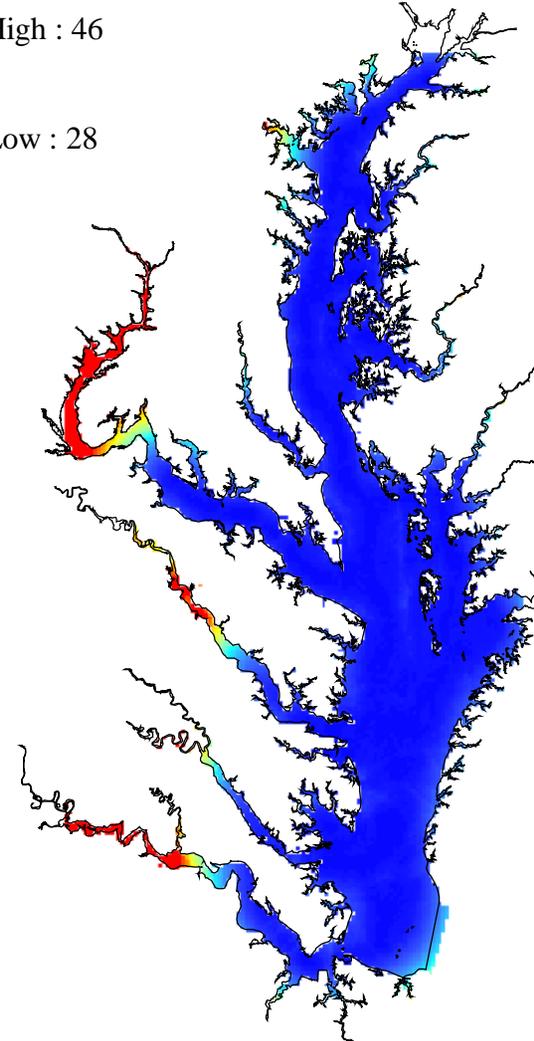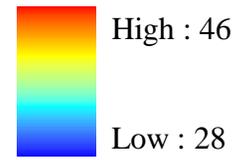
Figure 14.
a. 1992 Blue crab density

b. Standard error of blue crab density

Blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 143

Low : 72
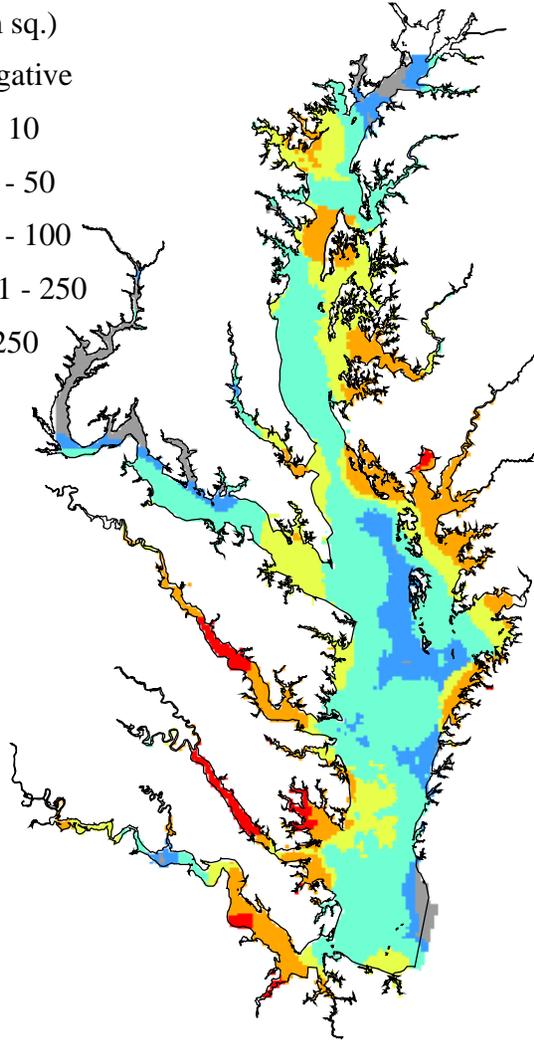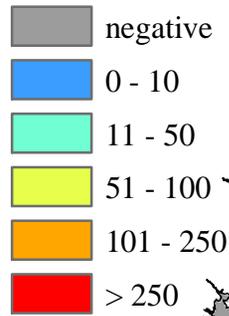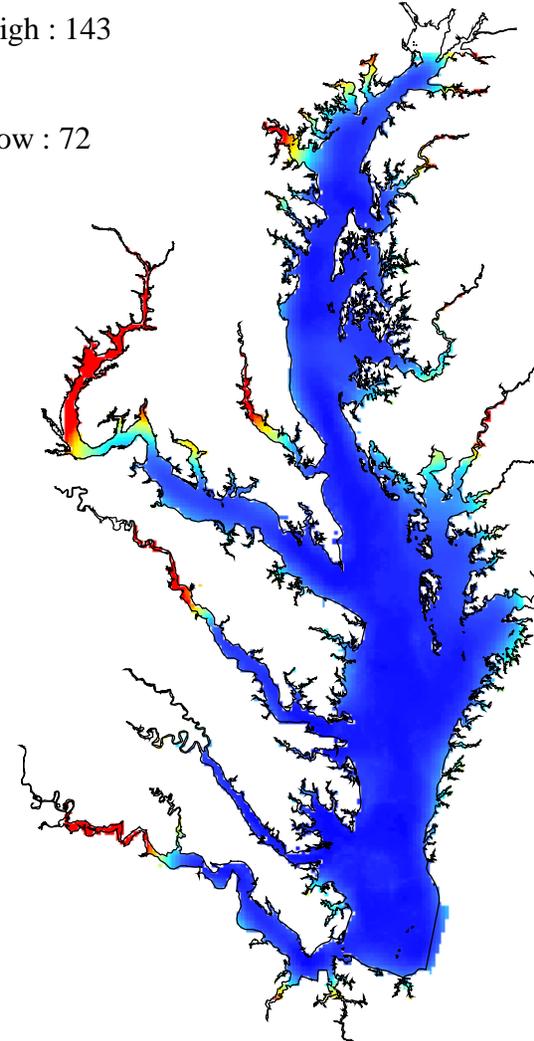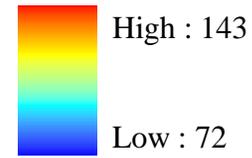
Figure 15.
a. 1993 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)
- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250
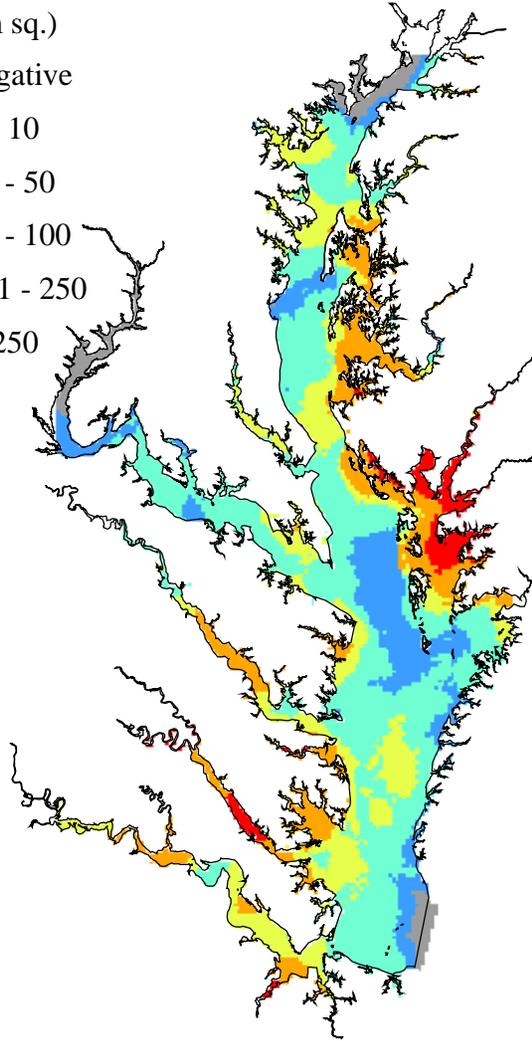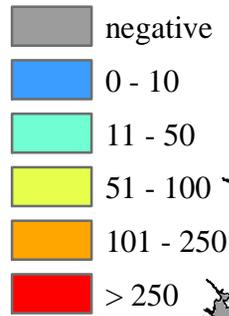
Standard Error
High : 120
Low : 52
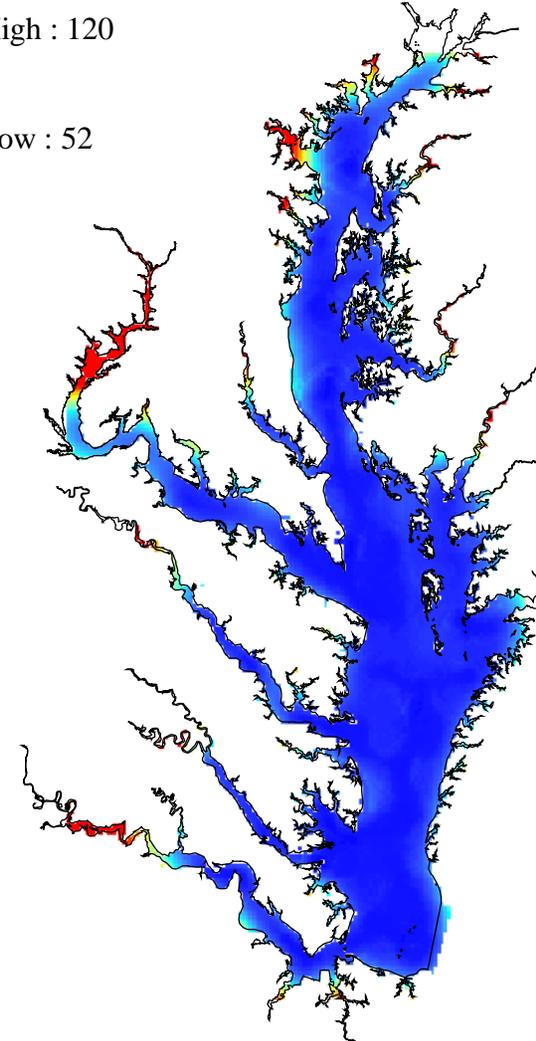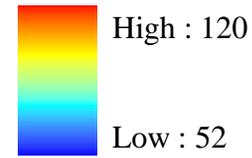
Figure 16.
a. 1994 Blue crab density

b. Standard error of blue crab density

Blue crab density

(#/1000 m sq.)

negative

0 - 10

11 - 50

51 - 100

101 - 250

> 250

Standard Error

High : 92

Low : 31
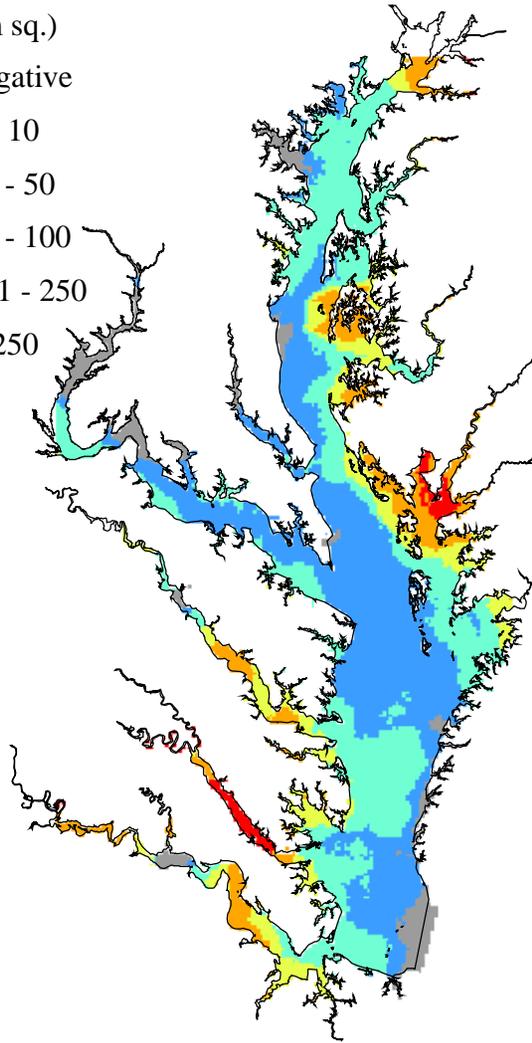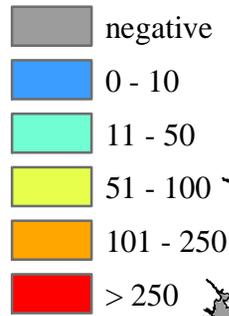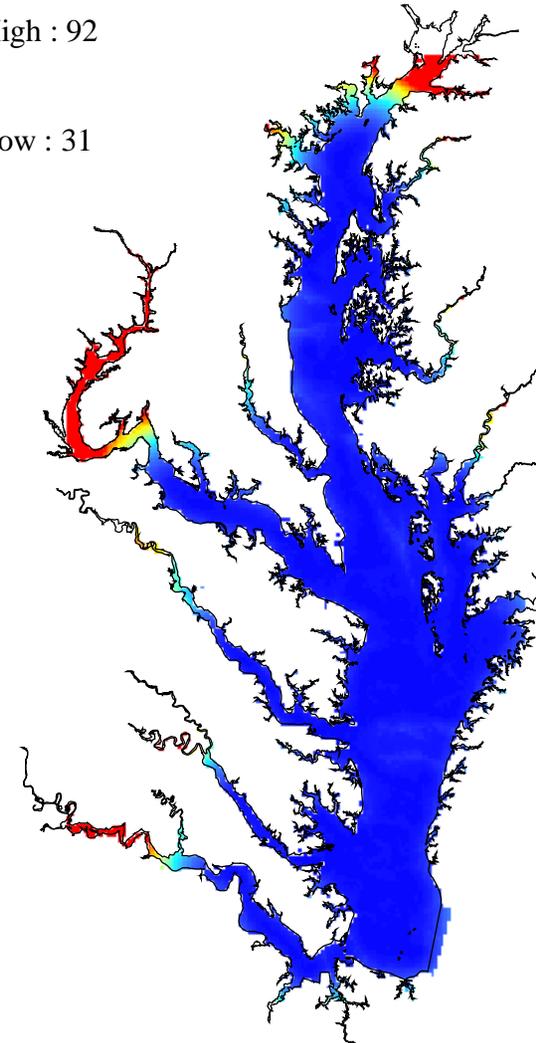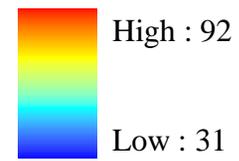
Figure 17.
a. 1995 Blue crab density

b. Standard error of blue crab density

Blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 139

Low : 59
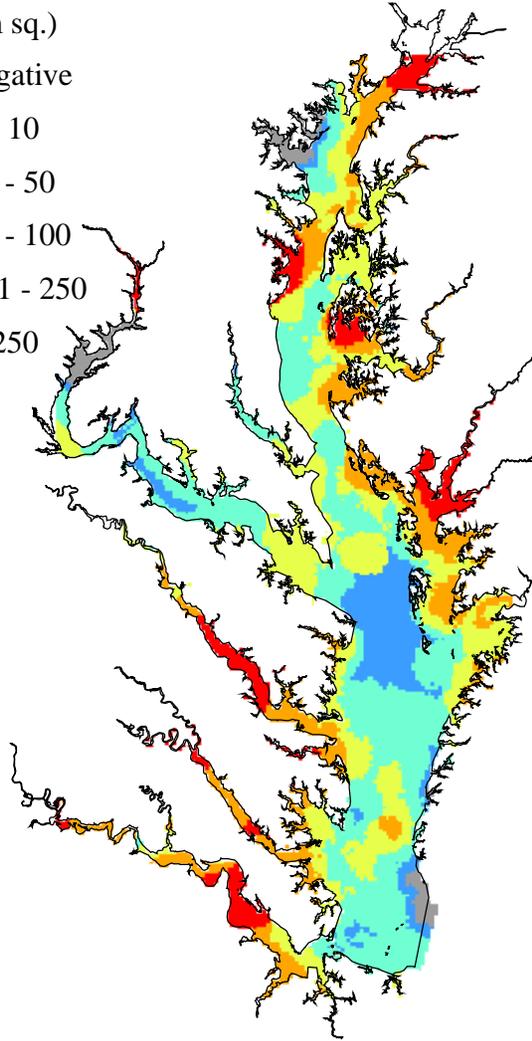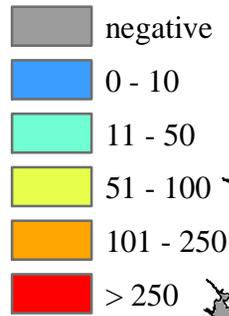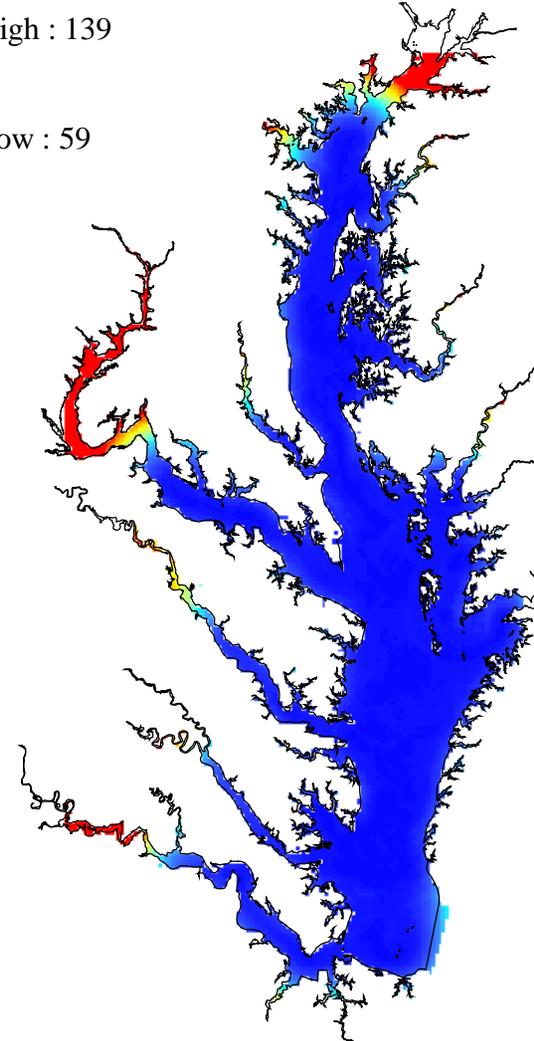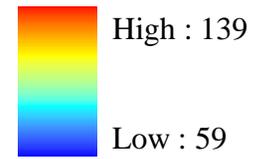
Figure 18.
a. 1996 Blue crab density

b. Standard error of blue crab density

Blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 244

Standard Error

High : 63

Low : 42
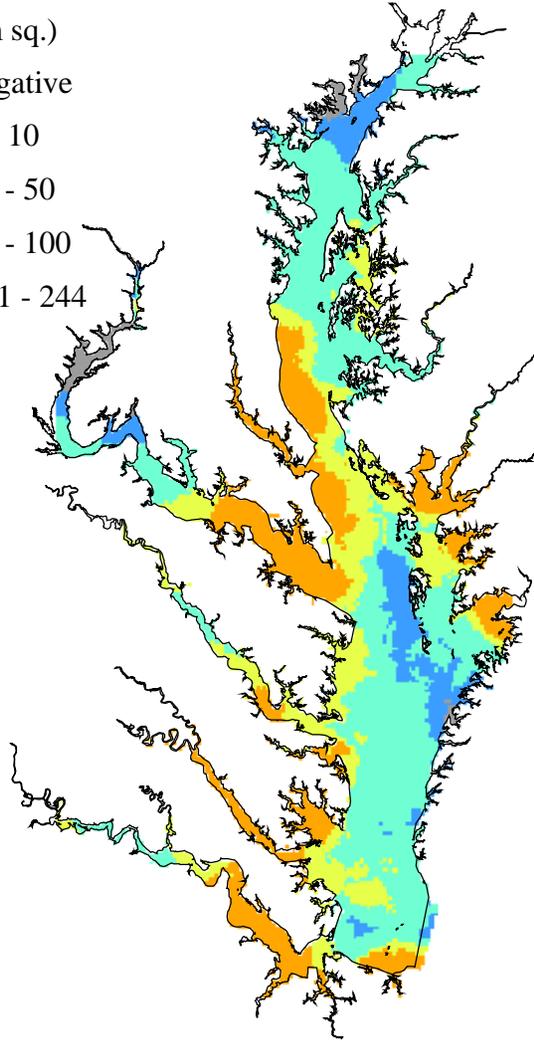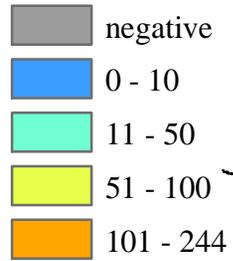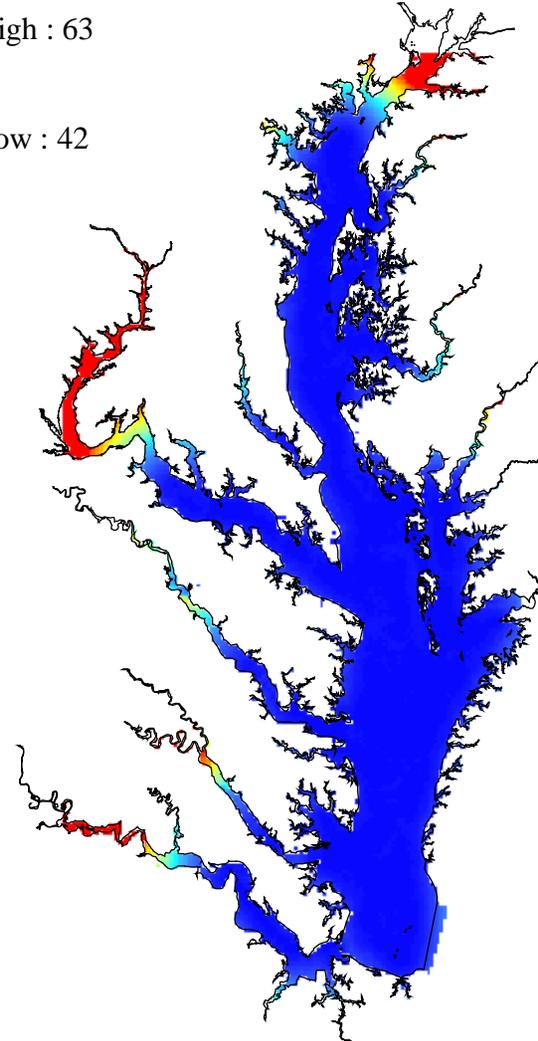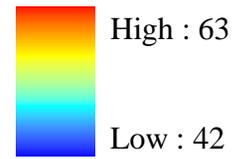
Figure 19.
a. 1997 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 59

Low : 28
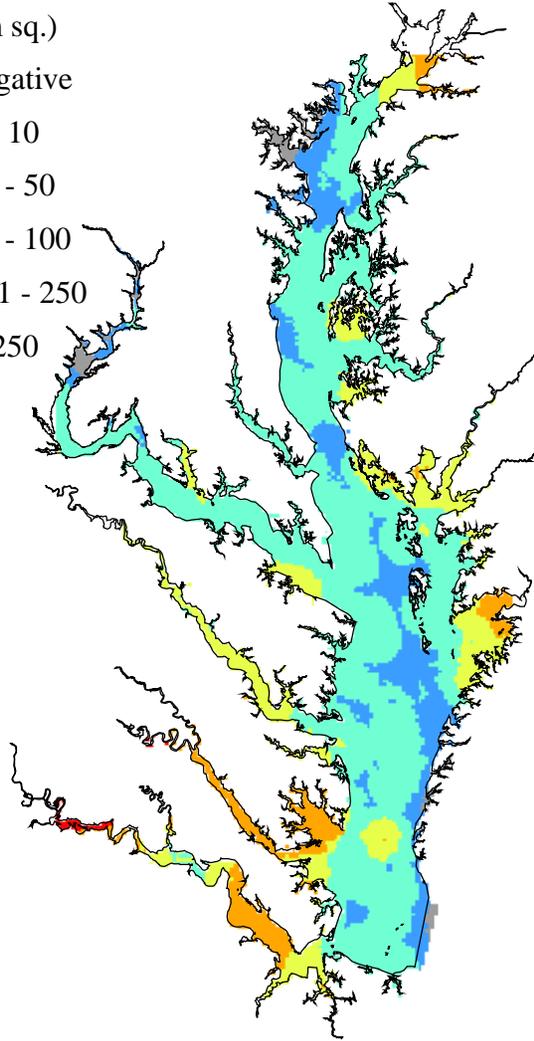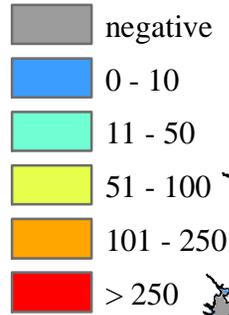
Figure 20.
a. 1998 Blue crab density
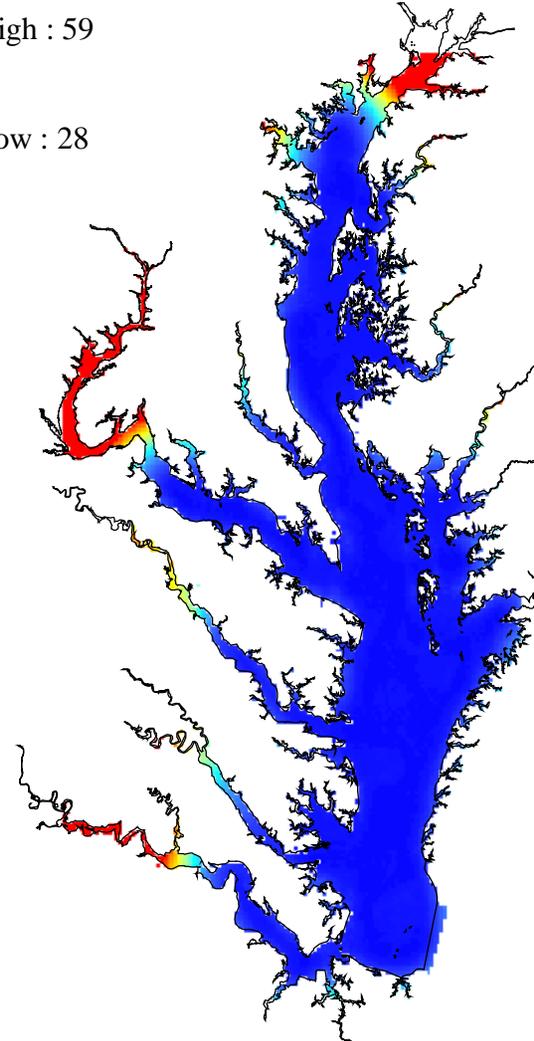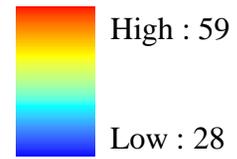
b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 53

Low : 21
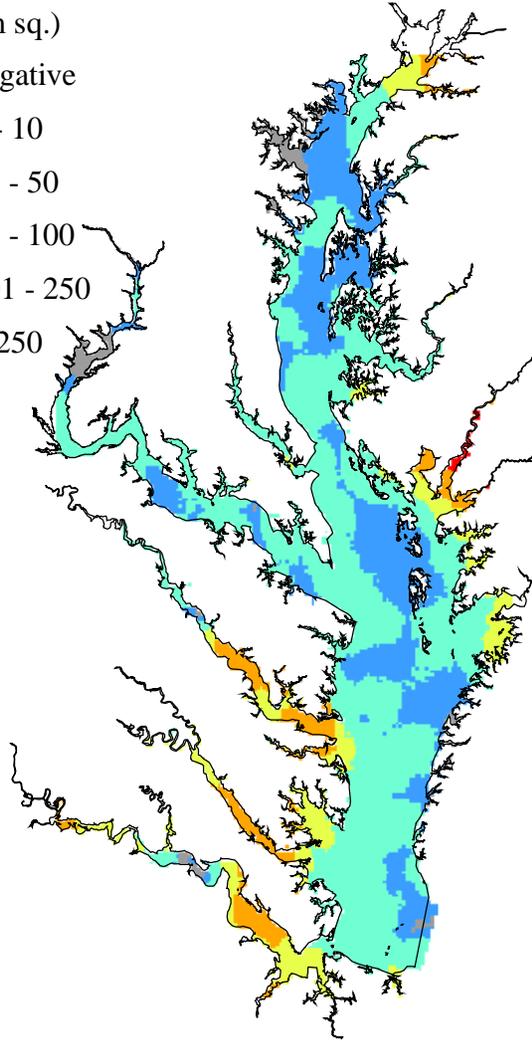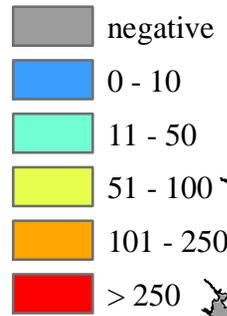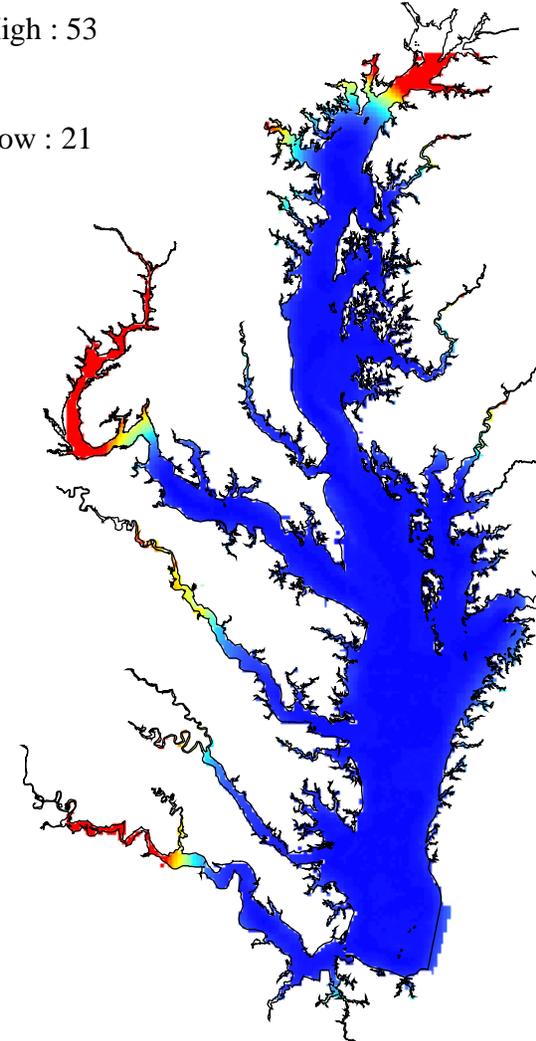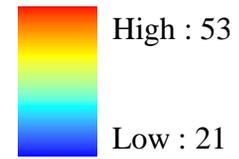
Figure 21.
a. 1999 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 208

Standard Error

High : 35

Low : 16
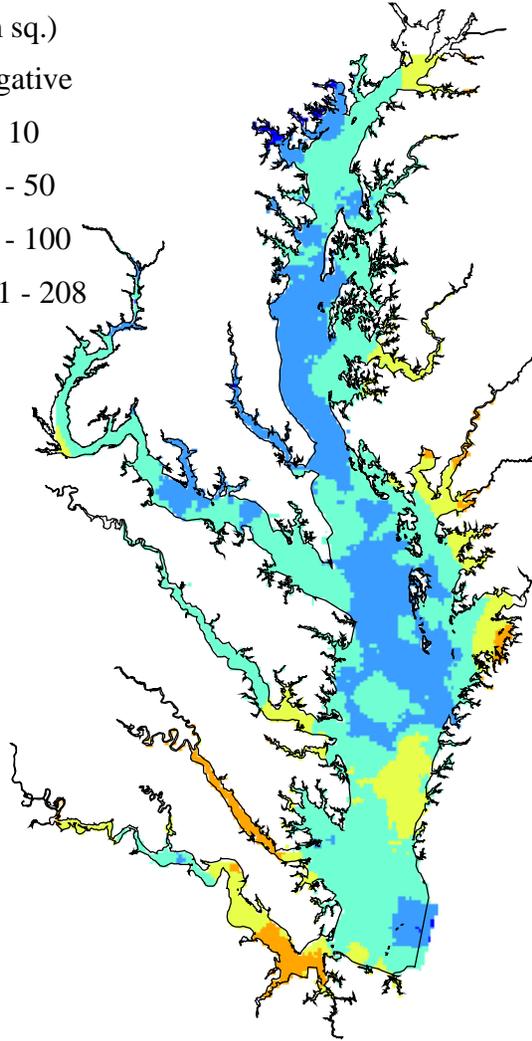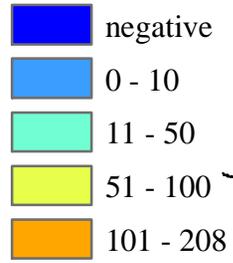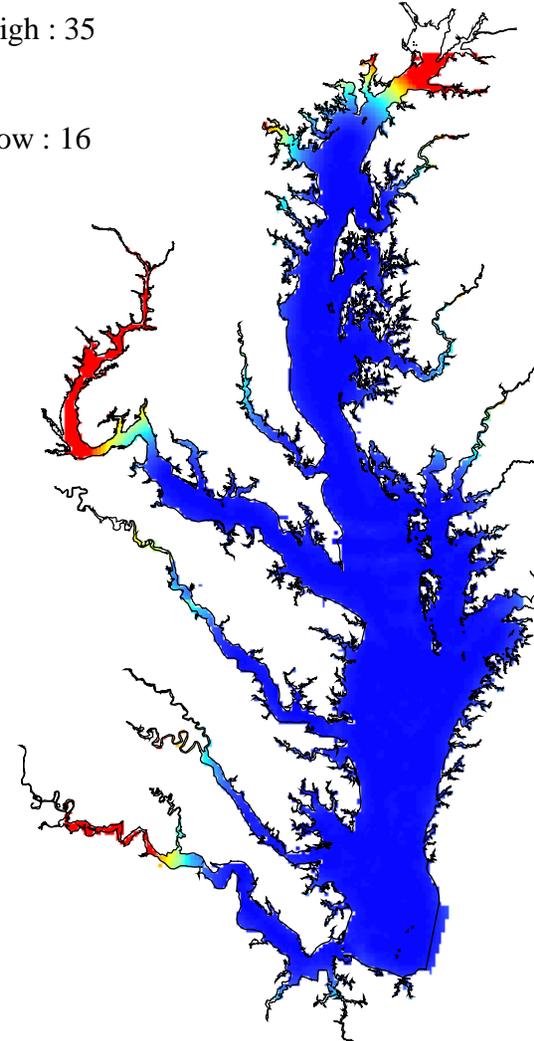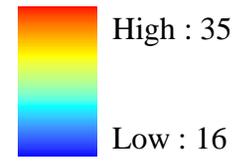
Figure 22.
a. 2000 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)
- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250
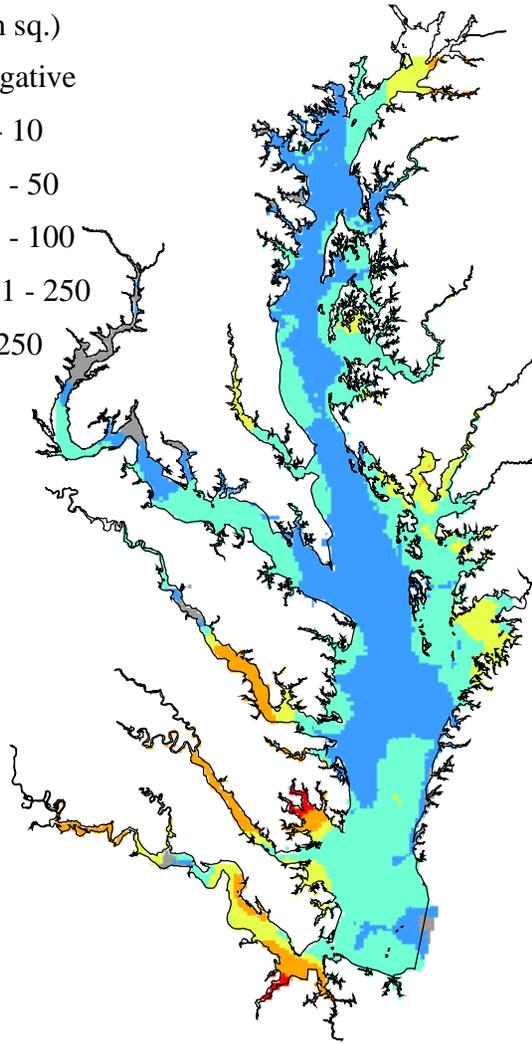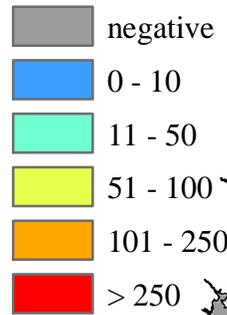
Standard Error
High : 41
Low : 14
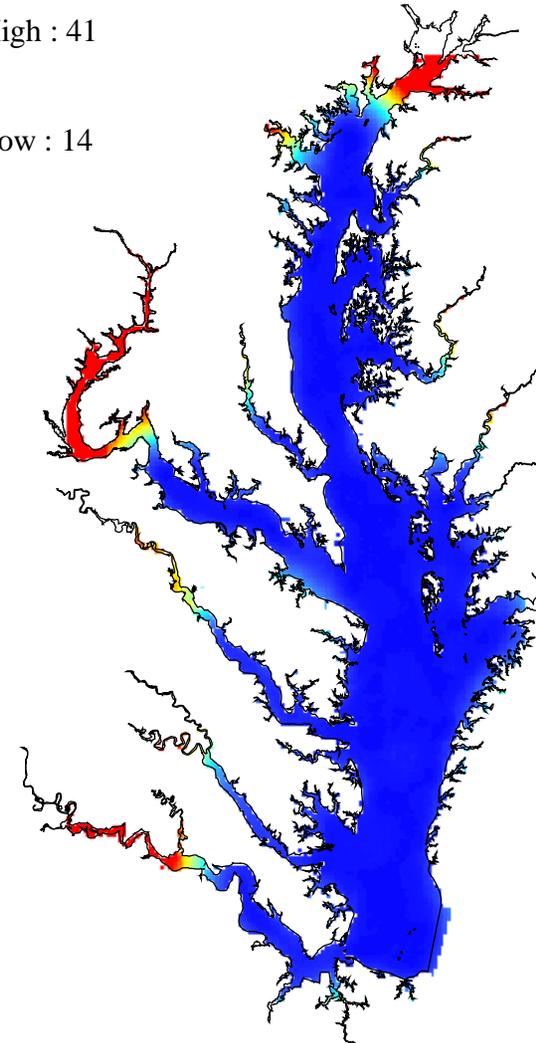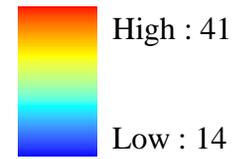
Figure 23.
a. 2001 Blue crab density

b. Standard error of blue crab density

Blue crab density
(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 250
- > 250

Standard Error

High : 43

Low : 16
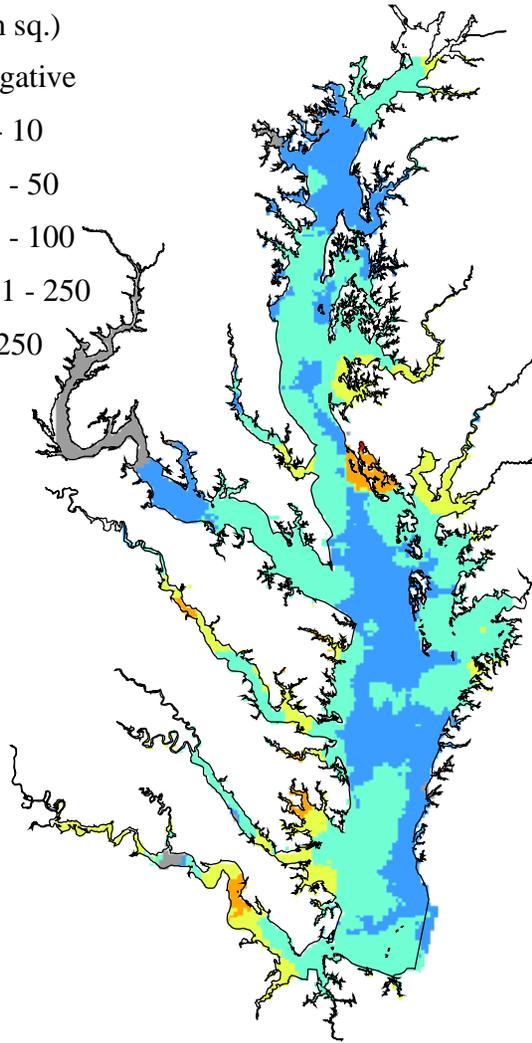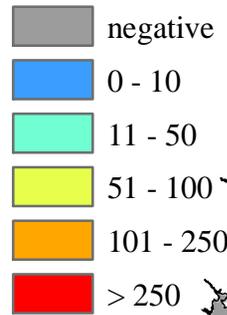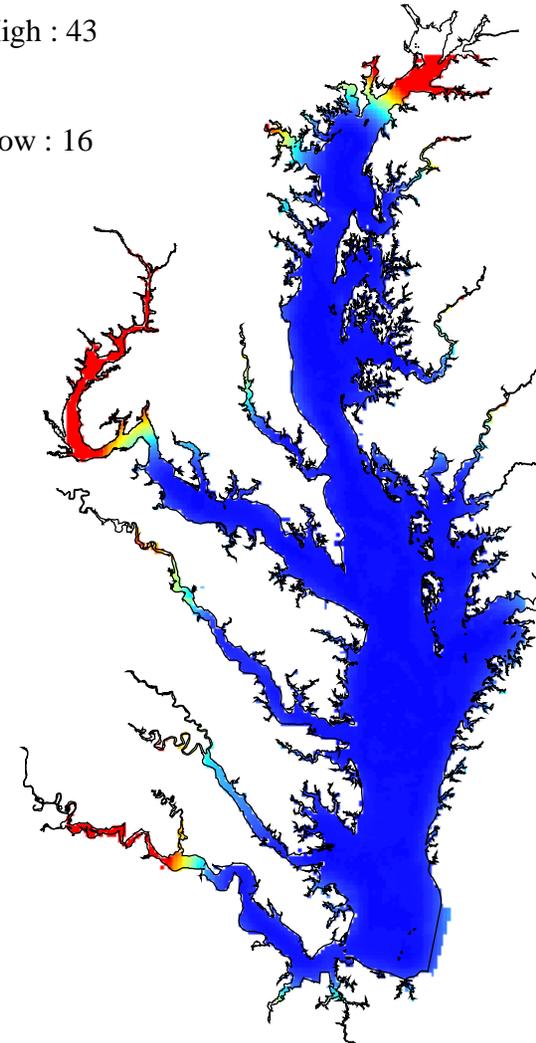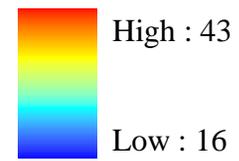
Figure 24.
a. 2002 Blue crab density

b. Standard error of blue crab density

Mean blue crab density

(#/1000 m sq.)

- negative
- 0 - 10
- 11 - 50
- 51 - 100
- 101 - 249

Trend in blue crab density

- strong decline
- moderate decline
- no change
- increase
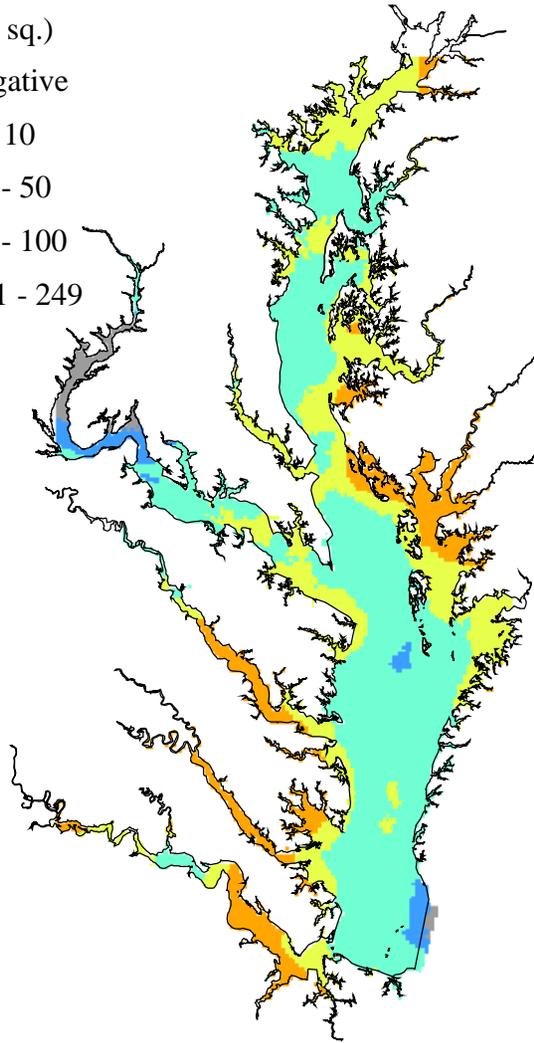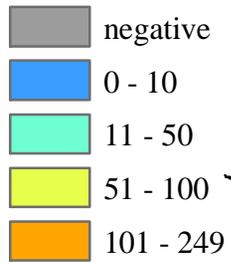
Figure 25.
a. Mean blue crab density
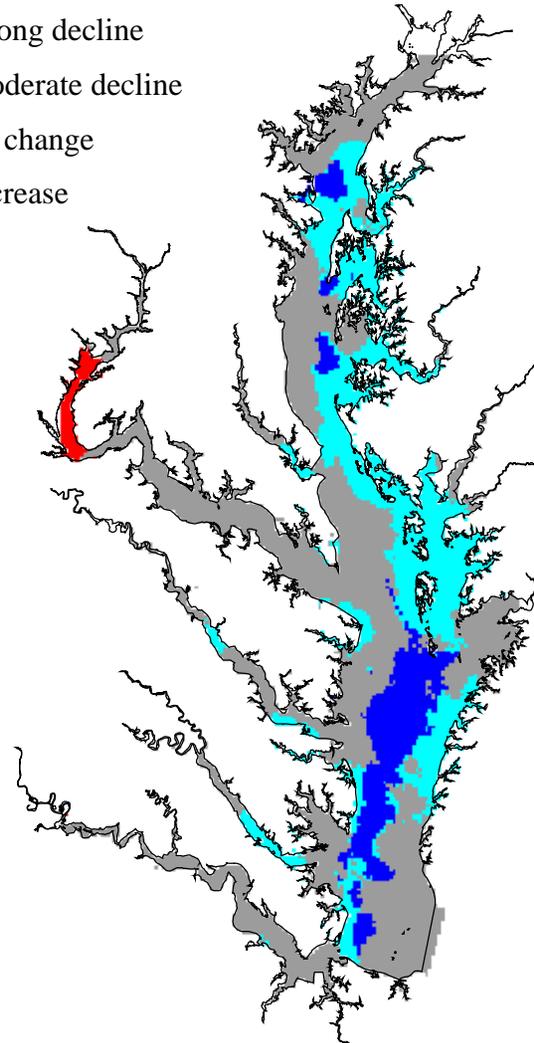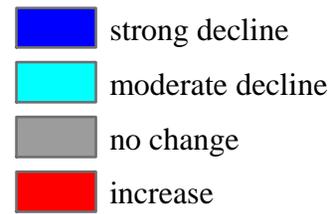
b. Trend in blue crab density

Figure 26.

Figure 27.

$R^2 = 0.5873$

$R^2 = 0.3073$

CPUE (pounds per license).

□ Geostatistical
◆ Design-based
—— Linear (Geostatistical)
—— Linear (Design-based)

Estimated Baywide Abundance (10^6)

Figure 28.

$R^2 = 0.469$

Figure 29.

$R^2 = 0.7805$

Latitude of Centroid (degrees)

Baywide Abundance (10^6)

Figure 30.

Figure 31.

Figure 32.

$R^2 = 0.0535$
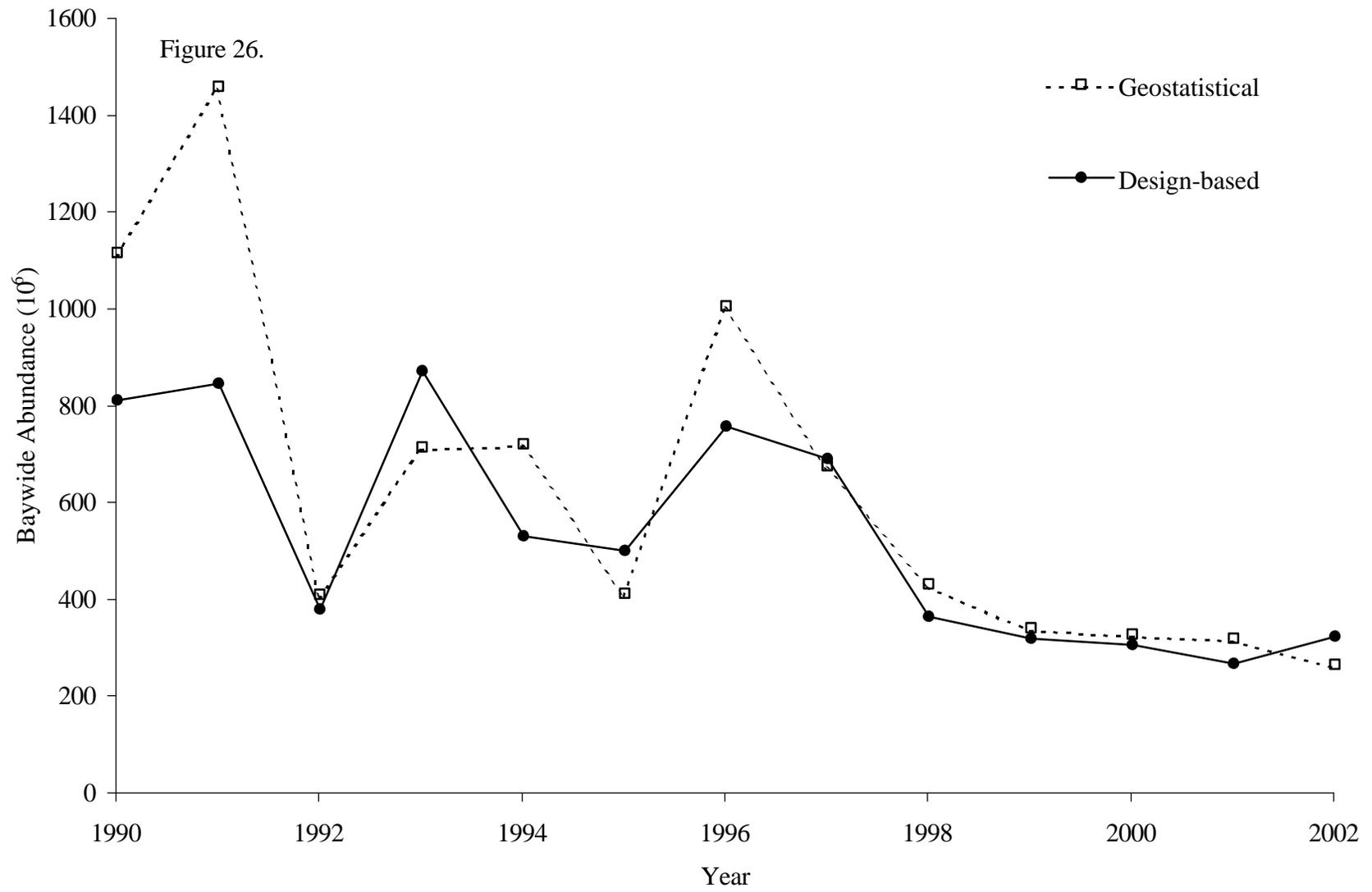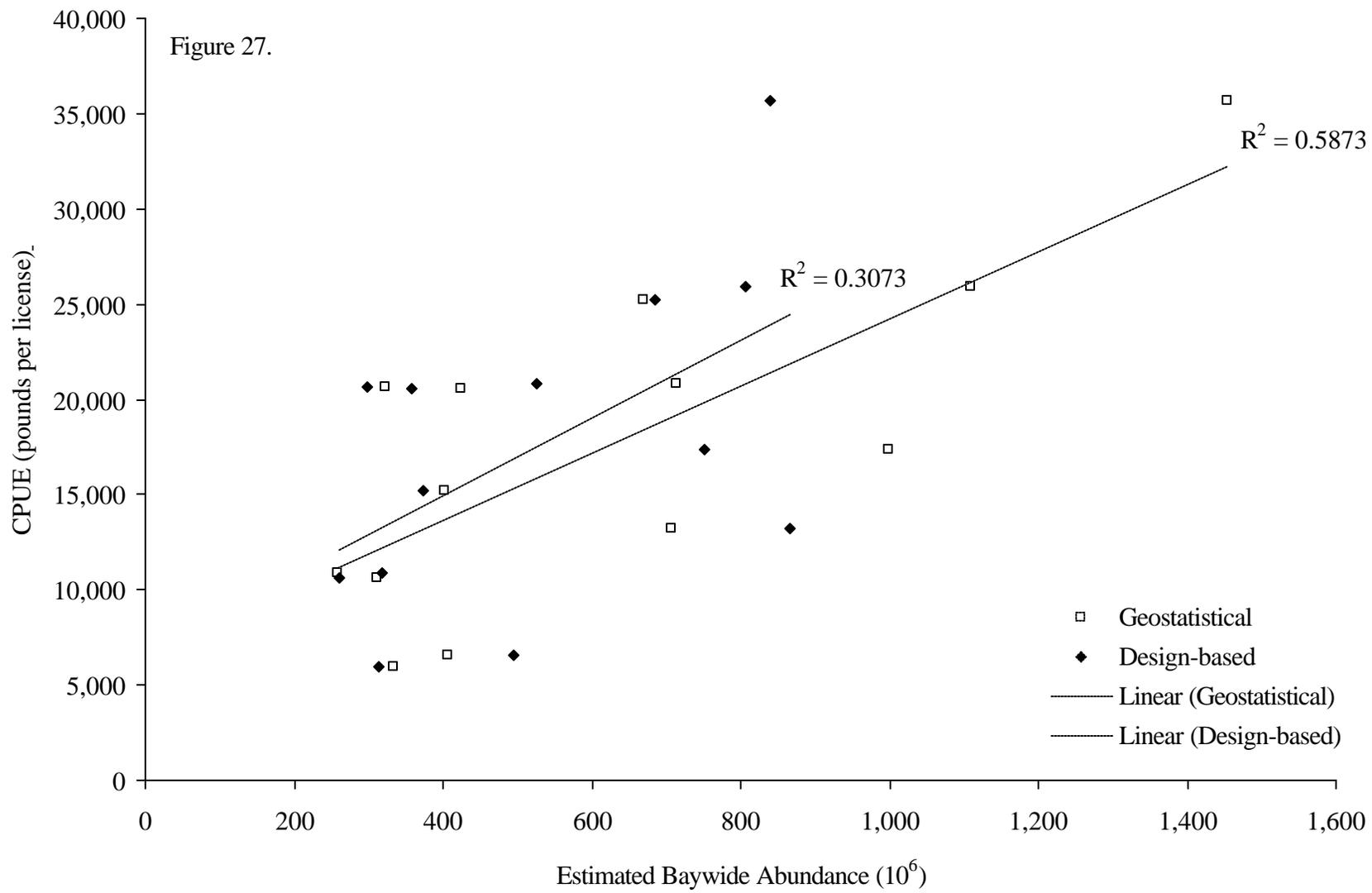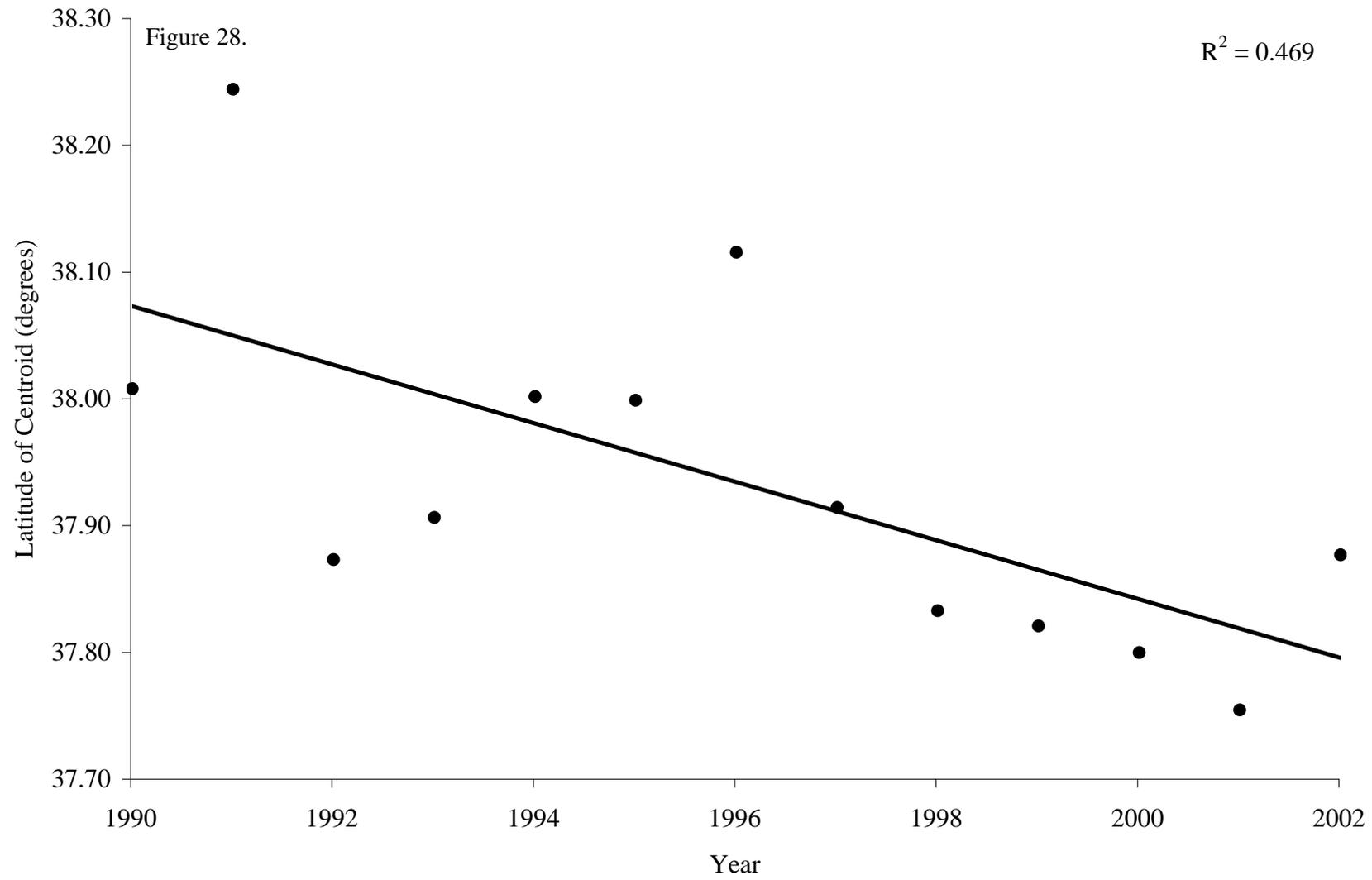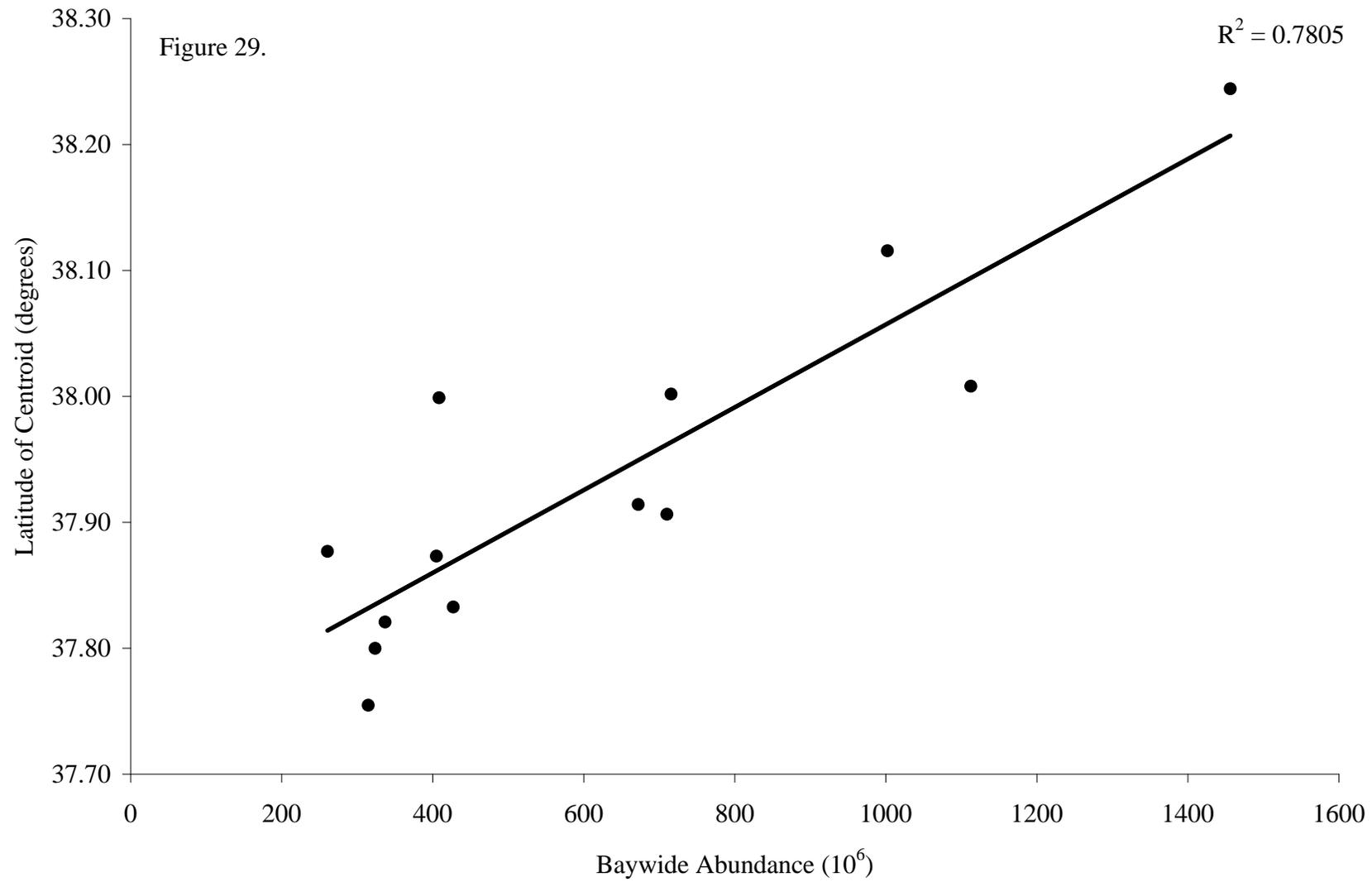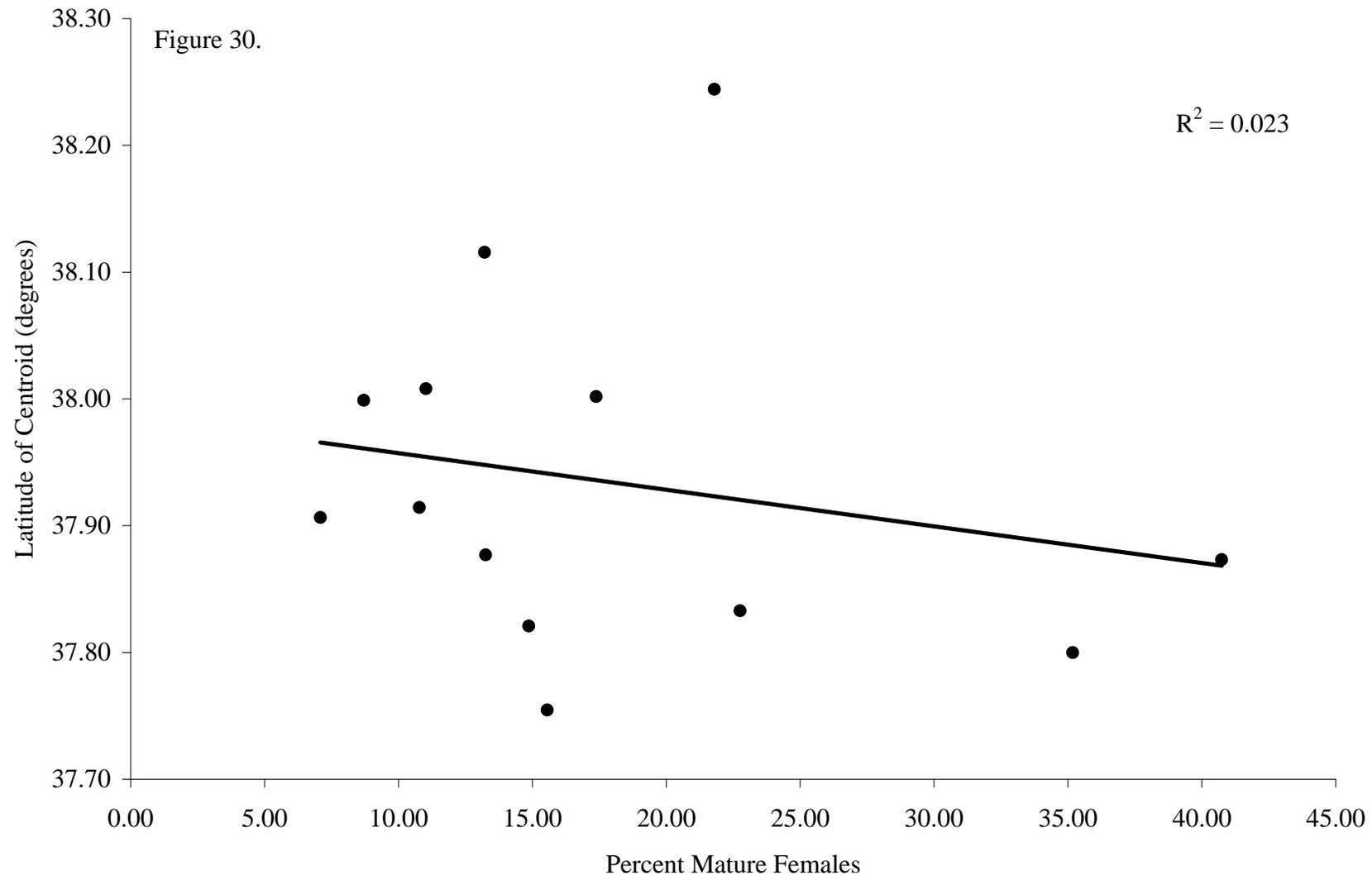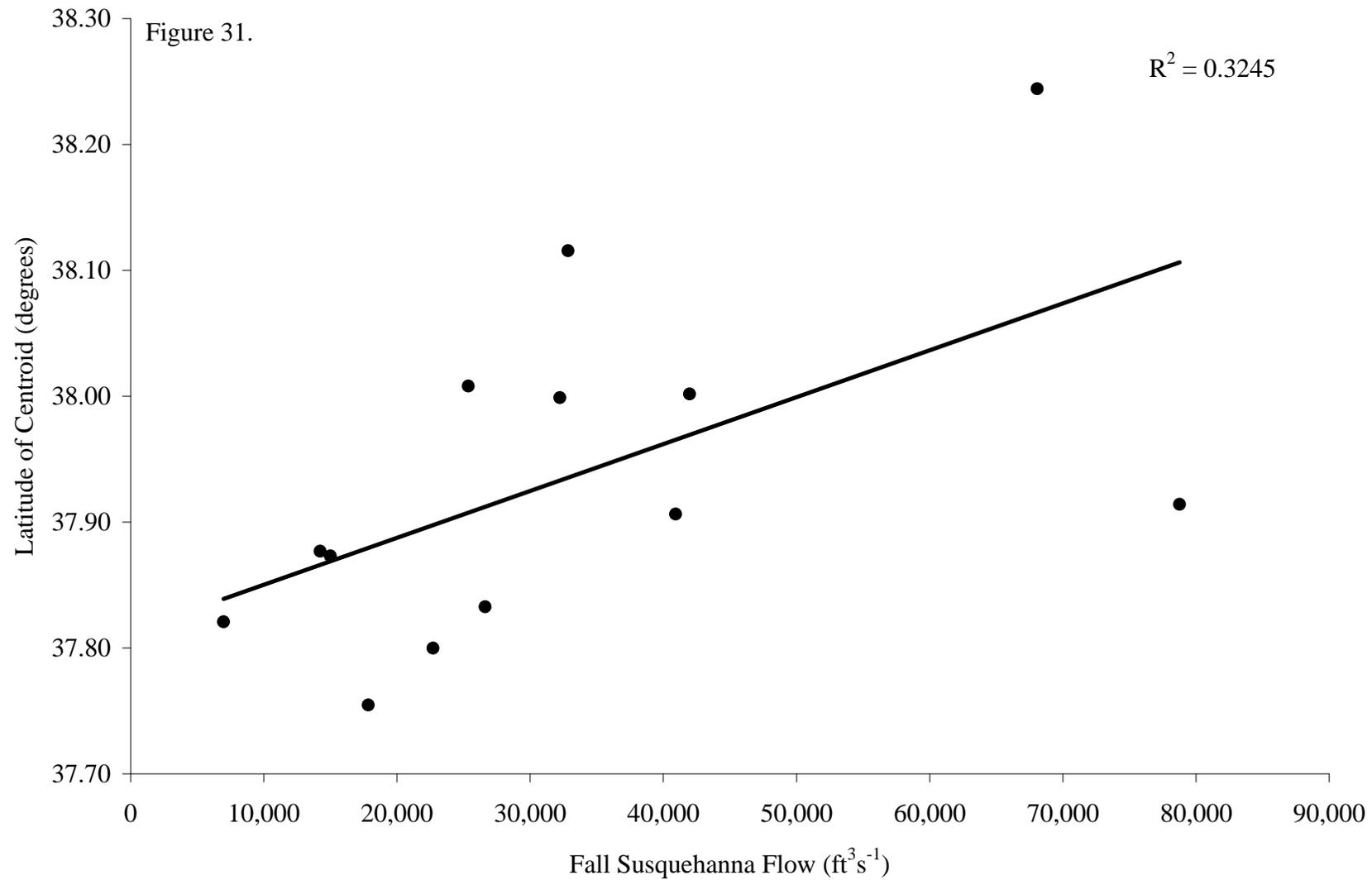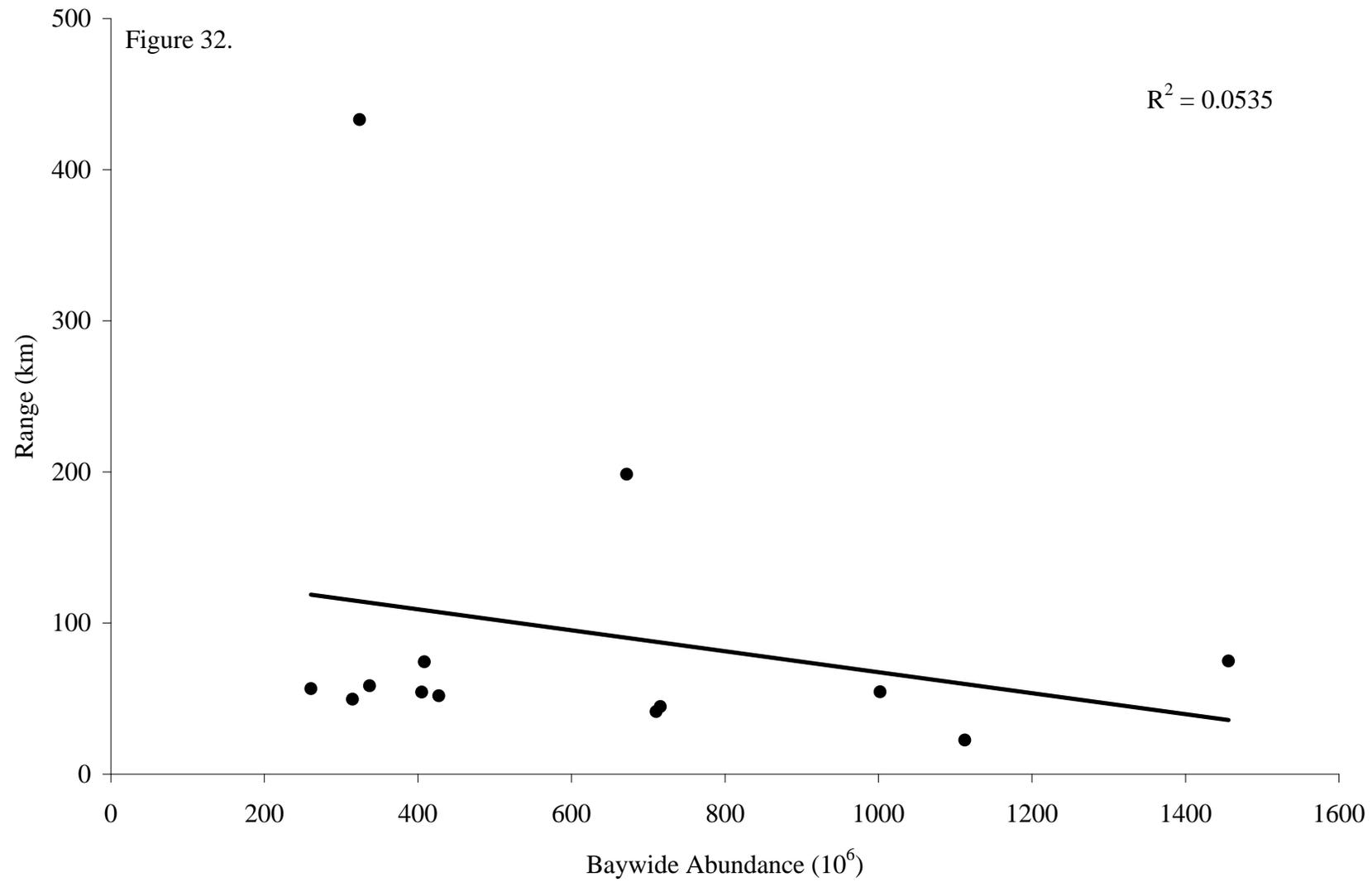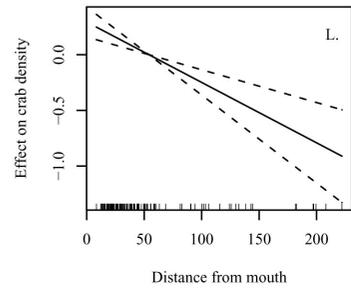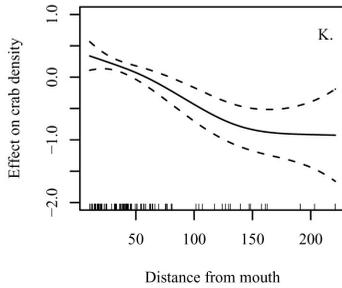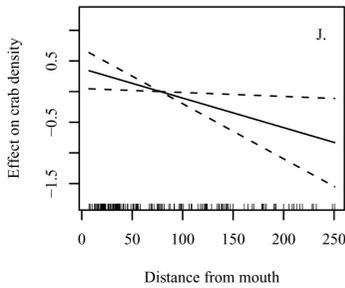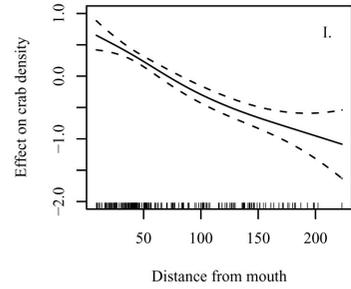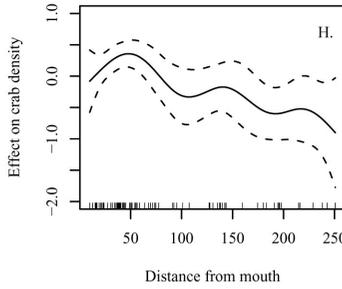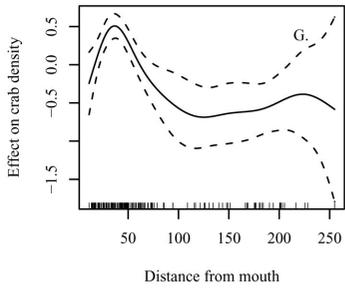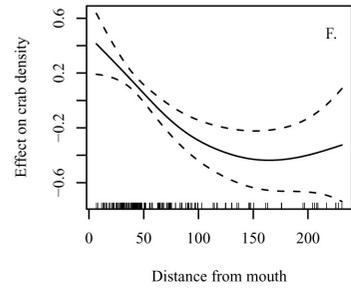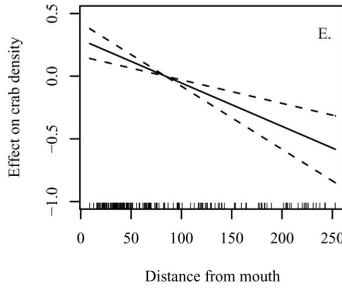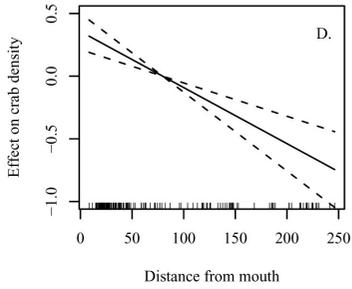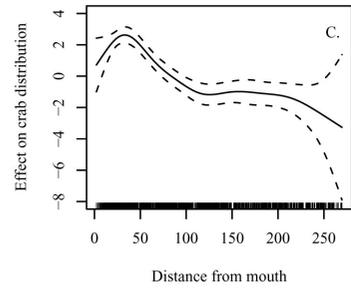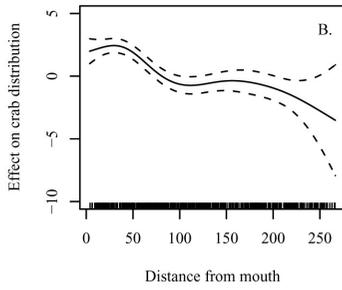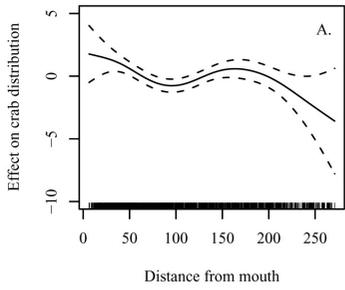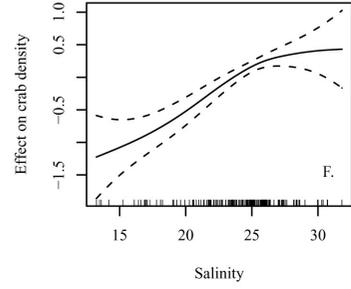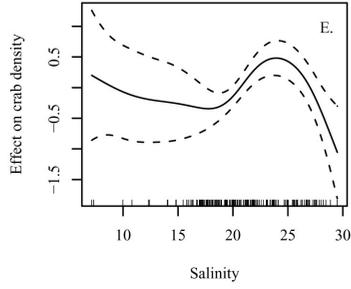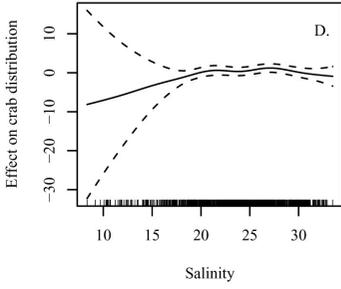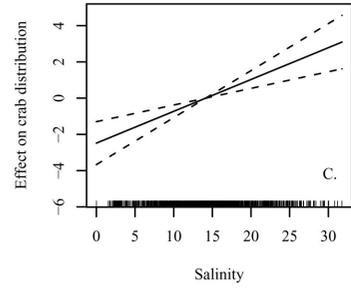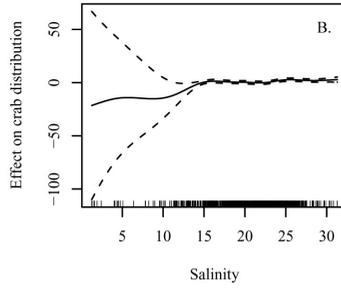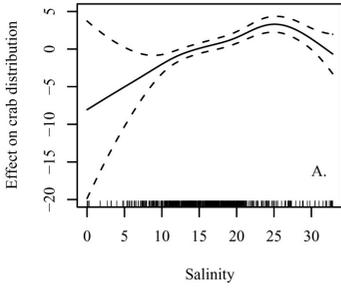
Figure 33.

Figure 34.

Figure 35.

Figure 36.

Figure 37.

$y = 1.0765x - 0.0408$
$R^2 = 0.3465$

One-to-One

Linear (Observed)
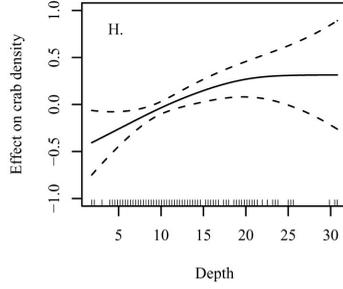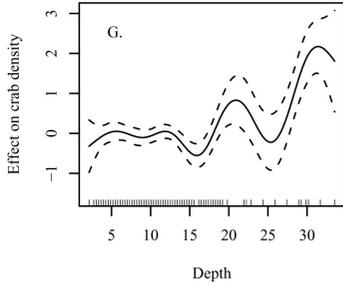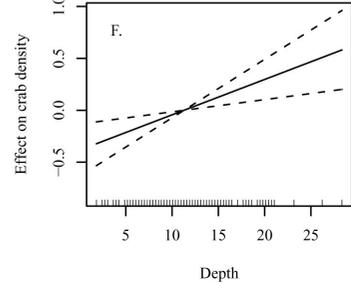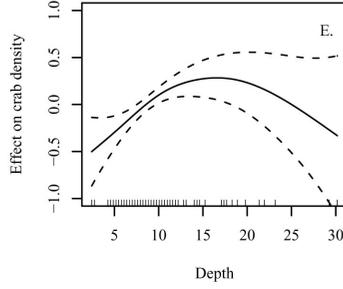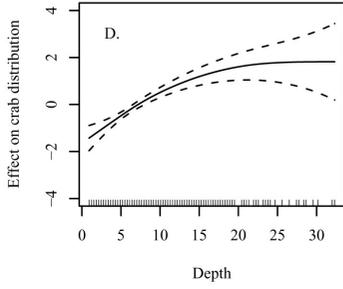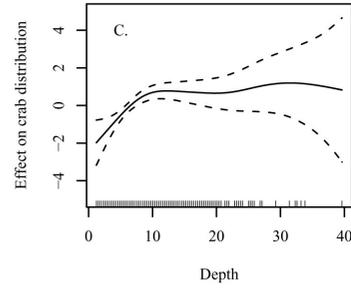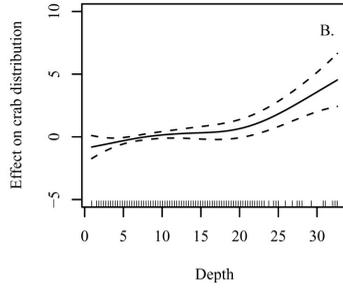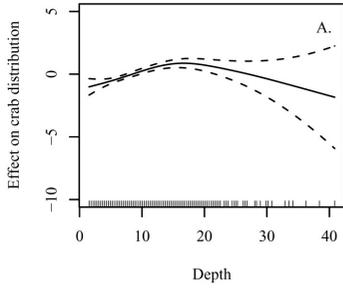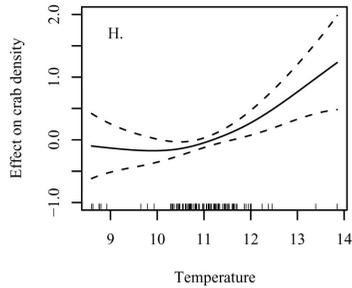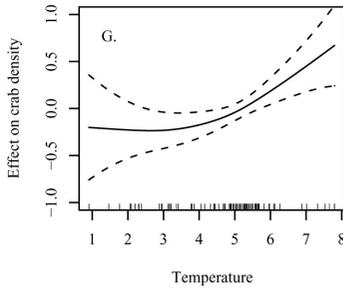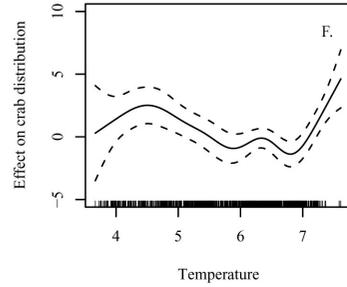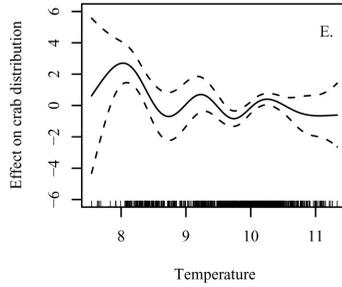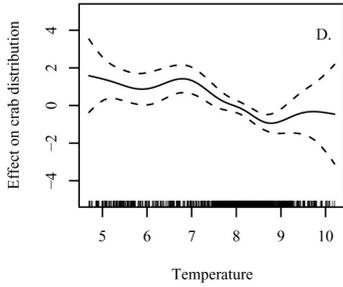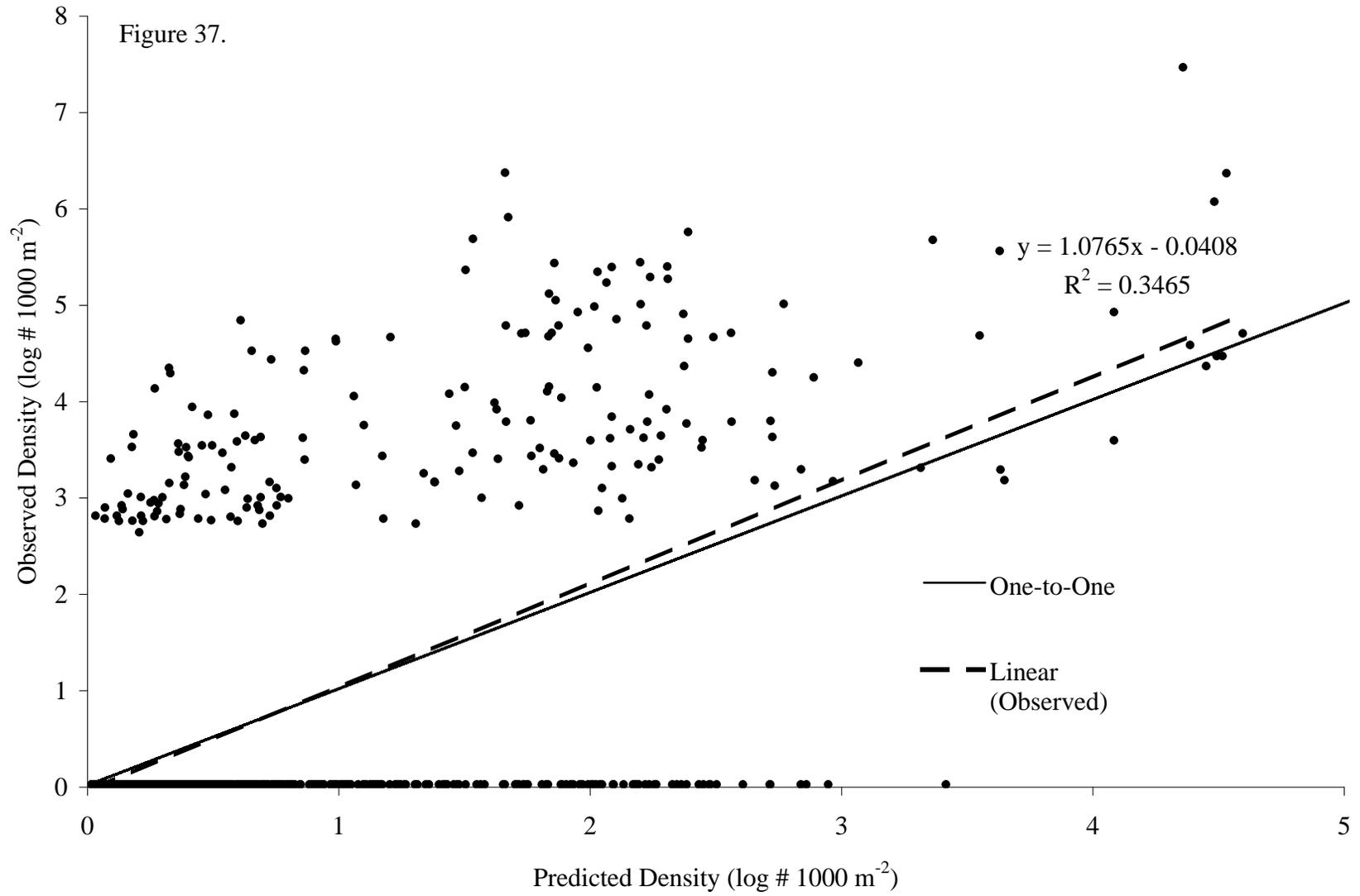
1998 Stage I
Probability of presence
- [ ] 0.00 - 0.15
- 0.16 - 0.46
- 0.47 - 0.98
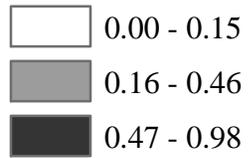
1998 Stage II
Predicted log density given presence
- [ ] 2.11 - 2.87
- 2.88 - 3.39
- 3.40 - 4.86
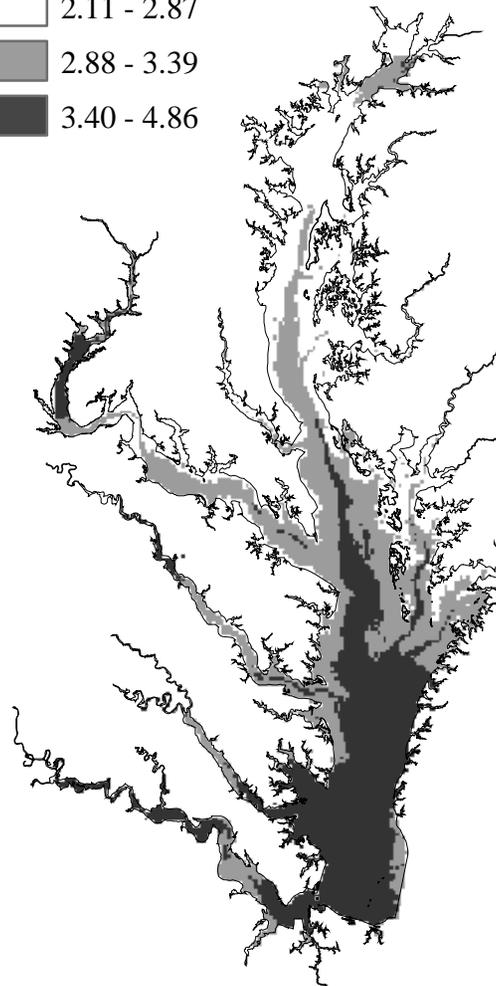
1998 Combined
Predicted log density
- [ ] 0.00 - 0.1
- 0.11 - 0.5
- 0.51 - 4.69

Figure 38.
a. Stage I

b. Stage II
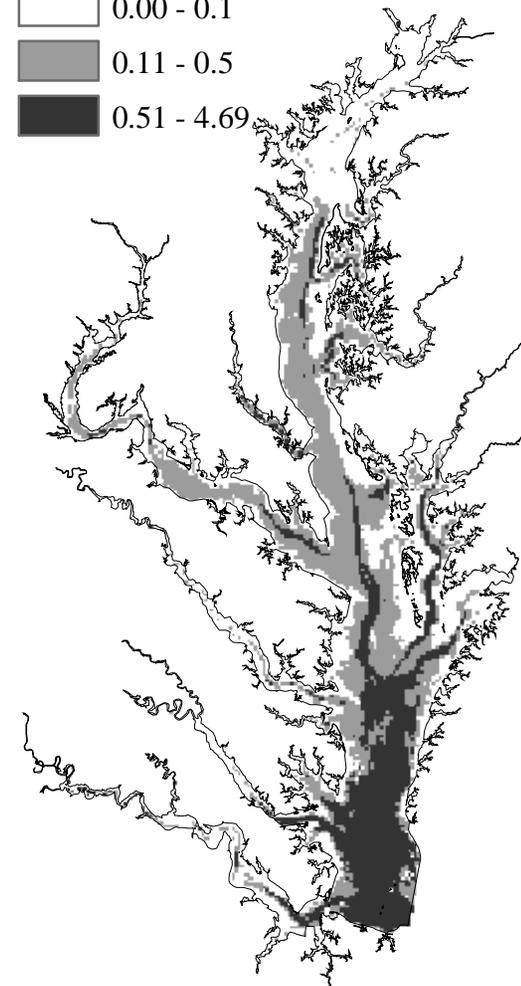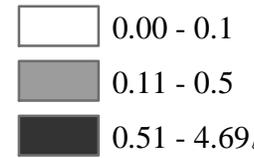
c. Combined

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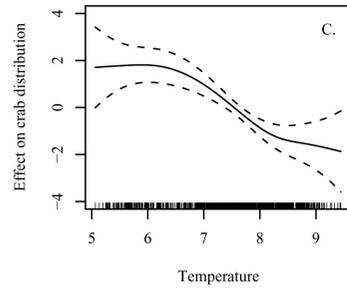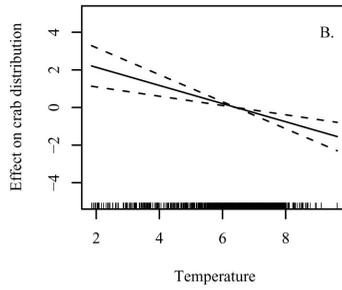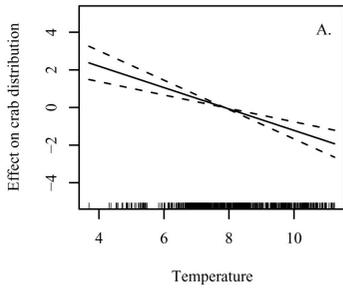Bez N (2002) Global fish abundance estimation from regular sampling: the geostatistical transitive method. Canadian Journal of Fisheries and Aquatic Science 59:1921-1931

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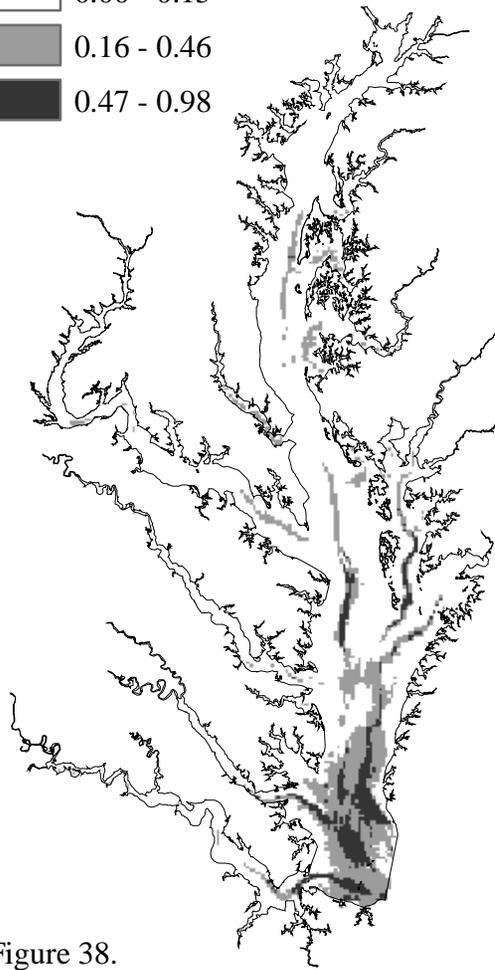
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