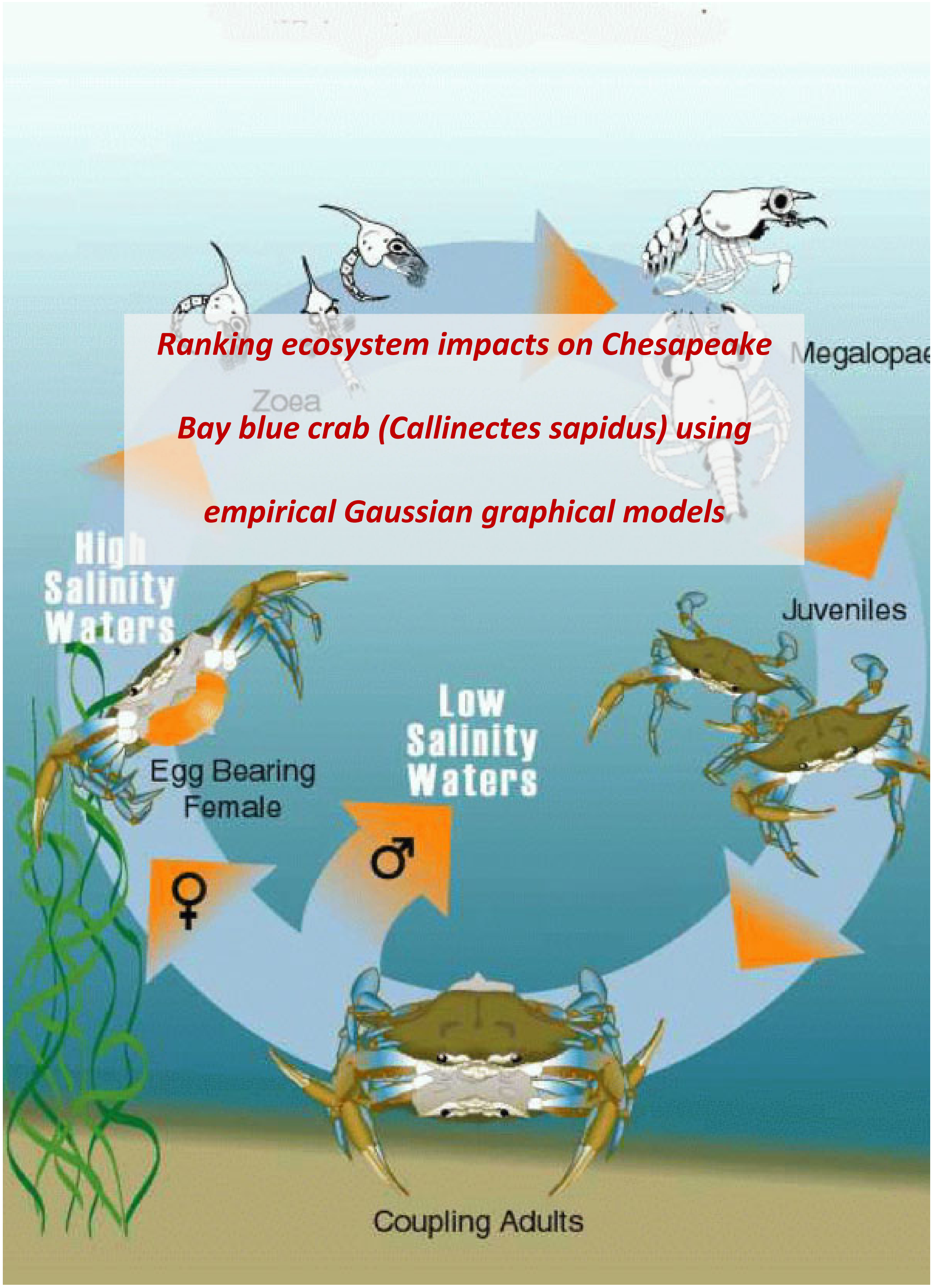
Ranking ecosystem impacts on Chesapeake Bay blue crab (Callinectes sapidus) using empirical Gaussian graphical models



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Ranking ecosystem impacts on Chesapeake Bay blue crab (Callinectes sapidus) using empirical Gaussian graphical models

Final Report

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Abstract

We applied probabilistic belief network analysis to understand variables influencing the dynamics of blue crab in Chesapeake Bay to support ecosystem approaches to manage this species. We compared multiple hypotheses regarding the role of climatic, water quality and biotic factors on the level and variability of recruitment in blue crab using a Gaussian graphic modeling (GGM) approach. Estimates of blue crab recruitment and variability in the Chesapeake Bay for 1990-2017 were derived from the winter dredge survey using model-assisted methods. Climatic variables considered included the North Atlantic Oscillation (NAO), Susquehanna River discharge, and wind forcing at Norfolk, VA. Water quality variables considered included water temperature and salinity in the Bay derived from Chesapeake Bay program monitoring program, and the hypoxic volume in the Bay. We considered the abundance of striped bass, a potential predator of blue crab, derived the Marine Recreational Fisheries Information Program as a biotic variables in our GGMs. A graph representing all possible direct and indirect pathways by which these variables affect recruitment contained 820 links. We examined three graphs modeling informative hypotheses with up to 390 links modeling 783 potential pathways of ecosystem impacts on blue crab recruitment and resilience. Both direct and indirect ecosystem effects were significant elements in the most parsimonious models for both the level and variability in blue crab recruitment. The graph for the level of recruitment was less connected than the graph for the variability in recruitment. For the level of recruitment, direct effects of age-1+ crabs and summer salinity were significant. Significant indirect effects on the level of recruitment included the phase of the NAO in summer, spring, summer and winter discharge, and the hypoxic volume. For the variance in recruitment, significant direct effects of age-1+ crabs, striped bass abundance and wind speed were detected. Hypoxic volume was the only significant indirect effect of water quality on the variability in recruitment, which in turn was significantly affected by the phase of the NAO in summer, and summer and winter discharge. Given that in the Chesapeake Bay, blue crab that recruit in the autumn of a year likely reach

market size before the next autumn, our findings of significant ecosystem effects on recruitment also suggest that exploration of ecosystem-based approaches to understanding and possibly managing harvests of this species is warranted.

Introduction

The importance of conducting fisheries management, even single species approaches, within an ecosystem-based context is becoming increasingly clear (Link 2010). Often these approaches are motivated by a desire to account for the impacts of a fishery on non-target species (Crowder et al. 2008), or by concerns over providing sufficient forage biomass to support ecosystem services (Pikkitch et al. 2012). Environmental impacts on fisheries production, whether through helping to explain variability in stock-recruitment relationships (Carscadden et al. 2000), or as a result of regime shifts (Chavez et al. 2003), or more recently in response to climate change (Nye et al. 2010) are other common motivations for ecosystem-based approaches. To account for these concerns, assessment scientists has developed a number of tools to provide advice to managers. These tools range in complexity from the addition of environmental correlates to single species models (Maunder and Watters 2003) to whole ecosystem models containing dozens of functional groups (Buchheister et al. 2017). However, scientific, regulator and financial issues can constrain application of these tools (Fogarty 2014). Assessing the importance of different interaction pathways within the fishery ecosystem is one way to help direct limited resources when initiating ecosystem-based fisheries management.

The blue crab (*Callinectes sapidus*) is an important component of estuarine ecosystems throughout its range along the Atlantic seaboard of North and South America. Blue crab supports important fisheries in many parts of its range, particularly in the Chesapeake Bay (Kennedy et al. 2007). In the Chesapeake Bay, blue crab is managed by single species limit and target reference points for biomass and exploitation rate (Miller et al. 2011). However, there is growing interest in the development of ecosystem based fisheries management for the Chesapeake Bay as a whole (Chesapeake Fishery Ecosystem Plan Technical Advisory Panel 2006), and for blue crab in particular (Maryland Sea Grant

2010). The abiotic and biotic factors that have driven development of ecosystem-based fisheries management in other systems and species are evident for blue crab. Environmental factors have been shown to impact recruitment (Applegate 1983, Tang 1985, Lipcius and Van Engel 1990). Mechanistic studies have indicated a role for seasonal patterns of wind speed and direction on annual recruitment (Olmi et al. 1990, Johnson 1995). Previous research has suggested roles for environmental factors in regulating crab populations (Hurt et al. 1979, Bauer and Miller 2010b, a). Recent research has examined the potential impacts of climate change on the dynamics of blue crab populations (Glandon et al. 2017, Glandon and Miller 2017, Glandon et al. in press). Trophodynamic relationships involving blue crab in the Chesapeake Bay have been well described (Maryland Sea Grant 2010). A full ecosystem model that includes adult and juvenile blue crab as separate nodes in the food web has been developed (Ma et al. 2010). However, an ecosystem approach to managing blue crab in the Chesapeake Bay has yet to be adopted, in part because of the scientific, regulatory and financial constraints evident in other cases (Fogarty 2014).

Empirical approaches exist to identify the important abiotic and biotic factors forcing the dynamics of fishery ecosystems. For example, Fu et al. (2012) used partial least squares regression to assess the importance of fisheries, trophodynamic and environmental drivers of productivity in 13 northern boreal marine ecosystems. These authors concluded that temperature related variables were correlated most to total system biomass across ecosystems, and that trophodynamic factors were most related to indices of ecosystem complexity. In a similar analysis, Mcowen et al. (2015) investigated the role of a suite of abiotic and biotic factors in regulating fisheries production in 47 marine ecosystems using dynamic factor analysis. Mcowen and colleagues concluded that bottom up forcing dominated in highly productive, overfished ecosystems, whereas predation dominated in under-exploited ecosystems. These empirical approaches seek to elucidate generalities among ecosystems. Can empirical approaches be used to explore the importance or strength of interactions within a single ecosystem as a guide to prioritizing data collection and modeling in developing an ecosystem approach to fisheries management?

Network models offer a potential approach to addressing this challenge. Networks can be defined as “n nodes that can be arbitrarily linked to one another,” (Varis 1995). The presence of a link or path between two nodes indicates a statistical relationship between the nodes. A sequence of paths between adjacent nodes reflects a pattern of conditional dependences in which the effect of the first variable on the last is conditional on the intermediate variables. In this way, the network represents a hypothesis of how the independent variables affect the dependent variable that we are seeking to understand (Fig. 1). There are at least two common approaches to the application of network analysis to understanding abiotic and biotic impacts on species: Probabilistic belief network analysis (PBNA) and Gaussian Graphical Models (GGM).

PBNA is an objective methodology in which the prior hypotheses regarding the nature, pattern and strength of interactions (paths) between nodes within a network are used to estimate the posterior probabilities of each path or sequence of paths (Varis 1995). The relationships represented by the specific hypothesis can be generated from results of previous pairwise empirical analyses, expert judgement, or can represent proposed mechanistic relationships. PBNA then iteratively solves for the most likely network configuration. The iterative PBNA algorithm seeks to identify the variables, among those introduced, most relevant to a specific problem, and to define links in the best possible way (Varis 1995). Varis (1995) provides an example of the application of PBNA to Salmon (*Salmo salar*) in the Baltic Sea. More recently, Varis has refined the method further (Varis 1998, Varis et al. 2012). Malick and colleagues (2015) used probabilistic belief networks to identify drivers of recruitment of Coho Salmon (*Onchrynchus kisutch*) in the California Current. They found networks that included the Pacific Decadal Oscillation were four times more likely to estimate recruitment than those that contained the Pacific Gyre Oscillation or the Oceanic Niño Index. However, PBNA methods have some characteristics that currently constrain their application to questions of ecosystem–based fisheries management. For example, the performance of such models in networks of greater than 30 variables is an area of developing statistical methodology and is poorly defined. Moreover, PBNA approaches represent the biotic and abiotic elements of the environment as categorical variables rather than continuous ones – in this way the method functions more as a branching network.

GGMs can potentially overcome both constraints of PBNA approaches. GGMs represent a wide class of models for undirected graphs in which two nodes are connected if and only if the corresponding variables are conditionally dependent (Koller and Friedman 2009). More specifically, GGMs that consider path dependencies are assumed to be multivariate normally distributed, although Liu et al. (2009) showed that conditional independence is maintained under monotonic and differentiable transformation, and proposed specifically a copula transformation to enable GGM-based analyses of data with non-normal marginal distributions. Importantly, GGMs do not share the same constraint as PBNAs in terms of the size of the network, as it is possible to apply GGMs to very large networks(n>~100's – e.g., Ni et al. 2015, Jia et al. 2017). There have been a diversity of statistical tools developed for the analysis of GGMs (Rue and Held 2005, Meinshausen and Bühlmann 2006, Yuan and Lin 2007, Banerjee et al. 2008, Friedman et al. 2008, Friedman et al. 2010, Wang 2012, 2015).

The role of abiotic and biotic factors or variables in affecting the dynamics of blue crab can be represented as a network of interactions (Fig. 1). The pathways through the network and the relative importance of each pathway represent a suite of hypotheses regarding how factors combine to influence, directly and indirectly, blue crab dynamics. The likelihood of the different influence pathways can be evaluated by their relative probabilities. Here we apply GGMs to understand the relative importance of climatic, water quality and biotic variables on the abundance and variability of blue crab in Chesapeake Bay. We have selected these variable categories to reflect previously published hypotheses on what controls blue crab abundance. Our goal is to identify and rank influence pathways in determining blue crab abundance as a guide to developing an ecosystem approach to fisheries management for the species.

Materials and Methods

We selected a suite of candidate independent variables representing categories of factors: climate, water quality and biotic. These variables were used to estimate their relative influence on estimates of juvenile and adult blue crab abundance and variability. Here we describe the data sources.

Blue crab variables

The abundance of blue crab in the Chesapeake Bay has been estimated annually by the Winter Dredge Survey (WDS), a fishery-independent, stratified random survey. The survey has been conducted at approximately 1,200 stations each year during winter months when blue crab are dormant and quiescent in the sediments. Data were available for the winter 1989-1990 (termed the 1990 winter) to winter 2017. Design-based (Sharov et al. 2003), model assisted (Liang et al. 2017) and geostatistical (Jensen and Miller 2005) approaches have been used to develop estimates. Because we were interested in both the level and variation of estimates of crab abundance, all GGMs used estimates from the Liang et al. (2017) model-assisted approach. Time series of juvenile (age-0) and adult (age-1+) abundances, with their associated uncertainties, are shown in Fig. 2.

Climatic variables

i) North Atlantic Oscillation (NAO). The NAO is a broad scale climate index related to atmospheric pressure differences between Iceland and the Azores. It has been shown to have skill in explaining recruitment patterns in a number of fish species in the mid-Atlantic Bight (Wood and Austin 2009), and to influence spatial patterns of recruitment in blue crab (Colton et al. 2013). In both cases, the influence of the NAO was lagged temporally from the dependent variable. Data were accessed from the US National Oceanic and Atmospheric Administration's National Center for Environmental Prediction (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). Data were summarized as monthly mean values for 1990-2018 so that time lags between NAO and blue crab dynamics could be evaluated.

ii) River discharge. The Chesapeake Bay is a large estuary with complex dynamics, representing the balance between freshwater input and tidal input from the coastal ocean. Over 50% of the freshwater entering the Bay is derived from flow from the Susquehanna River, which drains land in New York, Pennsylvania and Maryland. The flow from the Susquehanna River has been shown to affect copepod dynamics (Kimmel and Roman 2004, Kimmel et al. 2006), oyster recruitment (Kimmel and Newell 2007) and recruitment in several fishes (Wood and Austin 2009). Data were accessed from a United States Geological Survey flow gauge at a dam near Conowingo, MD on the Susquehanna River (https://waterdata.usgs.gov/usa/nwis/uv?01578310). Data were accessed as monthly means for each year of analysis.

iii) Wind forcing. Female blue crab release offspring near the mouth of the Chesapeake Bay during summer months. These larvae are advected out into the coastal ocean where they develop for 4-8 weeks. Previous research has shown the importance of wind forcing in ensuring their return to the Chesapeake Bay in early autumn. To represent the complex potential influence of wind speed on blue crab recruitment, we accessed data from the U.S. National Oceanic and Atmospheric Administration's National Climate Data Center for Norfolk, VA airport (www.ncdc.noaa.gov/cdo-web/search?datasetid=GHCND). We used the average NW wind speed and the cumulative count of the number of autumn days with wind gusts > 12 $m.s^{-1}$.

Water quality variables

i) Water temperature and salinity. Temperature and salinity are known to influence the abundance, productivity and distribution of a range of species in the Bay. Water quality monitoring has been conducted biweekly during summer and monthly otherwise at long term monitoring stations in the main stem of the Bay. To account for these influences we accessed Bay wide summer average surface temperature and the average surface salinity during autumn months for the lower Bay (datahub.chesapeakebay.net)

ii) Hypoxic volume. Hypoxia is a characteristic feature of the Chesapeake Bay during summer months as the phytoplankton produced during the spring bloom decay in the thermally stratified water column. Hypoxia is known to alter the distribution and mortality rates of blue crabs in the Bay, ultimately causing blue crab to walk out of the water, in a process known as a crab jubilee, as they become squeezed as an internal seiche brings low oxygen water to the edge (Eggleston et al. 2005). Hypoxic waters have also been shown to alter the distribution of blue crab at sub lethal levels (Eby and Crowder 2002). We accessed estimates of the summer time extent and volume of hypoxia from the United States Environmental

Protection Agency's Chesapeake Bay Program's Data Hub (datahub.chesapeakebay.net) using a three dimensional interpolator.

Biotic variables

i) Submerged aquatic vegetation (SAV) is believed to be important for juvenile blue crab as it provides structure thereby reducing predation on these vulnerable stages (Orth and Montfrans 1987, Hovel and Lipcius 2002, Etherington et al. 2003, Johnston and Lipcius 2012). The dynamics of SAV in the Chesapeake are complex, and include a period of rapid decline in the 1970's following Hurricane Agnes, followed by a period of management-driven recovery (Orth et al. 2017). The extent of SAV in Chesapeake Bay has been surveyed annually by multispectral aerial photography that is ground-truthed by field observations. Data for 1981-2018 were accessed for our analyses from http://web.vims.edu/bio/sav/SegmentAreaTable.htm.

ii) Striped bass was selected as an important predator of blue crab. There are several potential predators of blue crab, including blue crab themselves, as they are highly cannibalistic. We selected striped bass as a candidate predator because we viewed data for this species as more reliable. The abundance of fish species in the Chesapeake Bay is available from several sources: both fishery-independent and fishery-dependent. We used a catch per unit effort index derived from the U.S. National Marine Fisheries Service's Marine Recreational Fisheries Information Program. Data for 1981-2019 were assessed for our analysis from www.st.nmfs.noaa.gov/st1/recreational/MRIP_Estimate_Data/.

Evaluation of hypotheses

We constructed three hypotheses for ecosystem impacts on blue crab in the form of three graphs. With the graphs, the nodes represent ecosystem factors and links connecting nodes indicate dependencies (or lack of) among the variables. The networks consist of three types of variables: (i) climatic factors with no incoming links, (ii) regional factors with incoming and outgoing variables, and (iii) blue crab recruitment index with only incoming links. The networks were organized in a spatial manner to represent bottom-up forcing on blue crab recruitment. Specifically, large-scale climatic factors were conditionally independent in the network and directly influence a set of regional-scale water quality variables such as temperature and salinity. These water quality factors then influence regional-scale biological variables (e.g., predation), which were directly connected with blue crab recruitment.

We specified GGMs with direct and indirect impact pathways and fit the GGMs to observed data on environmental factors and blue crab recruitment indices. We used partial rank correlation coefficients to quantify the strength of each link in the network graphs. Specifically, coefficients were computed for each link by correlating two variables connected by a link while accounting for the effects of other variables that were linked to the variables. For example, the partial rank correlation coefficient between adult blue crab abundance and recruitment index in the first hypothesis (Fig. 1) is computed by correlating two variables, after removing the effects of wind, temperature, salinity, habitat and predator on both adult and juvenile blue crab indices. We allowed for uncertainty in networks by assuming a certain unknown probability of each hypothesized link to be included in the network. To help identify the statistically significant and strong associations between pairs of variables, we averaged the partial correlation coefficients according to the posterior probabilities of each link in the network, and computed the 90% posterior interval for each coefficient. Links with 90% posterior interval excluding zero were considered statistically significant.

Network parameter estimation

All networks took the form of GGMs where the copula transformed latent variables were assumed multivariate normal. We took a Bayesian approach to network parameter estimation. For the prior distribution of the graph, we considered a non-informative prior. We consider the G-Wishart prior for the precision matrix (Roverato 2002). We applied a Markov chain Monte Carlo (MCMC) method to simulate both the latent Gaussian variables and the posterior distributions. Specifically the MCMC algorithm iteratively explored each of the hundreds proposed links in a network space to obtain a current estimate of the network. Given the network estimate, the corresponding parameters of the local distributions associated with each variable were estimated after the copula transformation. Model fitting was performed using R (R Core Team, 2019) and the graphical analysis package BDgraph (Mohammadi et al. 2017). Ten parallel MCMC chains were run for 7 million iterations with the initial 3 million discarded as burn-in. Each chain was thinned by 5,000 to reduce the autocorrelation in MCMC chains. Convergence diagnostics were conducted using trace plots of individual network parameters and network size, as well as the Brook Gelman and Robin tests. The 8,000 post-burn in iterations were used for posterior inference.

Multiple networks, each of which represented alternative hypothesized ecosystem impacts on age 0 blue crab, were fit to the recruitment indices and ecosystem variables. For comparison purposes, a model with a fully connected graph was also fit to the data, representing a non-informative graphical learning scenario lacking prior hypotheses. Model fits were compared using the deviance information criteria (DIC, Spiegelhalter et al. 2002) across alternative hypotheses to identify the most parsimonious models. We computed the DIC focused on the recruitment indices, instead of the whole multivariate distribution including environmental variables. Due to the intractable extended likelihood (Hoff 2007), we approximated the DIC using the copula-transformed values of the recruitment indices. DIC values were compared based on leave one out information criterion (Plummer 2008, Vehtari et al. 2017). The converged optimal models were visualized as diagrams, and only links with statistically significant rank coefficients were shown by lines.

Posterior predictive analyses

Using the fitted GGMs, we quantified the joint effects of the environmental variables on recruitment (i.e. the total effect of all pathways connecting the environmental variable and recruitment index). We first discretized predictor environmental variables into two categories, above or below the median (Malick et al. 2015). We then estimated the conditional posterior probabilities for a range of blue crab recruitment values from the recruitment indices given above or below average environmental condition. We then compared the cumulative probability distributions for blue crab recruitment index between these two conditions. Due to limited sample sizes (n=29), we did not consider conditioning on multiple environmental variables.

We estimated the conditional cumulative probability distribution by conducting posterior predictive simulations. For example, to estimate the conditional cumulative probability of recruitment given that wind was above average in the fitted network, we retained from each posterior sample all years when wind was above average. The empirical cumulative distribution function (ECDF) of recruitment was then computed. The uncertainty band in ECDF was quantified by Monte Carlo integration across the MCMC samples. We computed posterior median and 90% credible intervals bands for the ECDFs. Such posterior analyses provide a probabilistic framework to rank each environmental factor, by accounting for all pathways connecting the environmental variable and the recruitment, and considering the uncertainty about the hypothesized networks.

Results

The fully connected graph contained 820 links, only 4 links were statistically significant, none of them between different ecosystem factor variables. We examined three graphs modeling informative hypotheses (Fig. 1) with up to 390 links modeling 783 potential pathways of ecosystem impacts on blue crab recruitment and resilience. All models converged yielding networks with approximately 120-195 links. Around 35-40 links were found to be statistically significant. For the recruitment level of blue crab, the fitted graph from the first hypothesis (Fig. 1) was associated with the best fit, the least complexity and the lowest DIC (Table 1). The lowest DIC for this model was significantly lower than for other models. For the recruitment variability, the fitted graph from the combined hypotheses (Fig. 1) was associated with the best fit. The fit was not as parsimonious as that from the first hypothesis, but overall still the lowest DIC (Table 1). For both recruitment indices, the fits from a fully connected graph were worse than that from any of the hypotheses (Table 1).

Pathway and link strength

Six significant pathways were identified in the recruitment level network (Fig. 3). The pathway with the highest average link strength included the summer NAO, DO/hypoxic volume, and age 1+ crab (mean absolute coefficient = 0.19). The pathway with the second highest relative strength included spring discharge and summer salinity (mean absolute coefficient = 0.17). No significant direct pathway was identified between climatic factors and recruitment.

Age 1+ crab was the only variable with a direct effect on recruitment, and had a positive relationship with the recruitment level. This indicates that stronger adult population is associated with stronger recruitment (Fig. 3). The summer salinity and DO/hypoxia had indirect effects on recruitment. The summer salinity pathway suggested that lower salinity was associated with lower recruitment. The summer DO/hypoxia pathway indicated that higher summer hypoxia volume was associated with lower adult crab abundance and consequently lower recruitment level.

Nine significant pathways were identified in the recruitment resilience network (Fig. 4). Three significant direct pathways were found between the climatic factors fall wind, summer NAO, and winter NAO and age 0-crab variability. The indirect pathway with the highest average link strength included the summer NAO, DO/hypoxic volume and age 1+ crab (mean absolute coefficient = 0.14), and the pathway including winter discharge, DO/hypoxia and predator abundance (mean absolute coefficient=0.13). The strengths of two direct pathways (wind and summer NAO, absolute coefficient = 0.20) were higher in link strength than the indirect pathways.

In the resilience network, the fall wind and summer NAO variables both had direct and significantly negative effects on age 0 crab variability, indicating that stronger fall wind or summer NAO are associated with higher variability in recruitment (Fig. 4). Between these two variables, fall wind had a slightly stronger association with recruitment variability than summer NAO. The environmental variables with an indirect effect on recruitment variability (summer DO/hypoxia) had a negative relationship with resilience. Summer DO/hypoxia is positively associated with recruitment variability through age 1+ crab, indicating that higher summer hypoxia volume is associated with weaker adult crab abundance and larger variability in recruitment. Alternatively, summer hypoxia is negatively associated with recruitment variability through predator abundance, indicating that higher summer hypoxia volume is associated with higher predation and larger variability in recruitment.

Environmental impact ranking

In the recruitment level network, the variable with the strongest joint effect on the probability of recruitment was the contemporary spawning stock size (Table 2). Age 1+ crab had a $\Delta p = -0.20$ (90% credible interval = -0.27, -0.13), indicating that recruitment is larger when age 1+ is above average. The climatic variables discharge and wind had the next strongest influences on recruitment level ($\Delta p = -0.10$). Among the three large-scale climatic variables, wind had the strongest association (Fig. 5). The cumulative probabilities between above average and below average wind were negative during years with large recruitment (CPUE > 100 million), when stronger recruitments were observed with above average wind. For NAO and discharge, the cumulative probabilities were nearly identical based on the overlapping 90% credible interval bands. For three water quality variables, no significant difference was found. Among the three biological variables, recruitment was consistently larger when spawning stock size was above average (Fig. 5), while SAV abundance had a negative joint effect on recruitment during years when CPUE exceeded 100 million. The cumulative probabilities were nearly identical between above average and below average predation.

For the resilience network, wind had the strongest effect on recruitment variability with $\Delta p = 0.30$ (Table 2). Predation and DO/hypoxia had the next strongest effects on recruitment variability with $\Delta p = -0.23$ and -0.20 respectively, indicating jointly positive associations with the recruitment variability. Among the three climatic variables, wind had the strongest overall effects, with the ECDF of below average wind dominating the ECDF of above average wind (Fig. 6). Thus, stronger wind was consistently associated with lower recruitment variability across all years. In contrast, for NAO and discharge, the cumulative probability distributions were nearly identical based on their 90% credible intervals. Among the three water quality variables, DO/hypoxia and surface temperature had similar overall effects, although the difference for surface temperature was consistently positive (16%) across all years, while the difference for DO/hypoxia was negative (-20%) only during years with moderate recruitment variability (CV < 30%).

Among the three biological variables, predator abundance had the strongest overall effects, with average difference around 22%. Higher predator abundances were associated with higher recruitment variability, especially during years when the estimated CV of CPUE was below 30%.

Discussion

We successfully applied GGMs to explore abiotic and biotic variables important to blue crab recruitment and the variability in recruitment. Both direct and indirect ecosystem effects were significant elements in the most parsimonious models for both the level and variability in blue crab recruitment. The graph for the level of recruitment was less connected than the graph for the variability in recruitment. For the level of recruitment, direct effects of age-1+ crabs and summer salinity were significant. Significant indirect effects on the level of recruitment included the phase of the NAO in summer, spring, summer and winter discharge, and the hypoxic volume. For the variance in recruitment, significant direct effects of age-1+ crabs, striped bass abundance and wind speed were detected. Hypoxic volume was the only significant indirect effect of water quality on the variability in recruitment, which in turn was significantly affected by the phase of the NAO in summer, and summer and winter discharge. Given that in the Chesapeake Bay, blue crab that recruit in the autumn of a year likely reach market size before the next autumn, our findings of significant ecosystem effects on recruitment also suggest that exploration of ecosystem-based approaches to understanding and possibly managing harvests of this species is warranted.

There were significant rank correlations between age-1+ crab abundance and both the level and variability in recruitment, although we note an inverse relationship between age-1+ abundance and the variation in recruitment. These findings confirm the results of earlier analyses that indicate the presence of a significant stock-recruitment relationship for blue crab in Chesapeake Bay (Applegate 1983, Lipcius and Van Engel 1990, Fogarty and Lipcius 2007). Although the rank correlation between spawning stock and recruitment is not as strong as one may wish to permit management strategies that are highly responsive to variation in abundance, our results indicate the importance of maintaining the focus on sustaining blue crab spawning stock biomass as a central management objective. This conclusion provides support for the continued application of single species-derived female-based reference points that have been used to manage the fishery since 2008 (Miller et al. 2011).

The extent to which ecosystem factors modify this recruitment in blue crab is more equivocal. In the Chesapeake Bay, Applegate (1983) and Tang (1990) indicated significant roles for ecosystem effects on recruitment. However, other authors noted that these complex stock recruitment relationships explained a lower fraction of the variation in the data (Lipcius and Van Engel 1990). Environment effects have been reported in other regions. Guillory (2000) reported significant effects of salinity and water discharge on blue crab recruitment in Louisiana. Although not measuring recruitment directly, Sanchez-Rubio et al. (2011) reported the importance of broadscale climatic variables in determining blue crab abundance in the Gulf of Mexico. Our results further the case for a significant role for environmental factors in affecting recruitment in blue crab. Our results indicate that biotic and abiotic variables do have a significant effect on the level and variation in blue crab recruitment, even though they were weaker than the direct effect of spawning stock biomass. Climatic factors, water quality variables and biotic factors were determined to be significant determinants of blue crab recruitment. For example, large-scale climatic patterns were shown to influence both the level and variation in blue crab recruitment. The mode of action of these climatic variables on blue crab recruitment remains poorly understood. Some effects may be direct, by altering wind and tidal patterns at the mouth of the Chesapeake Bay, which affect larval ingress (Johnson 1995, Roman and Boicourt 1999). The effects of these low frequency climate variations may also be less direct, as has been suggested for bivalves (Kimmel and Newell 2007), copepods (Kimmel and Roman 2004) and fish (Wood and Austin 2009). Because of the short life span of blue crab, impacts of the NAO on recruitment this year has the potential to affect commercial harvest the next year. Thus, we recommend that the utility of using the phase of NAO to understanding stock performance be explored further as a management tool.

Water quality variables, particularly dissolved oxygen levels, were shown to influence both the level and variation in blue crab recruitment. This was not a surprise. Both Applegate (1983) and Tang (1985) reported significant effects of environmental variables on blue crab stock-recruitment relationships for the Chesapeake Bay, although Lipcius and Van Engel (1990) noted that these more complex relationships may have explained less of the variation in the relationship than a direct stock vs recruitment relationship. Elsewhere, Guillory (2000) reported a negative relationship between salinity and recruitment of blue crab in coastal Louisiana, USA. We found that dissolved oxygen concentrations influence both the level and variability in blue crab recruitment at the population scale. Hypoxia has been shown to affect the distribution of blue crab at a scale of 10’s of kilometers in a North Carolina estuary (Eby and Crowder 2002). Eggleston and colleagues have shown that hypoxia can affect the movement, feeding, and mortality of blue crab (Bell et al. 2003b, a, Eggleston et al. 2005). In a modeling study Aumann et al. (2006) illustrated how these behavioral changes may integrate to effect crab mortality. However, our finding of a population level response is novel. Annual measurements and forecasts of the level of hypoxia are available for the Chesapeake Bay (Testa et al. 2017). We suggest that an evaluation of the extent to which hypoxia forecasts can inform forecasts of commercial blue crab harvest in the Chesapeake Bay one or two year later is warranted.

Here, we employed GGMs to explore the ecosystem context of blue crab recruitment. GGMs have been used already in some biological fields, notably genetics (Yin and Li 2011) and proteomics (Wang et al. 2016). This is the first application of GGMs in a fisheries context to our knowledge. Several features of

GGMs make them potentially valuable tools in assessing ecosystem effects in fisheries management. First, GGMs are capable of analyzing networks sufficiently large to represent entire ecosystems and the wide suite of potential environmental forcing variables. This is not the case with other multivariate techniques, such as principal components analysis in which the number of variables that can be considered is often constrained by the data available. Second, GGMs can be cast in a structured learning context in which efficient algorithms compare multiple alternative network configurations quickly to identify the most parsimonious networks. Finally, using appropriate transformations, GGMs can analyze non Gaussian networks and so the assumption of multivariate normality is less restrictive in GGMs than is the case in other analytical frameworks.

We have shown that ecosystem considerations do influence the level of recruitment in blue crab in the Chesapeake Bay and its variability. We suggest that consideration of particular ecosystem components may have advantages to adjusting commercial harvest limits in particular years because of the close relationship between the abundance of juvenile blue crab and the subsequent harvest in the following year. The application of GGMs to evaluate the efficacy of an ecosystem approach to management in blue crab is general and can be applied readily to other species such as striped bass and Atlantic menhaden. Earlier efforts at developing an ecosystem approach to fisheries in the region recommended a concerted and integrated effort to undertake such analyses but lacked the appropriate statistical tools (Chesapeake Fishery Ecosystem Plan Technical Advisory Panel 2006). Here, we have shown that GGMs represent a feasible approach to addressing such challenges.

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Table 1. Deviance Information Criteria (DIC) focused on (a) age 0 abundance index of Baywide Catch Per Unit Effort using Winter Dredge Survey data and (b) age 0 resilience index, the model assisted estimate of total variance using Winter Dredge Survey data. Dbar and pD denote model fit and complexity respectively. Smaller values denote better fit or more parsimonious model.

		Hypotheses			
Response	Deviance	H0	H1	H2	H1 or 2
(a)	Dbar	22.4	**20.1**	23.3	22.6
	pD	14.1	**2.4**	7.6	7.9
	DIC	36.5	**22.5**	30.9	30.5
(b)	Dbar	17.0	15.0	6.3	**5.6**
	pD	11.4	**2.1**	3.4	3.7
	DIC	28.4	17.1	9.7	**9.3**

Table 2. Average difference in the cumulative probabilities (posterior estimate and 90% credible interval) for abundance and resilience networks. Each difference is the cumulative probability that recruitment is below a given level when the environmental variable is above average minus that when the environmental variable is below average. Variables are defined in the method section.

	Abundance		Resilience	
Variable	Estimate	90% CI	Estimate	90% CI
NAO	0.03	(-0.05, 0.10)	0.02	(-0.06, 0.11)
Discharge	-0.11	(-0.18, 0.00)	-0.09	(-0.23, 0.05)
Wind	-0.11	(-0.20,-0.03)	0.30	(0.24, 0.36)
Surface Temp.	0.01	(-0.05, 0.08)	-0.16	(-0.23,-0.11)
Surface Salinity	0.12	(0.03, 0.20)	-0.03	(-0.07, 0.03)
DO/Hypoxic Vol.	0.07	(-0.01, 0.13)	-0.20	(-0.25,-0.14)
Age1+ Crab	-0.20	(-0.27,-0.13)	0.07	(0.01, 0.17)
Predator	0.08	(0.02, 0.15)	-0.23	(-0.30,-0.15)
SAV	0.08	(0.01, 0.14)	-0.09	(-0.15,-0.05)

Figure 1.

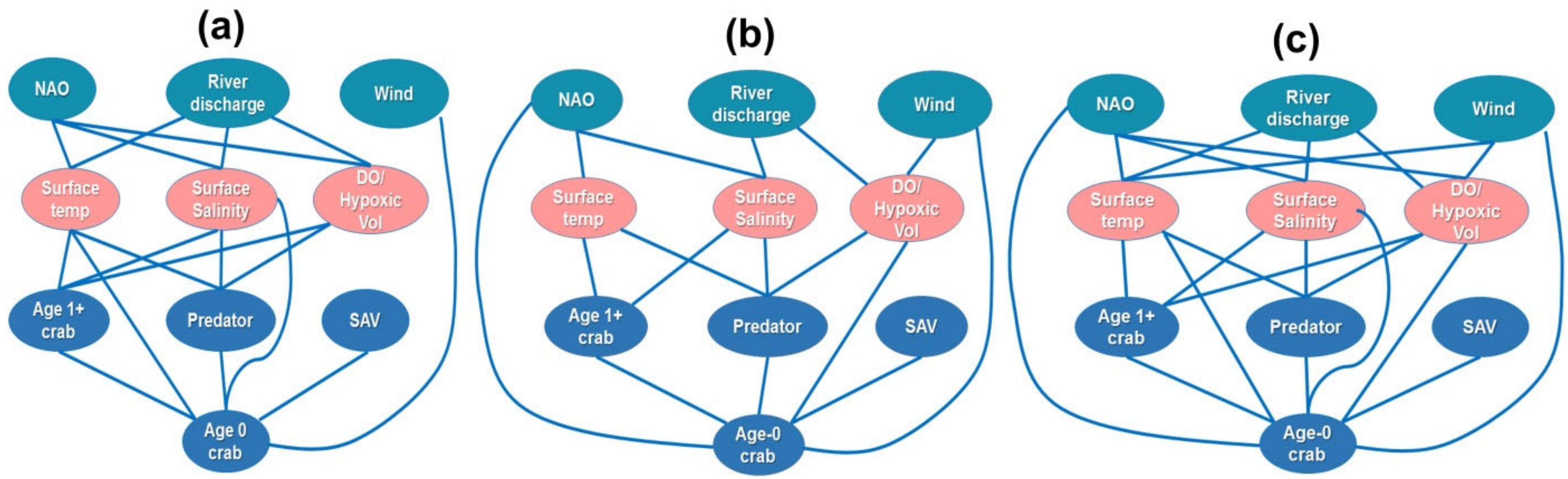

Figure 1. Schematic of pathways linking large-scale climatic processes and blue crab recruitment presented as different hypothesized mediated effects of water quality and biotic factors, represented as (a) hypothesis 1; (b) hypothesis 2; and (c) the union of hypotheses 1 and 2. A fully connected graph (not shown) was also used to model lack of prior knowledge about ecosystem impacts.

Figure 2

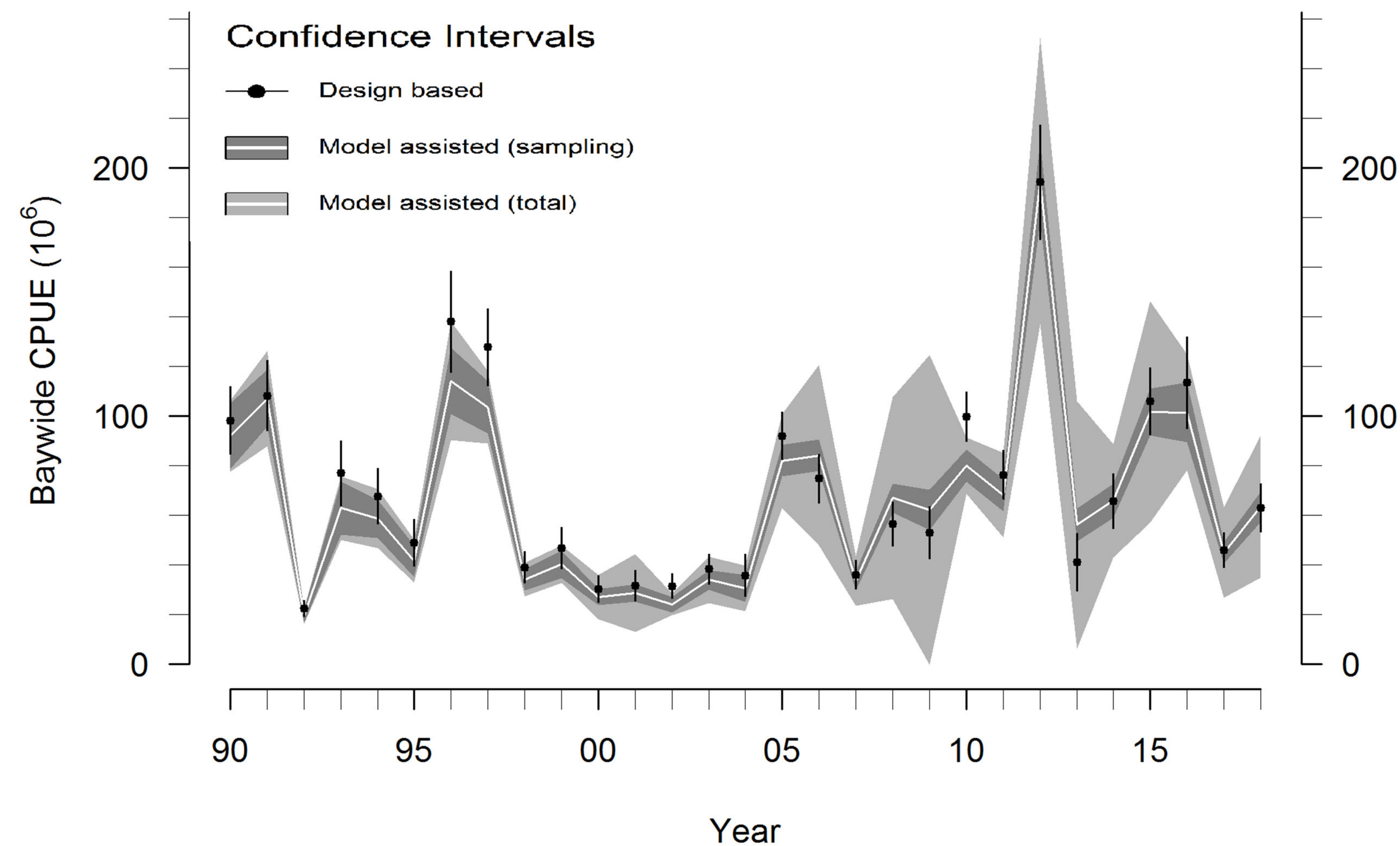

Figure 2. Time series plot of design and Bayesian calibrated estimates and standard errors (based on sampling and based on total variance including crab distribution) of Baywide Catch Per Unit Effort (CPUE) in millions.

Figure 3.

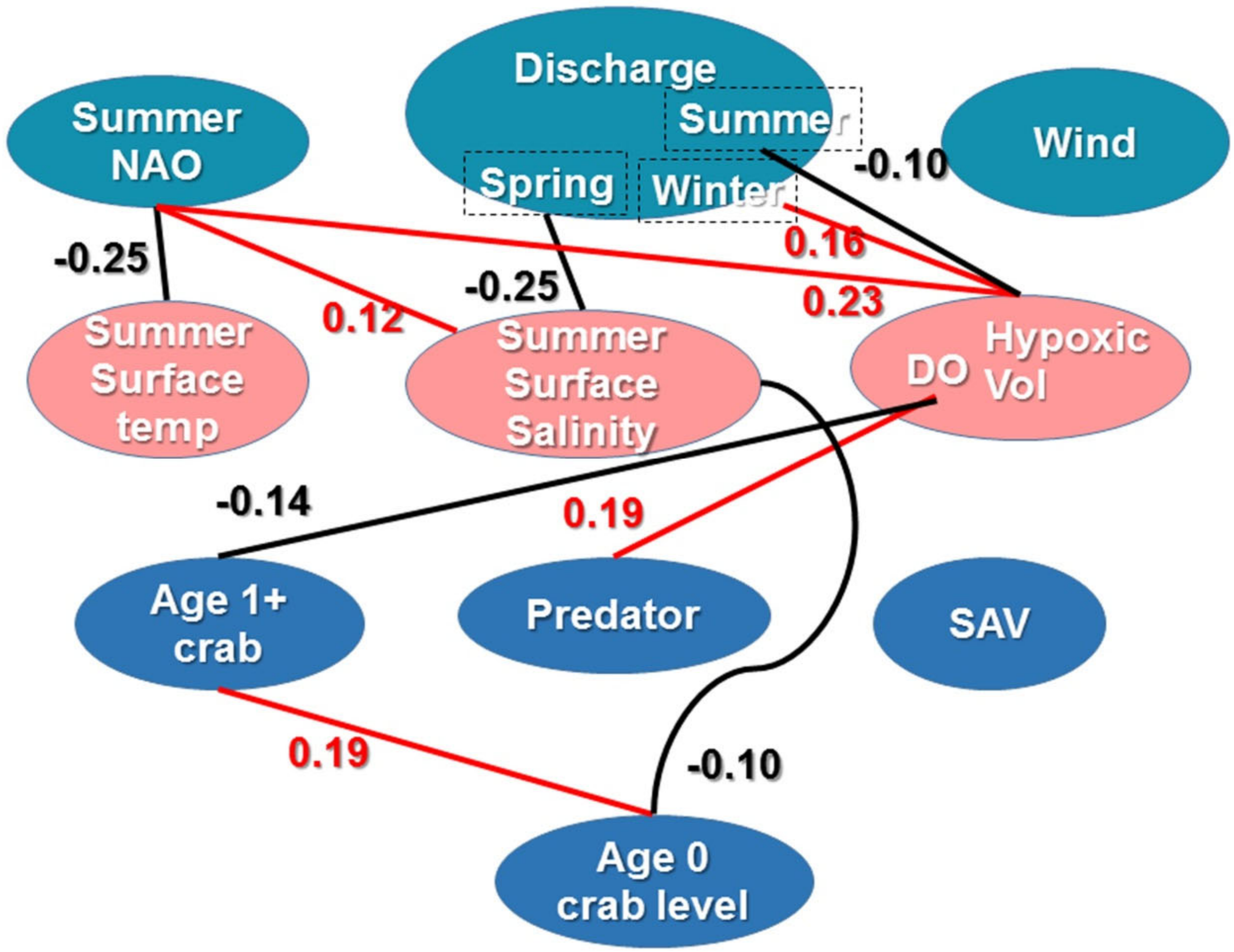

Figure 3. Graph of the GGM analysis using estimated Baywide CPUE as recruitment level. Ovals represent variables and links indicate dependencies among variables within the network. Numbers next to each link are the partial rank correlation coefficients. Red and black lines denote positive and negative rank correlations respectively.

Figure 4

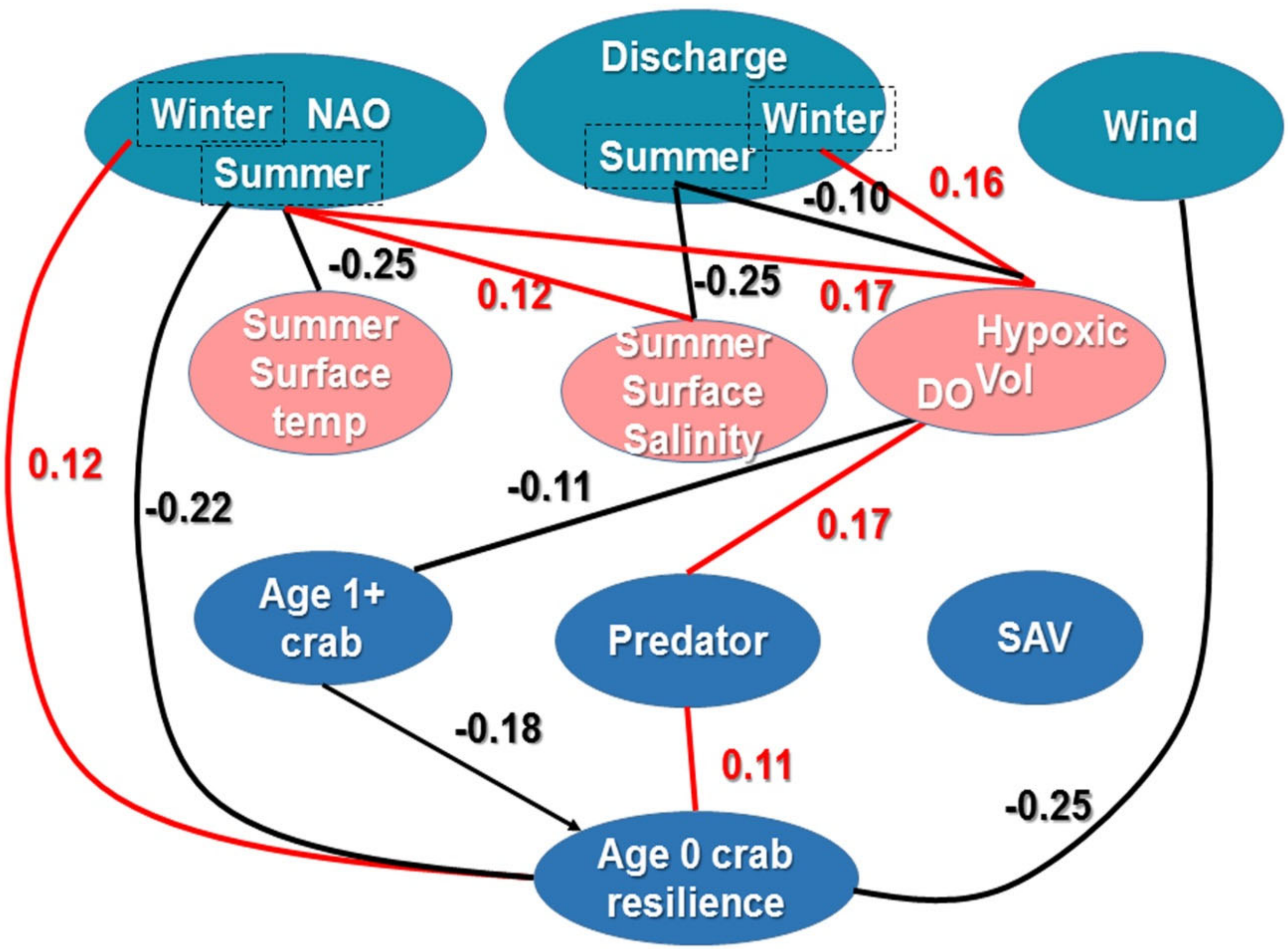

Figure 4. Graph for the GGM analysis using estimated total variance in CPUE estimate as recruitment resilience. Ovals represent variables and links indicate dependencies among variables within the network. Numbers next to each link are the partial rank correlation coefficients.

Figure 5

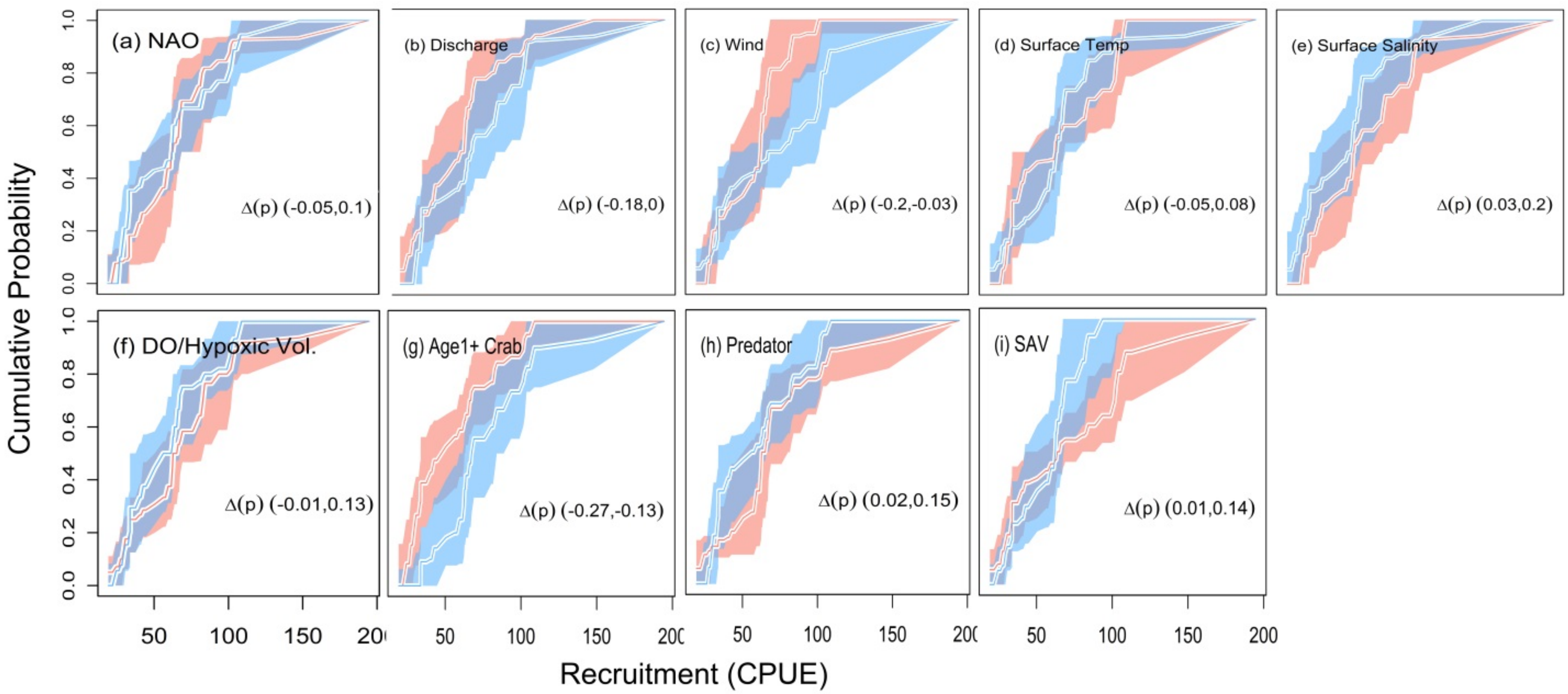

Figure 5. Cumulative probability distribution of blue crab recruitment from the most parsimonious network, conditional on each variable in the network. The blue curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas the red curves show cumulative probability when the environmental variable is less than average. Shades with the same color denote 90% credible intervals. The Δp gives the difference in cumulative probability (posterior estimate and 90% credible interval) that recruitment below a given level when the environmental variable is above average minus that when the environmental variable is below average.

Figure 6

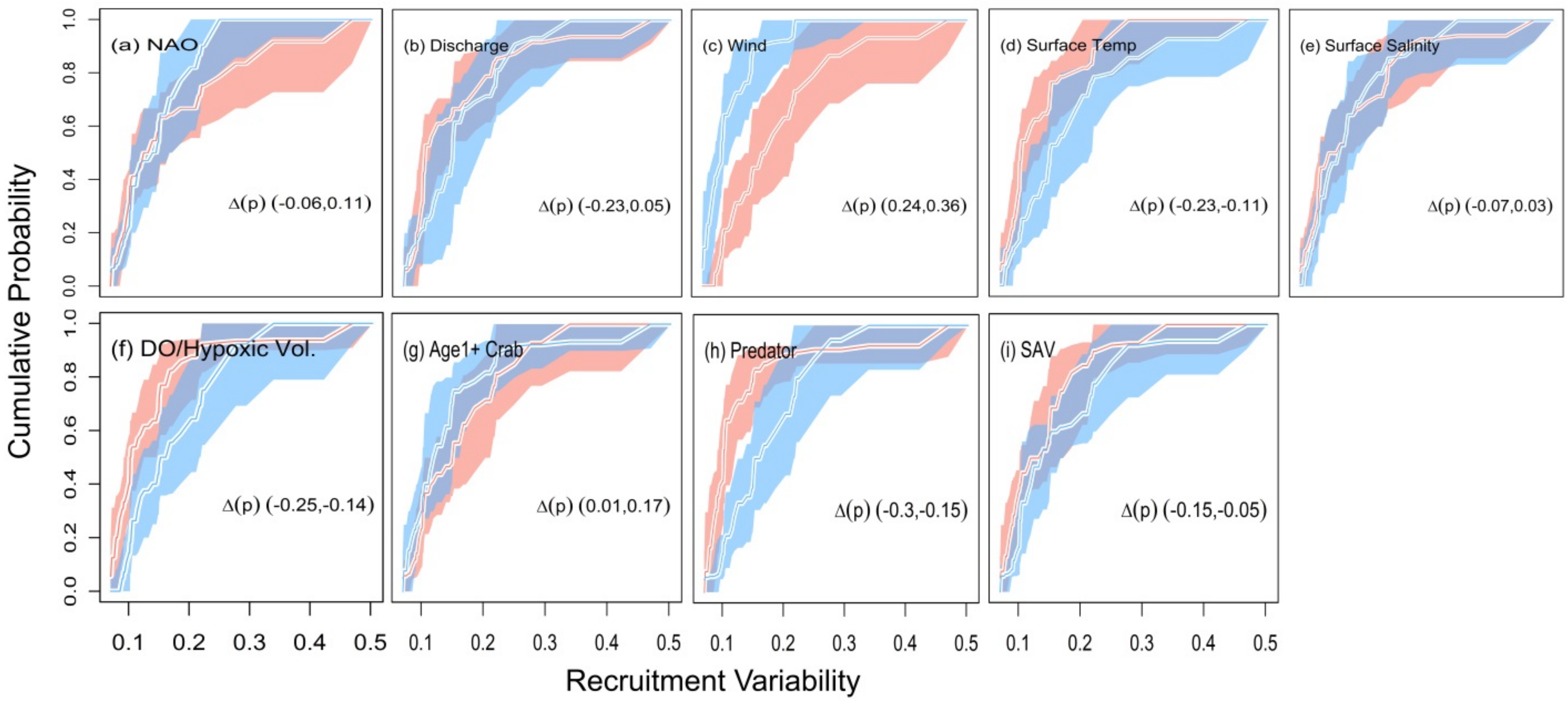

Figure 6. Cumulative probability distribution of blue crab resilience from the most parsimonious network, conditional on each variable in the network. The blue curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas the red curves show cumulative probability when the environmental variable is less than average. Shades with the same color denote 90% credible intervals. The Δp gives the difference in cumulative probability (posterior estimate and 90% credible interval) that recruitment below a given level when the environmental variable is above average minus that when the environmental variable is below average.