



An evaluation of the synchronization in the dynamics of blue crab (*Callinectes sapidus*) populations in the western Atlantic

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ABSTRACT

Interannual variability in the abundances of blue crab (*Callinectes sapidus*) in populations along the U.S. east coast is well documented, but the mechanisms driving these fluctuations remain poorly understood. Using principal component analysis and dynamic factor analysis we quantified the patterns in variability and the degree of synchrony among blue crab populations along the U.S. east coast to gain insight into the mechanisms regulating the dynamics of these populations. We determined that a latitudinal pattern in the variability in abundance among the states existed and that a combination of the Gulf Stream Index, southern winter temperature, and larval mixing in the coastal ocean may be important drivers for the observed fluctuations of blue crab. The blue crab population in the Chesapeake Bay appeared to be an anomaly in that its abundance did not match the latitudinal trend seen in the other states. Understanding the dynamics of blue crab throughout its range may help managers determine which population responses reflect local dynamics and which may reflect shared, regional responses.

Key words: blue crab, Gulf Stream Index, Moran effect, Northern Atlantic Oscillation, population dynamics, western Atlantic

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INTRODUCTION

Understanding the mechanisms responsible for the observed coherence in interannual variations in abundances of populations remains a central challenge in ecology. In some cases, populations appear to be regulated through density-dependent processes that act to maintain a population at or close to a stable equilibrium (Murdoch, 1994; Berryman, 2002; Turchin, 2003). In such cases, the level of variability in abundance is believed to vary inversely with the degree of density-dependent feedback. Two generally accepted density-dependent mechanisms, competition and predation, invoke intra-specific interactions to determine the degree of regulation in a particular population (Hixon *et al.*, 2002). Both of these processes can regulate population size by limiting population growth at high densities through either increased competition for resources or increased incidence of predation. Analyses of density-dependent mechanisms reveal characteristic lags in the responses of population abundances (May, 1974).

Density-independent control has also been used to explain the coherence of population abundances (Andrewartha and Birch, 1954). Under this modality, two populations may fluctuate in a similar manner due to a common external driver affecting both populations. This has been termed synchronization (Liebhold *et al.*, 2004). Two density-independent processes have been implicated in synchronization. Dispersal of individuals resulting from physical or biological processes may cause exchanges of individuals between different populations, thereby inducing synchronization in the dynamics of both populations (Cowen *et al.*, 2006). A common response to environmental factors can also induce synchronization (i.e., Moran effect; Moran, 1953). Moran effects have been identified in numerous terrestrial and aquatic studies for a variety of environmental factors, including broadscale climatic indices such as the El Niño Southern Oscillation (ENSO; Cheal *et al.*, 2007; Lima *et al.*, 2001, 2002) and the North Atlantic Oscillation (NAO; Fromentin and Planque, 1996; Post and Stenseth, 1999; Forchhammer *et al.*, 1998). Regardless of whether it is dispersal, a Moran effect or

another mechanism that is primarily responsible for density-independent synchronization, it has been hypothesized that the degree of synchrony will be inversely related to the geographic distance separating two populations (Liebhold *et al.*, 2004). This inverse relationship has been termed spatial synchrony (Liebhold *et al.*, 2004).

The blue crab, *Callinectes sapidus*, is one species whose populations could potentially be synchronized as a result of dispersal, environmental forces, or a combination of both due to its complex life history. Blue crabs are commonly found in estuarine and coastal ecosystems in the western Atlantic from Cape Cod, MA, USA, to northern Argentina, although they can be found as far north as Nova Scotia, Canada, during warm conditions (Williams, 1974). Genetic and conventional tagging data suggest the possibility of spatially separated populations along the Atlantic coast (McMillen-Jackson *et al.*, 1994; McMillen-Jackson and Bert, 2004). The geographic separation of populations suggests that the Moran effect could potentially play a role in the synchronization of adult blue crabs. The life cycle of each blue crab population follows a general pattern, although the timing of key events varies latitudinally (Hines *et al.*, 2010). Winter temperature appears to be an important control in regulating abundances and the timing of events (Bauer and Miller, 2010). Generally, adults mate in estuarine waters in autumn. Impregnated females subsequently migrate to the mouth of the estuary, overwinter, and release larvae into the coastal ocean in late spring. Larvae return to estuaries where they settle as juveniles and remain for the duration of their lives, with negligible migration to other estuaries.

The Atlantic seaboard of North America is characterized by a wide, shallow shelf that can be divided into a few connected, large marine ecosystems (LMEs; Sherman, 1994). Many marine and estuarine species are broadly distributed across this shelf (Longhurst, 2001) and, because of this, individual populations within these LMEs likely experience common patterns of forcing. Nye *et al.* (2013) recently evaluated the effects of climate forcing on north Atlantic marine ecosystems and demonstrated patterns of broadly coherent responses in the productivities and distributions of a number of ecologically and economically important coastal and marine species within the basin. There are several broad scale indices of climate forcing for the north Atlantic, including the Atlantic Multi-decadal Oscillation (AMO; Nye *et al.*, 2013), the NAO (Ottersen *et al.*, 2001) and the Gulf Stream Index (GSI; Taylor, 1996). Each index reflects different aspects of the climate system within the basin.

The AMO is an index of sea surface temperature (SST) anomalies for the region 0–60°N over a period of approximately 65–70 years (Nye *et al.*, 2013). Nye *et al.* (2013) summarize published correlations between the AMO and the distribution of phytoplankton and zooplankton species, the distribution and catches of marine and anadromous fishes, and the structure of fish assemblages. Because the AMO is a direct reflection of SST patterns, it is likely that the mechanisms behind the reported correlations between population and ecosystem effects and the AMO relate to the degree of stratification in the water column and its subsequent effects on productivity.

The NAO is a measure of the atmospheric pressure difference between the Arctic and subtropical Atlantic, and is a prominent and recurrent climate pattern within the basin (Hurrell *et al.*, 2003). A power spectrum of the NAO does not appear to exhibit a dominant frequency, although biennial variability is common (Hurrell *et al.*, 2003). Indices can be calculated for any period of time, but a winter (December–March) NAO index is the most common, largely because it exhibits the most variability and is most clearly correlated with broad spatial and temporal teleconnections (Hurrell *et al.*, 2003). Indeed, Hurrell and Deser (2009) reported that the summer (June–August) NAO index exhibits the minimum temporal variability. Accordingly, we use a winter NAO index hereafter. As with the AMO, the NAO has been correlated with a wide diversity of population and ecosystem effects in both terrestrial and marine ecosystems (Ottersen *et al.*, 2001). Brodziak and O'Brien (2005) have shown that the NAO influences recruitment anomalies of groundfish in the western Atlantic. Hare and Able (2007) have shown the NAO is a predictor of the abundance of Atlantic croaker, *Micropogonias undulatus*, in the mid-Atlantic. Peer and Miller (2013) have demonstrated a correlation of the NAO with the phenology of spawning of striped bass, *Morone saxatilis*. However, because the NAO is an index of atmospheric conditions, mechanistic explanations of the correlations reported above are less direct than they are for the AMO. For example, Hare and Able (2007) invoke a northward latitudinal displacement of a relatively cold water mass along the US mid-Atlantic coast to explain the increases in croaker abundances they document.

A third regional index of climate reflects the position of the north wall of the Gulf Stream, the GSI (Taylor, 1996). Taylor invoked a relationship between the sinuosity of the Gulf Stream and the path and frequency with which cyclonic weather systems traverse the Atlantic and plankton communities in the approaches to the English Channel. More recently,

Nye *et al.* (2011) have invoked changes in the path of the Gulf Stream to explain northward shifts in the distribution of silver hake, *Merluccius bilinearis*, in the northwest Atlantic. As with the NAO, the mechanisms behind the reported correlations are less direct than with the AMO, but they are likely related to changes in the distribution of warmer bottom water (Nye *et al.*, 2011).

In addition to the three broad climate indices discussed heretofore, indices that reflect local conditions can also be defined. Such local indices have also been shown to be correlated with local population and ecosystem responses. Frank *et al.* (2005) use indices of bottom water temperature and stratification on the Scotian Shelf, to explain a lack of recovery of Atlantic cod, *Gadus morhua*, and other groundfish even after a fishing moratorium was instituted. At a smaller scale, Collie *et al.* (2008) report a strong correlation between fish community structure in Narragansett Bay and Narragansett Sound, RI, and spring–summer SST. Often the mechanisms underlying the reported correlations at these smaller scales are clearer.

Analyzing the temporal responses of species to abiotic and climate factors, such as those discussed above, is a complex statistical problem. Often multivariate techniques, such as principal components analysis (PCA), have been used to detect patterns (Sirabella *et al.*, 2001). Although PCA has been successfully applied to detect abiotic influences on the dynamics and distributions of marine species, the technique assumes that observations are independent, thereby ignoring the autocorrelation inherent in time series data. However, traditional multivariate time series approaches require extensive time series for accurate parameter estimation. Recently, Zuur *et al.* (2003a) developed an approach for multivariate time series, termed dynamic factor analysis (DFA), which can reliably analyze shorter time series that are characteristic of ecological data. The approach decomposes time series into a finite number of common trends. Zuur and colleagues have used DFA to analyze patterns in both invertebrate and fish species (Zuur *et al.*, 2003b; Zuur and Pierce, 2004). In both cases, the fisheries time series were shown to parallel patterns evident in the NAO. More recently, Katara *et al.* (2011) have used the technique to evaluate drivers of the coherent dynamics of anchovy, *Engraulis encrasicolus*, and sardine, *Sardinops sagax*, in the eastern Mediterranean.

Here we evaluate patterns in the variability in populations of blue crab from Florida to Delaware Bay to assess the degree of synchrony among neighboring populations. Additionally, we seek to evaluate the potential role of several potentially key environmental

variables in influencing crab population dynamics: the NAO, the GSI, regional winter temperature and sun spot number. We considered the NAO and GSI separately even though they are significantly correlated ($r = 0.43$, $P = 0.01$) because the NAO is a more complex phenomenon than the GSI and therefore blue crab populations may be influenced more by one than the other. We included winter temperature as an explanatory variable because of its strong role in creating an underlying latitudinal gradient in the extent of overwintering: blue crabs north of South Carolina overwinter, whereas those in the south are active year-round (Bauer and Miller, 2010). We also included sun spot number in our analyses, following Hurt *et al.* (1979), who reported a significant relationship between abundance of blue crab in the Chesapeake Bay and sunspot activity.

Our approach was to use abundance time series developed from catch-survey stock assessment models previously applied to stocks throughout the study range (Colton, 2011). Time series of absolute abundance developed from the assessment models were analyzed first using PCA to determine the degree and extent of synchrony in the dynamics of blue crab stocks. We tested the hypothesis that stocks separated by smaller geographic distances will be more similar than stocks separated by larger distances, by correlating the Euclidean distance separating each population in the PCA ordination with their equivalent geographic separation distance. Subsequently, we used DFA to determine the extent to which environmental variables explain any of the synchronization evident in both age-0 and age 1⁺ blue crab populations.

METHODS

Stock assessments

Abundance time series from each of the seven principal blue crab stocks from the U.S. Atlantic coast (Delaware Bay, Chesapeake Bay, coastal MD and VA, North Carolina, South Carolina, Georgia, and Florida – Fig. 1) were derived from stock assessments. Details of the assessment methodology and results are provided in Colton (2011) and are only summarized here. Separate assessments were developed for each region. Each assessment involved a structured population model which propagates changes in abundances of pre-recruited and recruited crabs through time (Collie and Sissenwine, 1983; Miller *et al.*, 2011) and observation models which described the fit of the observed fishery independent surveys to the process model. The structured population model can be represented as:



Figure 1. Map of the Atlantic coast of North America showing the locations of the seven principal blue crab populations used in the analysis.

$$N_{t+1} = \left((N_t + R_t) \cdot e^{-M/2} - C_t \right) \cdot e^{-M/2} \quad (1)$$

where N and R are the abundances of recruited (age-1⁺) and pre-recruited (age-0) crabs, C is the annual catch, M is the intrinsic rate of natural mortality, and the subscripts represent time. The model assumes a pulse fishery operating halfway through the year (Collié and Sissenwine, 1983; Miller *et al.*, 2011). Observed survey time series were incorporated in observation models which prescribed the fit between observed and model abundances for each survey. Specifically,

$$n_t = q_n \cdot N_t \cdot e^{\eta_t} \quad (2)$$

$$r_t = q_r \cdot R_t \cdot e^{\delta_t} \quad (3)$$

where N , R and t are as defined above, n and r are the survey estimates of the abundance of recruited (age-1⁺) and pre-recruited (age-0) crabs, q is a stage-specific catchability, and η and δ are lognormal error terms. Estimates of q_n were generated for each survey from:

$$q_n = \exp \left(\frac{\sum (\log(n_t) - \log(N_t))}{k} \right) \quad (4)$$

and q_n was calculated as a ratio. Likelihood components for each survey, assuming lognormal error, and penalty terms that penalized estimation of negative abundances and extreme exploitation rates were summed to provide an overall objective function. In model fitting, the objective function was minimized using a non-linear search algorithm in AD MODEL BUILDER (Fournier *et al.*, 2012). Full details are provided in Colton (2011).

Statistical analyses

We conducted three suites of analyses to determine whether synchronization was present among blue crab populations in the time series of age-0 (i.e., R_t), age-1⁺ (i.e., N_t) or total abundance (i.e., $R_t + N_t$) generated by the assessment models. The most elementary analysis was a simple linear correlation analysis, which sought to document the level of correlations among the seven different stocks. These analyses assume statistical independence both within and among

abundance time series. As such, the analyses ignore the potential role of temporal autocorrelation within the time series.

We subsequently employed a PCA to assess the extent of synchronicity among populations (McGarigal *et al.*, 2000). A PCA was conducted for total abundance of each stock using the correlation matrix. A scree plot and the percent (%) of variation explained were used to determine how many principal components to retain in the analysis. PCA was conducted using the `princomp` function in R (Package `stats` version 2.16.0). To quantify the degree of similarity in the dynamics of pairs of stocks for total blue crab abundance, we calculated the Euclidean distances between the two points representing each pair of stocks based on their coordinates on the first two PCA axes, since these two axes explained 69.4% of the variance and therefore explained most of the variability in blue crab abundance relationships among the states. This matrix of PCA separation distances was compared with the matrix of geographical distances between populations to evaluate the hypothesis that correlations will be inversely related to separation distance. Geographical distances were determined by estimating the geographic center of each state or region using ARCGIS (ESRI Corporation, Redlands, CA, U.S.A.) (Colton, 2011). Linear regressions were used for each state or region to assess the relationship between geographic and PCA distances. Similar PCA analyses were conducted for age-0 and age-1⁺ abundance time series. The results of these analyses, not reported here, were broadly similar to those for total crab abundance.

A dynamic factor analysis (DFA) was used to evaluate the relationship between stock dynamics and individual explanatory environmental factors. The underlying DFA model may be written as:

$$\mathbf{y}_t = c + \mathbf{Z}\boldsymbol{\alpha}_t + \mathbf{D}\mathbf{x}_t + \mathbf{e}_t \quad (5)$$

where \mathbf{y}_t is a vector of landings at time t , c is a constant level parameter that allows the trends to move up or down to better fit the time series, $\boldsymbol{\alpha}_t$ is a vector of common trends at time t which is multiplied by a matrix \mathbf{Z} of factor loadings for each region onto those common trends, \mathbf{x}_t is a vector of explanatory variables at time t which is multiplied by matrix \mathbf{D} of regression parameters for each region in relation to those explanatory variables, and \mathbf{e}_t represents random error with the assumption that $\mathbf{e}_t \sim N(0, \mathbf{H})$, where \mathbf{H} is a symmetric, non-diagonal covariance matrix (Zuur *et al.*, 2003a).

Two sets of DFA analyses were conducted to examine possible trends among the different blue crab populations along the western Atlantic: one set for age-0 and one for age-1⁺ crabs. For large-scale

environmental variables we used winter NAO averaged for the December–March period for each year (data obtained from the National Weather Service Climate Prediction Center, College Park, MD, USA), the GSI averaged annually (data obtained from Marine Biological Association of the United Kingdom, Plymouth, UK) and sunspot number (SSN) averaged annually (data obtained from NASA Marshall Flight Space Center-Solar Influences Data Analysis Center, Huntsville, AL, USA). For a small-scale environmental variable we used northern and southern winter temperature (Colton, 2011). In fitting the DFA to N populations, we examined between 1 and $N-1$ common trends for each of the explanatory variables and without any explanatory variables included. Akaike's information criterion (AIC) was used to determine which of the model runs was best for describing the abundance data for each age class and region. All DFA analyses were conducted in R v. 2.11.1 (R Core Development Team 2008) using a commercial interface designed specifically to implement DFA algorithms (BROD GAR v. 2.6.6 – Highland Statistics Ltd, Newburgh, Scotland).

RESULTS

Stock assessment models fitted to data from each region indicate how well each survey is explained by the modeled population abundances for both age-0 and age-1⁺ crabs (Table 1). Surveys associated with a high R^2 statistic are better indices of abundance. For example, in Delaware Bay the Delaware trawl does a much better job at predicting abundance given the parameters in the model than the New Jersey trawl does for both age classes of crabs (Table 1). Therefore, the model's estimate of absolute abundance for Delaware Bay has a pattern similar to the Delaware trawl survey (Fig. 2). The models produced absolute abundance estimates of age-0 and age-1⁺ blue crabs for each region for the period 1990–2008 (Fig. 3; Colton, 2011). Each state had at least one survey that was highly correlated with the output time series from the model and we felt confident in our estimates to be able to use the absolute abundance time series predicted by the models in our analyses.

The linear correlation analysis provided preliminary evidence that the abundances of some blue crab stocks are correlated along the western Atlantic (Fig. 4). In particular, the three southernmost states (SC, GA and FL) of the study area demonstrated significant correlations ($r > 0.65$). Abundance of crabs in the Chesapeake Bay was also significantly correlated with abundances in these three states ($r > 0.68$).

Table 1. Results for the stock assessment models. The negative log-likelihood values are for the overall model and the R^2 values represent the correlation between the observed and predicted values for each fishery-independent survey that went into the model.

	-LL	R^2
<i>Delaware Bay</i>	94.52	
Age-0		
New Jersey Trawl		0.17
Delaware Trawl		0.43
Age-1 ⁺		
New Jersey Trawl		0.03
Delaware Trawl		0.72
<i>Chesapeake Bay</i>	248.26	
Age-0		
VIMS Trawl Age-0		0.34
Maryland Trawl Age-0		0.03
Winter Dredge Age-0		0.65
Age-1 ⁺		
VIMS Trawl Age-1 ⁺		0.55
Maryland Trawl Age-1 ⁺		0.26
Winter Dredge Age-1 ⁺		0.74
CHESMMAP Age-1 ⁺		0.14
<i>Coastal Maryland and Virginia</i>	31.60	
Age-0		
Maryland Seine		0.45
Maryland Trawl		0.72
Age-1 ⁺		
Maryland Seine		0.27
Maryland Trawl		0.67
<i>North Carolina</i>	-69.47	
Age-0		
North Carolina Trawl		0.07
Age-1 ⁺		
North Carolina Trawl		0.997
<i>South Carolina</i>	33.76	
Age-0		
South Carolina Trawl		0.22
Age-1 ⁺		
South Carolina Trawl		0.90
<i>Georgia</i>	1.94	
Age-0		
Georgia Trawl		0.76
Age-1 ⁺		
Georgia Trawl		0.92
<i>Florida</i>	16.04	
Age-0		
North Indian River Lagoon (IRM)		0.03
Northeast Florida (JXM)		0.72
Age-1 ⁺		
North Indian River Lagoon (IRM)		0.74
Northeast Florida (JXM)		0.41
South Indian River Lagoon (TQM)		0.48

Coastal MD and VA, NC, and SC abundances were moderately but not significantly correlated with each other. There was little evidence of a linear correlation between abundances in Delaware Bay and the other states ($r < 0.28$).

The first two axes of the PCA for the assessment-derived total abundance of blue crabs in each region explained 69.4% of the variation in abundance. All of the regions loaded negatively on the first principal component (PC1; Table 2, Fig. 5). A latitudinal pattern was evident on the second principal component (PC2), with northern and southern regions clearly separated. Delaware Bay, the MD and VA coastal bays, and North Carolina loaded negatively on PC2. In contrast, South Carolina had a slightly negative loading, whereas Georgia and Florida loaded positively. Chesapeake Bay had a slightly positive loading, which did not follow the general latitudinal pattern.

The PCA scores (years) form a pattern on the plot, with the early 1990s being negatively loaded on PC1 and positively loaded onto PC2, the mid-late 1990s negatively loading on both PC1 and PC2, the early 2000s positively loading on PC1 and negatively loading on PC2, and the mid-late 2000s loading positively on both principal components. Therefore, the early 1990s associated with the southern states in the PCA space and the mid-late 1990s associated very closely with the northern states, suggesting a temporal pattern in addition to the spatial pattern.

Further support for the presence of spatial synchrony came from regressions of geographic distances to PCA distances for each region (Fig. 6). The stocks towards the edges of the study range (Delaware Bay, Georgia, and Florida) exhibited a strong positive relationship between the two distance measurements, whereas the states in the middle of the study range had a slope close to zero and did not exhibit a very good fit (Fig. 6). These results suggest that the northern regions exhibited broadly similar patterns in abundance and that these patterns were different than those demonstrated by the southern regions, which were also internally coherent. The mid-Atlantic regions had no distinguishable relationship because they are between the two groups of populations and therefore potentially have characteristics of each. This latitudinal grouping was reinforced if Chesapeake Bay was dropped from the regression analysis as anomalous (Colton, 2011).

Because the PCA suggested spatial separation between the northern and southern regions, we ran DFAs separately for northern (Delaware Bay – NC) and southern (SC – FL) regions. Chesapeake Bay was included in the northern DFA because even though

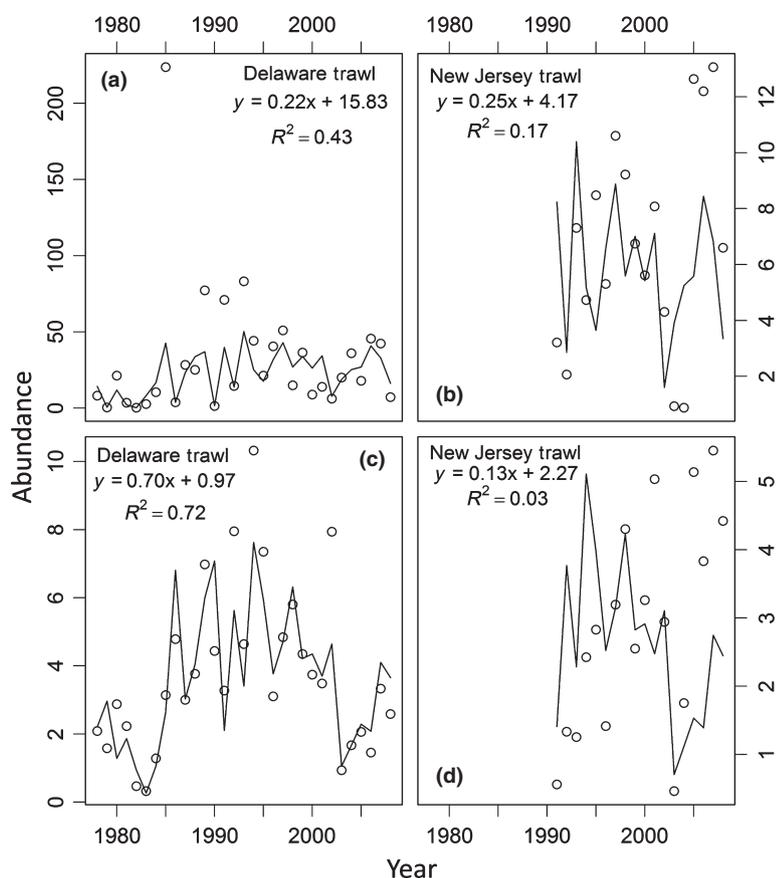


Figure 2. Model fits in the catch survey models for (a) Delaware trawl age-0 crabs, (b) New Jersey trawl age-0 crabs, (c) Delaware trawl age 1⁺ crabs and (d) New Jersey trawl age 1⁺ crabs. The observed time series is represented by the open points and the fitted time series from the model is depicted by the line. R^2 values represent the correlation between observed and predicted values.

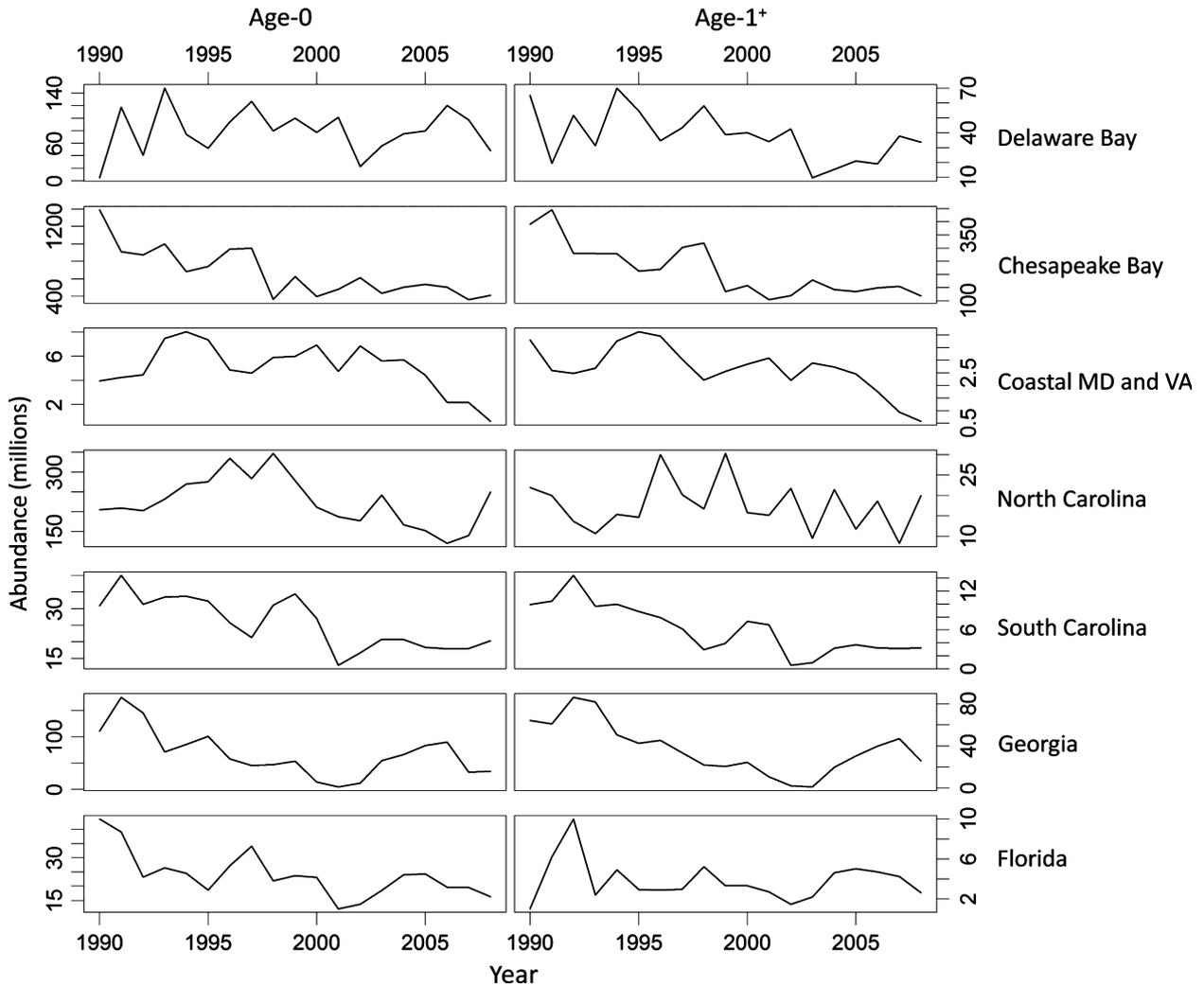
the PCA suggests it followed the pattern of the southern states, it is geographically located in the north and therefore would be influenced by northern environmental variables. Since the main goal of the DFA is to examine how the environment influences blue crab abundance we included the Chesapeake Bay in the northern analyses. We ran separate analyses for age-0 and age-1⁺ blue crabs with the goal of determining whether one life stage was more important for synchronization than the other.

The age-0 abundance data for the northern regions were best explained by a DFA model with one common trend and the GSI as an explanatory variable (Table 3). One other model exhibited a $\Delta\text{AIC} < 2$ (GSI with two trends) and was therefore also well supported by the data (Table 3). Considering the best fitting model, the Chesapeake Bay, the coastal bays of Maryland and Virginia, and North Carolina all loaded positively onto the trend, suggesting their abundances were most closely related to the trend. The model fit North Carolina well ($R^2 = 0.725$), and Chesapeake Bay and the coastal MD and VA bays moderately well ($R^2 = 0.425$ and 0.424). The fit for Delaware Bay was poor ($R^2 = 0.018$). The common trend can be

interpreted to imply that blue crab populations were decreasing during the 1990–2008 period in North Carolina, the Chesapeake Bay and the MD and VA coastal bays (Fig. 7a). The GSI was strongly and negatively correlated with North Carolina (Table 4). The other parsimonious model had the same environmental covariate, but two common trends instead of one. Like the model with one trend, the GSI was strongly and negatively correlated with North Carolina (regression parameter = -0.547). However, the first trend of the two-trend model best explained the variation in the coastal bays of MD and VA (factor loading = 0.462) and North Carolina (factor loading = 0.396), whereas the second trend best explained only the Chesapeake Bay (factor loading = 0.386). Both trends suggested a decline in blue crab abundance over the time series. The fits for this model were better for all four regions ($R^2 = 0.034$ for Delaware Bay, 0.829 for Chesapeake Bay, 0.779 for coastal MD and VA, and 0.764 for North Carolina) than for other models, suggesting that treating Chesapeake Bay as a separate trend may be appropriate.

The adult abundance data for the northern regions were best explained by a DFA model with one

Figure 3. Time series of abundances for age-0 (left) and age-1⁺ (right) blue crab estimated from application of a catch-survey model to fishery catch and survey abundance times series for each stock. For more details on the assessment methodology, see Colton (2011). Note differences in vertical scale on individual panels.



common trend and no explanatory variables included (Fig. 7b). The model fit Chesapeake Bay and the coastal MD and VA bays well ($R^2 = 0.71$ and 0.61) but provided a much poorer fit for Delaware Bay ($R^2 = 0.28$) and North Carolina ($R^2 = 0.07$). As with the age-0 northern DFA, other models (NAO with one trend and GSI with one trend) exhibited $\Delta\text{AIC} \leq 2$ and therefore were similarly supported by the data (Table 2). All three of the parsimonious models identified in the DFA contained a single common trend that showed a decrease in blue crab abundance over the course of the time series. The models differed in which, if any, covariate was included.

The DFA results for age-0 crabs in the southern region indicated that five of the 14 models examined were equally parsimonious (Table 3). These five

models varied in the number of trends and in which environmental covariates, if any, were included in the model. Those models with two trends principally separated South Carolina from Georgia and Florida. The trends in all models suggested a decrease in blue crab abundance until about 2005, when there was evidence of a possible recovery occurring up until 2008; the end of the time series. Since all parsimonious models suggested a similar pattern in abundance, results for the DFA model that had one common trend and southern winter temperature as an important explanatory variable are presented as an example. All three states were strongly and positively correlated with the trend (Fig. 7c). Southern winter temperature was strongly and positively correlated with South Carolina and Florida (Table 4). The model fit Georgia and Florida

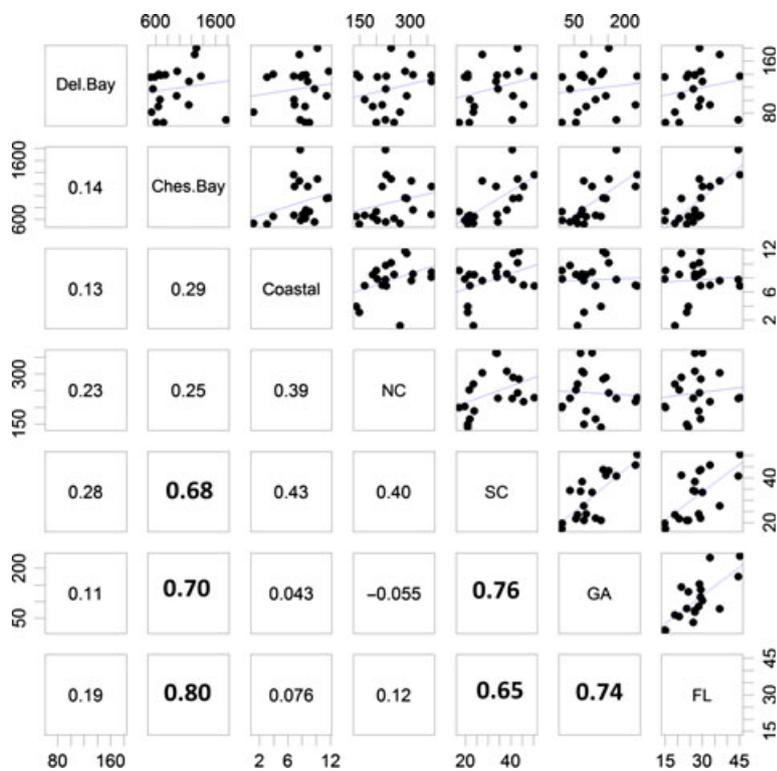


Figure 4. Results of correlation analysis among total abundances of blue crab populations. The upper panels show the scatter plot of abundances with the best fit line and the lower panels report the correlation coefficient for the corresponding two populations. Correlation coefficients that were significant ($P < 0.05$) are shown in bold type.

very well ($R^2 = 0.87$ and 0.78) and fit South Carolina moderately well ($R^2 = 0.53$).

The age-1⁺ DFA for the southern regions with the lowest AIC was the model with one common trend and the GSI as an explanatory variable (Table 3). The trend for the best model was very similar to that of the age-0 crabs except that there is a 1-year lag when the increase in the early 2000s and the subsequent decrease towards 2008 occurs. All states were strongly, positively correlated with the trend (Fig. 7d). The GSI was strongly, positively correlated with South Carolina (Table 4). The model fit South Carolina and Georgia very well ($R^2 = 0.86$ and 0.98) but fit Florida poorly ($R^2 = 0.20$). There were three other parsimonious models for age 1⁺ blue crabs (Table 3). All but one of these models suggested that one common trend was needed to best explain the data. The model that suggested two common trends were needed only moderately explained South Carolina and was weakly correlated with Georgia and Florida. The models differed in which environmental covariate, if any, were needed to best explain the data, with the GSI was important in two out of the four parsimonious models.

DISCUSSION

Our analyses provide evidence for the existence of synchrony among blue crab populations along the east

coast of the USA. The synchrony was revealed as a latitudinal gradient in which stocks from northern regions, broadly defined, were internally coherent and different from populations in southern regions that themselves were internally coherent. Specifically, based on the results of the PCA, abundances of blue crab populations in Delaware Bay, the coastal bays of Maryland and Virginia, and North Carolina exhibit similar trends to each other that differ from abundance trends in South Carolina, Georgia, and Florida, which themselves demonstrate synchrony. The Chesapeake Bay population was a notable anomaly to this pattern. All DFA trends indicated an overall decline in abundance in blue crabs over the last two decades, regardless of region or age-class. Models for the southern region indicated slight evidence of a recovery in abundance in the early 2000s, but these then decreased again so it is unclear if this region is in fact experiencing a recovery or if the increase in the last couple of years was due to natural fluctuation.

The latitudinal and temporal pattern we found among the abundance time series in blue crab from different populations clearly indicates that there is a geographic pattern in synchrony. The latitudinal pattern could be due to a Moran effect creating a northern and southern pattern in abundance. An alternative explanation would invoke patterns of larval crabs in the western Atlantic. However, little is known about

Table 2. Proportion of variance explained, loadings and scores from PCA for the total abundance of blue crab.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Proportion of variance	0.486	0.208	0.129	0.087	0.055	0.024	0.011
Loadings							
Del.Bay	-0.174	-0.295	0.900	-0.233	0.097	0.090	0.039
Ches.Bay	-0.479	0.108	-0.142	0.103	0.518	0.645	-0.208
Coastal	-0.211	-0.553	-0.400	-0.627	0.182	-0.127	0.218
NC	-0.197	-0.617	-0.059	-0.700	-0.128	0.020	0.266
SC	-0.495	-0.098	-0.048	-0.076	-0.543	-0.124	-0.653
GA	-0.446	0.37	0.004	-0.129	-0.453	0.197	0.636
FL	-0.462	0.261	0.064	0.174	0.416	-0.711	0.075
Scores							
1990	-2.851	1.741	-1.573	0.566	1.117	0.166	-0.366
1991	-3.503	1.477	0.537	0.029	-0.327	-0.381	-0.084
1992	-2.000	1.541	-0.668	-0.099	-1.058	0.214	0.087
1993	-2.044	-0.739	1.112	-1.077	0.526	0.700	-0.188
1994	-1.612	-1.368	-0.018	-0.805	-0.381	-0.172	0.073
1995	-0.873	-1.197	-1.048	-0.581	-0.861	0.472	0.203
1996	-1.115	-1.379	-0.088	1.122	0.306	0.289	0.338
1997	-1.107	-0.735	1.332	0.723	1.479	0.001	0.179
1998	-0.046	-1.758	0.448	1.075	-0.354	-0.394	0.197
1999	-0.269	-1.313	0.402	0.336	-0.364	-0.320	-0.299
2000	0.772	-0.846	-0.200	-0.682	-0.045	-0.859	-0.561
2001	2.414	-0.717	0.584	-0.698	0.318	0.461	-0.232
2002	2.597	-0.247	-1.562	-0.461	0.587	0.480	-0.159
2003	1.805	-0.291	-1.454	0.223	0.007	-0.109	0.276
2004	1.059	0.544	-0.668	-0.536	0.322	-0.624	0.258
2005	1.020	1.232	-0.109	-0.526	0.261	-0.433	0.433
2006	1.373	1.702	1.406	-0.500	-0.131	0.242	0.317
2007	2.021	1.469	1.453	-0.110	-0.084	-0.054	-0.159
2008	2.359	0.884	0.114	2.001	-0.847	0.292	-0.284

PCA, principal components analysis.

larval blue crab dispersal at this scale. Very few studies have been done on mixing of blue crab populations and the few that have, were largely focused in Delaware Bay. The published work (Epifanio *et al.*, 1989; Garvine *et al.*, 1997; Tilburg *et al.*, 2009) has centered on blue crab larval retention with the general conclusion that larvae released from Delaware Bay are either retained or transported southward and there is unlikely to be any transfer of larvae that originated in the southern estuaries into Delaware Bay. The abundance in Delaware Bay had the worst model fit in all DFAs and was not strongly correlated with any other stock in the Pearson correlations, which could potentially be a result of not receiving larvae from other estuaries.

The DFAs indicated that the GSI improves the model fit in the age-0 northern and the age-1⁺ southern abundance models, which suggests that this climatic index may relate to a transport mechanism within each region that generates the observed latitudinal pattern. We do not take this to necessarily

imply connectivity among populations. Rather we suggest that the GSI reflects conditions that promote transport of larvae back to their 'parental' estuary. Although the NAO is correlated with the GSI, the limited explanatory power of the NAO for the variability in crab populations suggests that the GSI explanatory power is due less to large-scale weather patterns and more to changes in local circulation that result from variations in the position of the Gulf Stream. However, the regression coefficients were only significant for North Carolina and South Carolina regions. The GSI reflects the position of the north wall of the Gulf Stream as it turns offshore at Cape Hatteras, so these two states may be more strongly affected simply because of their close proximity to the turning point of the Gulf Stream (Taylor, 1996). Motion of the north wall of the Gulf Stream is linked to on- and offshore modes of variability (Bane and Dewar, 1988), which may give rise to enhanced exchange between the Mid- and South-Atlantic

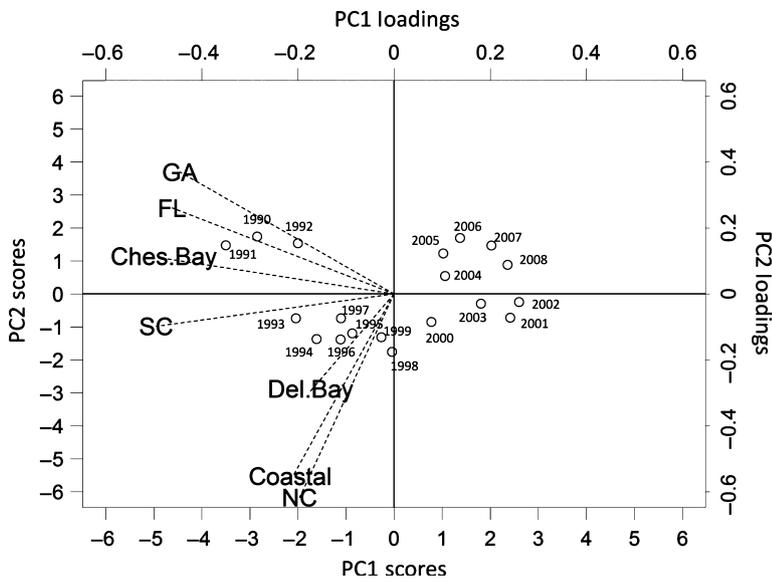


Figure 5. Principal components analysis (PCA) results for the 1st two principal components (69.4% of the overall variance explained) for total abundance. The state/regional labels represent the loadings of individual regions on each axis. The numbers represent scores for the individual years (1990–2008).

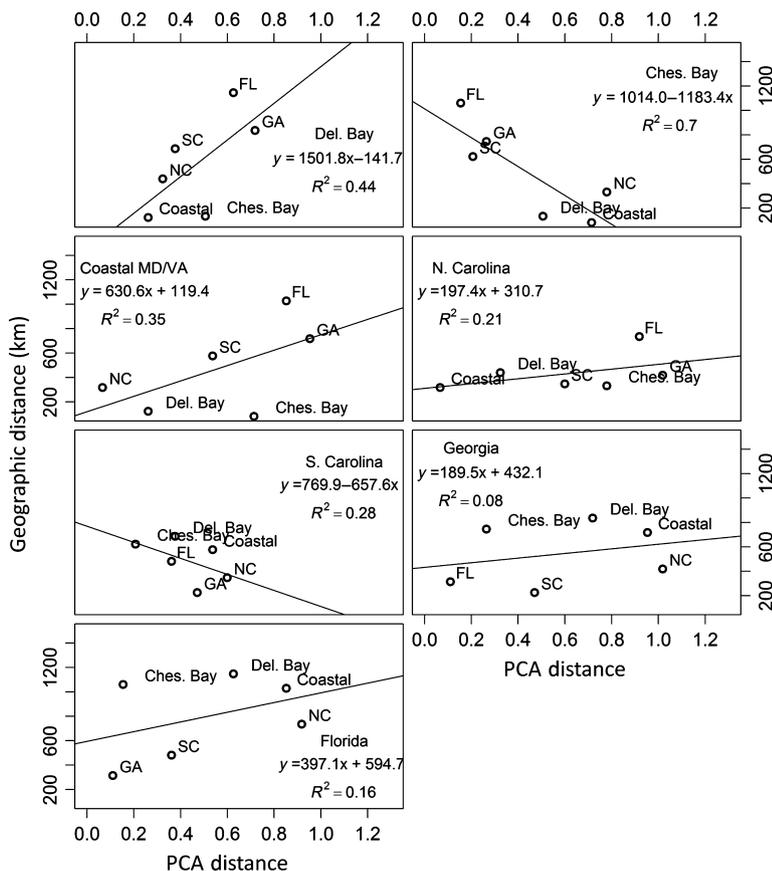


Figure 6. Plots showing relationship between Euclidean separation distances in the total abundance principal components analysis (PCA)-space from Fig. 5 and geographical distances between the indicated state/region and every other state region. Simple linear regression fits to the data are shown in each panel.

Bights, influencing the synchrony of the populations. Hypotheses that invoke larval transport processes are certainly not the sole viable explanations of the observed latitudinal grouping. For example, the

populations could be responding to variability at a regional scale in the abundance of important predators, which is itself driven by climatic forcing (e.g., Hare and Able, 2007). Alternatively, approaches to

Table 3. AIC values for DFA analyses. The best model (indicated by the lowest AIC value) is indicated in bold and is highlighted. Other potential models ($\Delta\text{AIC} \leq 2$) are indicated in bold.

	No Env.	NAO	GSI	SSN	N winter temp	S winter temp	Winter temp
NORTH Age-0							
1 trend	220.831	224.918	217.627	222.949	225.122	224.205	227.687
2 trends	221.564	221.341	218.978	261.465	225.123	227.672	231.028
3 trends	225.897	221.244	223.306	273.502	226.999	231.872	232.795
NORTH Age 1 ⁺							
1 trend	212.377	213.47	214.345	219.864	216.388	214.431	218.935
2 trends	217.264	218.345	218.586	388.931	233.599	220.47	228.561
3 trends	221.292	222.453	222.592	417.707	230.537	258.621	245.007
SOUTH Age-0							
1 trend	145.018	145.099	147.187	149.424	149.086	144.066	148.12
2 trends	145.475	145.949	147.334	153.424	152.351	148.097	154.187
SOUTH Age 1 ⁺							
1 trend	134.18	139.435	133.761	135.165	138.673	138.217	143.085
2 trends	136.05	141.221	135.68	139.165	141.475	142.217	145.118

AIC, Akaike's information criterion; DFA, dynamic factor analysis; SSN, sunspot number.

Table 4. Regression parameters (D matrix in Eqn 5) for the relationship between each region and the included explanatory variables in the best DFA analyses. Strong correlations are indicated in bold (by convention $|t| > 1.5$, Zuur *et al.*, 2003a, 2003b).

	Estimated parameter	SE	t-value
<i>Northern</i>			
Age-0, one trend, GSI			
DB	-0.167	0.267	0.626
CB	-0.061	0.217	0.281
coastal MD/VA	0.141	0.215	0.658
NC	-0.594	0.173	3.430
<i>Southern</i>			
Age-0, one trend, S temp			
SC	0.723	0.103	7.019
GA	-0.135	0.108	1.244
FL	0.588	0.105	5.624
Age-1 ⁺ , one trend, GSI			
SC	0.303	0.154	1.971
GA	-0.086	0.150	0.575
FL	-0.158	0.252	0.627

DFA, dynamic factor analysis; GSI, Gulf Stream Index.

management in the different regions might be responsible. For example, although management of blue crab is conducted at the state level, it could be argued that there is more exchange of ideas and approaches to management within the northern and southern states than there is between the two groupings: the northern states work within the Mid-Atlantic Fishery Management Council at the federal level, and the southern

states within the South Atlantic Fishery Management Council at the federal level.

Winter temperature was an important variable for age-0 southern crabs and was strongly correlated with South Carolina and Florida. Both of these states were positively correlated, suggesting that colder winters lead to lower abundances of blue crab. This is reasonable because crabs in the southern states do not overwinter and therefore colder temperatures are likely to lead to high mortality rates (Bauer and Miller, 2010; Hines *et al.*, 2010). There are also other potential environmental factors not examined in this study that may help explain latitudinal patterns in blue crab landings. Sanchez-Rubio *et al.* (2011) found that the AMO, NAO, and north-south wind momentum drive patterns in juvenile blue-crab abundance in the north-central Gulf of Mexico, explaining 25–28% of the variability. Sanchez-Rubio *et al.*'s (2011) evidence of environmentally driven abundance patterns in the Gulf of Mexico suggests that abundances of juvenile blue crabs could be synchronized through a Moran effect in the Gulf of Mexico also. Our results suggest a similar conclusion for the Atlantic seaboard.

It should also be noted that all but one of the parsimonious models that contained an environmental covariate included the NAO, GSI, or winter temperature. These three variables are correlated but differ with respect to their spatial domain. The NAO acts at the broadest scale, whereas temperature acts at the smallest scale (Hurrell and Deser, 2009). The correlations among these variables may explain why more than one model was deemed appropriate

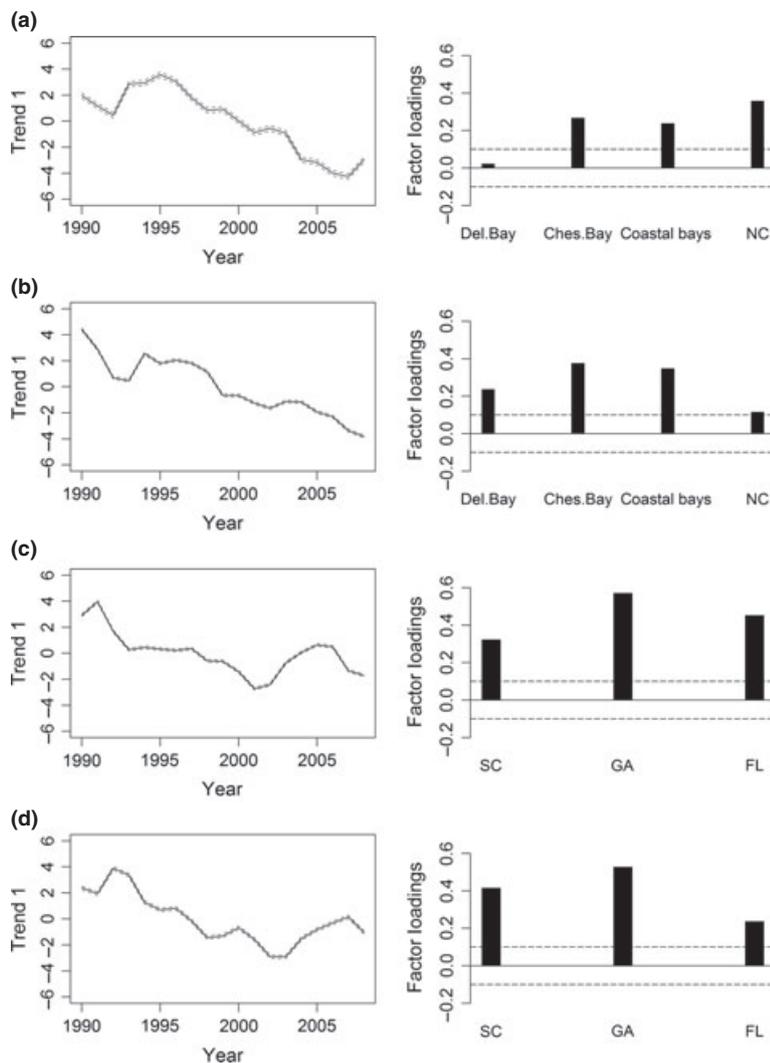


Figure 7. Results of dynamic factor analysis (DFA) analyses. Left column shows common trends from the DFA model with the lowest AIC value ($\pm 95\%$ CI) for (a) age-0 blue crabs in the northern region, (b) age-1⁺ blue crabs in the northern region, (c) age-0 blue crabs in the southern region and (d) age-1⁺ blue crabs in the southern region. Right-hand column shows equivalent factor loadings for each state/region on the common trend. Loadings falling outside the dotted lines are significantly correlated with the corresponding trend based on an arbitrarily chosen cut-off level of 0.1, which was suggested by Zuur *et al.* (2003b).

and how different models created very similar trends. The importance of climate variability in regulating abundances of blue crab could be expected to vary latitudinally *a priori* from a consideration of the species life history alone (Hines *et al.*, 2010). The shift from year-round growth in SC, GA, and FL to discontinuous growth in the more northern regions implies that seasonal restrictions on growth are likely to be more pronounced in the northern region, and thus potentially more responsive to environmental variability.

Variations in crab abundances in the Chesapeake Bay blue crab population were most similar to Florida and Georgia and thus were an anomaly to the latitudinal pattern evident among the other regions. However, when data from the Chesapeake Bay were included with the northern states for the DFA (based purely on geographic proximity), the dynamics of the

Chesapeake stock appeared broadly similar to the other stocks in the northern region, suggesting that the models for the northern regions adequately explain at least a portion of blue crab abundance trends in the Chesapeake Bay. However, it is possible that the northern age-1⁺ DFA fit is being driven primarily by the Chesapeake Bay data, as indicated by the poor fit of this DFA to the North Carolina and Delaware Bay data. The distinct dynamics in the Chesapeake Bay may reflect the fact that the Chesapeake Bay is different from other systems. This high level of productivity may impact the population dynamics of blue crab differently compared with estuaries of other stocks included in the analysis (Nixon, 1988). Another potential explanation could be that the pattern of fishing mortality in Chesapeake Bay is uniquely related to other estuaries and this drives the dynamics differently than in the rest of the coast. A closer look at what

makes the Chesapeake Bay different from its neighboring estuaries would be useful for a better understanding of where it fits into the pattern.

Overall, there are similarities in blue crab population fluctuations along the east coast and therefore some degree of synchrony is present. Density-independent mechanisms were found to drive this synchrony, with a combination of both mixing through dispersal and a Moran effect due to the GSI or winter temperature serving as these density-independent drivers, although they cannot explain all of the variability seen in the populations. Although this creates a foundation for better understanding the fluctuations in blue crab populations, more studies into the density-independent mechanisms driving blue crab fluctuations are needed to better inform management agencies along the east coast of the USA. A better understanding of the spatial variation of populations could provide more insight into what mechanisms drive fluctuations in abundance. With this information we may eventually be able to predict future blue crab abundance based on trends in ocean currents and environmental processes, which could lead to more effective management. Finally, this study presented evidence for separate northern and southern trends in blue crab abundances. A latitudinal split in synchrony suggests the need for the regional management of blue crab rather than the state-by-state management that is currently in practice.

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