

# Ranking ecosystem impacts on Chesapeake Bay blue crab (*Callinectes sapidus*) using empirical Gaussian Graphical Models

Dong Liang, Geneviève M. Nessler, Michael J. Wilberg, and Thomas J. Miller

**Abstract:** Moving toward ecosystem-based fisheries management requires integration of biotic and abiotic factors into our understanding of population dynamics. Using blue crab (*Callinectes sapidus*) in the Chesapeake Bay as a model system, we applied Gaussian Graphical Models (GGMs) to understand the influence of climatic, water quality, and biotic variables on estimates of key indices of blue crab recruitment for 1990–2017. Variables included the North Atlantic Oscillation (NAO), Susquehanna River discharge, wind forcing, hypoxic volume, submerged aquatic vegetation, and the catch per unit effort of striped bass (*Morone saxatilis*). Direct effects of age-1+ crabs and summer salinity on recruitment were significant. Phase of the NAO in summer and spring, summer and winter discharge, and hypoxic volume indirectly affected the recruitment. A simulation study showed that GGM model selection achieved nominal coverage and outperformed structural equation modeling (SEM) and Multivariate Adaptive Regression Splines (MARS). GGMs have the potential to improve ecosystem-based management of blue crabs in Chesapeake Bay. Specifically, the approach can be used to examine ecosystem impacts on blue crab productivity and to improve forecasts of blue crab recruitment.

**Résumé :** Le passage à une gestion écosystémique des pêches nécessite l'intégration de facteurs biotiques et abiotiques à la compréhension de la dynamique des populations. En utilisant le crabe bleu (*Callinectes sapidus*) de la baie de Chesapeake comme système modèle, nous avons appliqué des modèles graphiques gaussiens (MGGs) pour comprendre l'influence de variables climatiques, biotiques et relatives à la qualité de l'eau sur les estimations d'indices clés du recrutement de crabes bleus pour la période de 1990 à 2017. Ces variables comprennent l'oscillation nord-atlantique (ONA), le débit du fleuve Susquehanna, le forçage éolien, le volume hypoxique, la végétation aquatique immergée et les prises par unité d'effort de bars d'Amérique (*Morone saxatilis*). Les effets directs des crabes de plus d'un an et de la salinité estivale sur le recrutement sont significatifs. La phase de l'ONA en été et au printemps, le débit estival et hivernal et le volume hypoxique ont des effets indirects sur le recrutement. Une étude de simulation montre que la sélection de modèles MGG atteint la couverture nominale et donne de meilleurs résultats que les modèles d'équations structurales (MES) et la régression multivariée par splines adaptatives (MARS). Les MGG pourraient améliorer la gestion écosystémique des crabes bleus dans la baie de Chesapeake. L'approche peut notamment être utilisée pour examiner les impacts écosystémiques sur la productivité des crabes bleus et pour améliorer les projections de recrutement de crabes bleus. [Traduit par la Rédaction]

## Introduction

The importance of conducting fisheries management within an ecosystem-based context is becoming increasingly clear (Link 2010). Often ecosystem-based approaches are motivated by a desire to account for the impacts of a fishery on nontarget species (Crowder et al. 2008) or by concerns over providing sufficient forage biomass to support ecosystem services (Buchheister et al. 2017; Pikitch 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. Tools for incorporating the ecosystem in analyses to understand population dynamics 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). 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 (hereinafter referred to as the 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 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; Lipcius

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and Van Engel 1990; Tang 1985). Previous research has suggested roles for environmental factors in regulating crab populations (Bauer and Miller 2010a, 2010b; Hurt et al. 1979). Recent research has examined the potential impacts of climate change on the dynamics of blue crab populations (Glandon et al. 2018, 2019). Trophodynamic relationships involving blue crab in the 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 also been developed (Ma et al. 2010). However, an ecosystem approach to managing blue crab in the Bay has yet to be adopted.

Empirical approaches exist to identify the important abiotic and biotic factors forcing the dynamics of fishery ecosystems. Methratta and Link (2006) examined univariate and multivariate descriptors of ecosystem structure to identify a set of simple indicators. Although these approaches may be useful as system references, an approach that links the dynamics of individual species to abiotic and biotic drivers would still have utility for understanding causation and for projections. Simple multiple regression approaches are inappropriate because of the common presence of multicollinearity and strong autocorrelation in data from fishery ecosystems. Multivariate Adaptive Regression Splines (MARS), a class of flexible regression models that approximate high-dimensional data under nonlinearity, is an approach that can address these concerns (Friedman 1991). MARS has the advantage of computational efficiency given the gradient-based schemes and have been applied in estimating graphical models (Ayyıldız et al. 2017). Structural equation modeling (SEM) is another potential approach. SEM seeks to model empirical data to reveal the underlying relationships among the data categories, thereby testing alternative hypotheses of causation (Fan et al. 2016; Grace et al. 2010, 2012). The underlying relationship is quantified through latent variables. SEM approaches have the advantages that they offer flexibility in the form of the relationship among data classes and allow alternative hypotheses to be tested. SEM have been estimated through simple correlations, maximum likelihood, and Bayesian methods (Grace et al. 2010). For example, Fu et al. (2012) used partial least squares regression within an SEM framework 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 to total system biomass across ecosystems and that trophodynamic factors were most related to indices of ecosystem complexity. These analyses demonstrate the advances in understanding that result from being able to test multiple alternative hypotheses within a single analytical framework. Yet the performance of these methods remains largely unevaluated.

Empirical network analysis is an alternative approach that can examine the effect of multiple simultaneous drivers on population dynamics. There are at least two common approaches to the application of empirical network analysis to understanding abiotic and biotic impacts on a species: probabilistic belief network analysis or Bayesian networks and Gaussian Graphical Models (GGMs). A Bayesian network is an objective methodology in which 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 (Scutari and Denis 2014; Varis 1995). However, unless the network is relatively small (fewer than 30 nodes), exact inferences in Bayesian networks are difficult to achieve due to computational constraints (Cooper 1990).

GGMs can potentially overcome the computational constraints of Bayesian networks approaches and represent a third alternative to MARS and SEM. GGMs represent a class of models of undirected graphs in which two nodes are connected if and only if the corresponding variables are conditionally independent given other nodes in the graph (Koller and Friedman 2009; Rue and

Held 2005). GGMs consider data to be distributed according to a latent multivariate Gaussian distribution with the underlying network structure encoded in the inverse covariance or precision matrix. The functional form among dependent and independent variables is linear under the multivariate Gaussian assumption (Voorman et al. 2014), but flexibility can be achieved by transformations of the data. 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. The sparsity and latent normality enable GGMs of larger networks ( $n > \sim 100$ s; e.g., Jia et al. 2017; Ni et al. 2015). GGMs have received much interest and development in the statistical and machine learning literature (Banerjee et al. 2008; Friedman et al. 2008, 2010; Meinshausen and Bühlmann 2006; Rue and Held 2005; Wang 2012, 2015; Yuan and Lin 2007). To our knowledge, GGMs have not been used in fisheries applications.

Here we apply GGMs to understand the relative importance of climate, water quality, and biotic variables on the abundance and variance of abundance estimates of blue crab in the Bay. We have categorized the variables as climate, water quality, or biotic to reflect previously published hypotheses on what controls blue crab abundance. 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 blue crab dynamics directly and indirectly. The likelihood of the different influence pathways can be evaluated by their relative probabilities.

We conducted a simulation study to compare the performance of MARS, traditional Bayesian SEMs, and GGMs by generating sample data from known networks. We then fit all models to assess their structural learning sensitivity. Based on the performance of GGMs in the simulation, we use this framework to compare three hypotheses regarding how environmental factors affect blue crab recruitment. Our goal was 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.

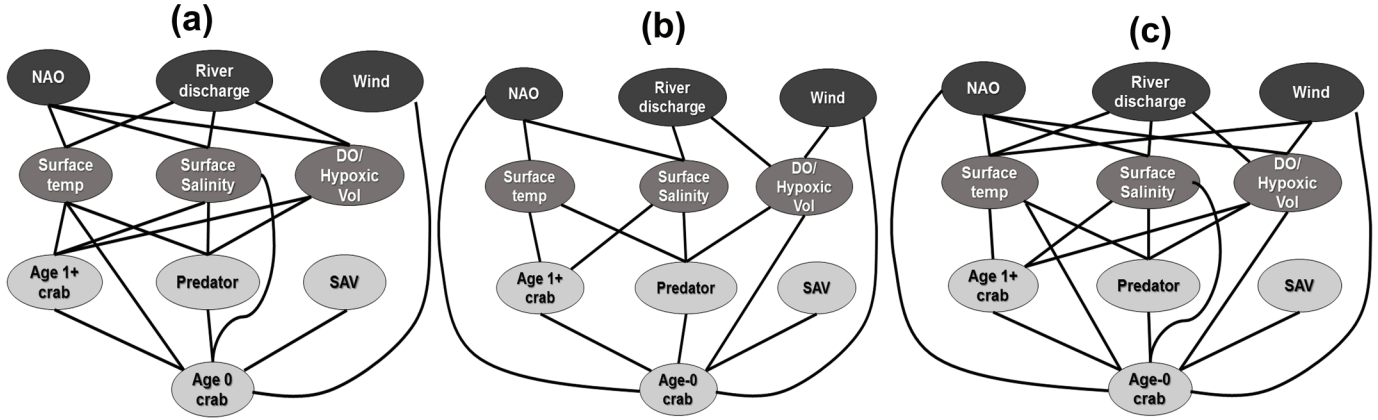
## Materials and methods

Our simulation study and application of GGMs was based on factors that affect recruitment (age-0) of blue crab in the Bay. We selected a suite of candidate independent variables representing four categories of factors that may affect blue crab recruitment: climate, water quality, external biotic, and internal population dynamic. Appropriate multiple time lags were evaluated for all factors and are described below (Table 1). We used data from 41 environmental variables to rank the strength of over 700 influence pathways on juvenile blue crab recruitment. The pathways were organized into three hypotheses. We estimated GGMs from the long-term data and conducted posterior simulations of blue crab recruitment given different scenarios for the environmental variables. Here we describe the data sources, the modeling process, and the simulation study.

### Blue crab variables

The abundance of blue crab in the Bay has been estimated annually by the Winter Dredge Survey (WDS), a fishery-independent, stratified random survey conducted at  $\sim 1200$  stations each year during winter months when blue crabs are inactive in the sediment (Sharov et al. 2003). Data were available for the winter 1989–1990 (termed the 1990 winter) to winter 2017. Size thresholds are used to separate age-0 recruit crabs from age-1+ adult crabs (Sharov et al. 2003). Three approaches have been used to develop abundance estimates: design-based (Sharov et al. 2003), model-assisted (Chen et

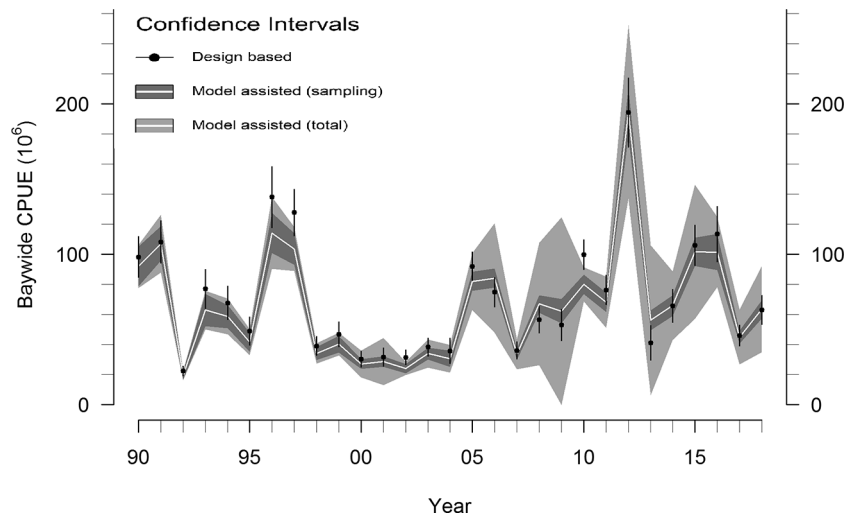
**Fig. 1.** Schematic of pathways linking large-scale climatic processes and blue crab recruitment presented as different hypothesized mediated effects of climate, water quality, and biotic factors, represented as (a) Hypothesis 1, (b) Hypothesis 2, and (c) Hypothesis 3: the union of hypotheses 1 and 2. A fully connected graph (not shown) was also used to model lack of prior knowledge about ecosystem impacts. NAO, North Atlantic Oscillation; DO, dissolved oxygen; SAV, submerged aquatic vegetation.



**Table 1.** The timing and spatial coverage of the different indices used in the exploration of ecosystem effects on blue crab.

Factor	Variable	$t-1$												$t$			Comments
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	
<b>Hypotheses 1-3</b>																	
Climate	NAO	Mid-Atlantic															Monthly values
	River discharge	Susquehanna River flow															Monthly values
	Wind													Norfolk, Va.			Seasonal average
Water quality	Surface temp.													Bay-wide			Seasonal average
	Surface salinity													Bay-wide			Seasonal average
	Dissolved oxygen													Bay-wide			Annual value
Biotic	SAV													Bay-wide			Seasonal average
	Predator	Bay-wide															Annual value
Dependent	Contemporary age-1+ crabs													Bay-wide			Annual value
	Age-0 crab													Bay-wide			Annual value

**Fig. 2.** Time series plot of design-based and Bayesian-calibrated estimates and standard errors (based on sampling and based on total variance including crab distribution) of Chesapeake Bay-wide catch per unit effort (CPUE) in millions.



al. 2004; Liang et al. 2017), and geostatistical (Jensen and Miller 2005). We used estimates of abundance from the model-assisted approach (Fig. 2), which allows for a more comprehensive treatment of sampling uncertainty (Liang et al. 2017).

We used several estimates of blue crab abundance from the WDS (Table 1). The abundance of female age-1+ crabs measured over the winter is referred to as the reproductive age-1+ abundance, as these females will release offspring in May–September

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of the same year (McConaugha et al. 1983). The offspring spend a period of time in the coastal ocean before re-entering the Bay in August–November (van Montfrans et al. 1995). These “recruits” continue to grow and become widely distributed throughout the bay. The abundance of these age-0 recruits is estimated in the WDS conducted in the subsequent year (Table 1). In analyses below we also examine relationships with age-1+ abundance in the contemporary year in which recruitment was based (Table 1). Additionally, we conducted analyses on the variation associated with estimates of recruitment (see online Supplemental materials 1<sup>1</sup>).

### Climatic variables

We used the North Atlantic Oscillation (NAO), a broad-scale synoptic index, to represent oceanic influences on early life stages of blue crab. The NAO 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. 2014). In both papers, and in our analyses here, NAO data represent the period in which early life stages are in the coastal ocean (i.e., the year before age-0 crabs are surveyed in the WDS; Table 1). For our analyses, NAO 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 12 monthly mean values for 1990–2018 so that time lags between NAO and blue crab dynamics could be evaluated.

Previous research has shown the importance of wind forcing in ensuring the return of final stage larval crab to the Bay in early autumn (Johnson 1995). To represent the complex potential influence of wind speed on blue crab recruitment, we accessed data from the US National Oceanic and Atmospheric Administration’s National Climate Data Center for the airport at Norfolk, Virginia ([www.ncdc.noaa.gov/cdo-web/search?datasetid=GHCND](http://www.ncdc.noaa.gov/cdo-web/search?datasetid=GHCND)). We used the mean northwest wind speed in autumn and the cumulative count of the number of autumn days with wind gusts greater than the third quantile long-term wind speed ( $12 \text{ m s}^{-1}$ ) for the year prior to which the recruits were surveyed in the WDS (Table 1).

After entry, early instar crabs become widely distributed throughout the lower half of the Bay (Orth and van Montfrans 1987). River discharge is important in establishing and controlling salinity gradients in the bay and likely affects crab distributions. Over 50% of the freshwater entering the bay is derived from Susquehanna River flow. Susquehanna River flow 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), and these data were used in our analyses to represent flow generally. Data were accessed from a United States Geological Survey flow gauge at a dam near Conowingo, Maryland, on the Susquehanna River (<https://waterdata.usgs.gov/usa/nwis/tuv?01578310>). Data were accessed as 12 monthly means of daily flow for the period before age-0 crabs are surveyed in the WDS (Table 1).

### Water quality variables

Water temperature and salinity influence the abundance, distribution, and productivity of a range of species in the Bay (e.g., Bauer and Miller 2010a, 2010b). Water quality monitoring has been conducted biweekly during summer and monthly otherwise for many years at long-term monitoring stations in the main stem of the bay. To account for temperature and salinity effects, we used bay-wide summer mean surface temperature and salinity and the mean surface temperature and salinity during autumn months for the lower bay ([datahub.chesapeakebay.net](http://datahub.chesapeakebay.net)) for the year before age-0 crabs were surveyed in the WDS (Table 1).

Hypoxia is a characteristic feature of the Bay during summer months. Hypoxia is known to alter the distribution and mortality rates of blue crabs (Eggleston et al. 2005), and hypoxic waters have also been shown to alter the distribution of blue crab at sub-lethal levels (Eby and Crowder 2002). We accessed summer mean bottom dissolved oxygen concentrations and 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](http://datahub.chesapeakebay.net)) using a three-dimensional interpolator (Bahner 2006) to index potential settlement habitat for recruits that are surveyed in the WDS in the subsequent winter.

### Biotic variables

Submerged aquatic vegetation (SAV) is believed to be important for juvenile blue crab, as it provides structure, thereby reducing predation on these vulnerable stages (Etherington et al. 2003; Hovel and Lipcius 2002; Johnston and Lipcius 2012; Orth and van Montfrans 1987). The extent of SAV in the Bay has been surveyed every summer by multispectral aerial photography that is ground-truthed by field observations (Orth et al. 2017). Summer SAV coverages for 1981–2018 were accessed for our analyses from <http://web.vims.edu/research/units/programs/sav/access/tables/index.php>. Summer SAV coverages were selected to index potential settlement habitat for recruits that are surveyed in the WDS in the subsequent winter (Table 1).

There are several potential predators of blue crab, including blue crab themselves, as they are highly cannibalistic. We selected striped bass (*Morone saxatilis*) as a candidate predator because blue crab can be a large portion of striped bass diets in the Bay (Overton et al. 2009; Walter et al. 2003) and because data available for this predator in the Bay are more reliable than that of many other predators of blue crab. We used a catch per unit effort (CPUE) index for 1981–2019 derived from the US National Marine Fisheries Service’s Marine Recreational Fisheries Information Program as an index of striped bass abundance ([www.st.nmfs.noaa.gov/st1/recreational/MRIP\\_Estimate\\_Data/](http://www.st.nmfs.noaa.gov/st1/recreational/MRIP_Estimate_Data/)). The trend in this index was comparable to fishery-independent estimates for 2002–2016 from the fishery-independent Chesapeake Bay Multispecies Monitoring and Assessment Program (Bonzek et al. 2019). An annual mean value was used to reflect predation pressure on newly settled blue crab that would be sampled in the subsequent WDS (Table 1).

### Evaluation of hypotheses

We constructed three hypotheses for ecosystem impacts on blue crab in the form of three graphs. We refer to these subsequently as H1, H2, and H3. H3 is defined as the union of H1 and H2. Although these hypotheses represented a small subset of all plausible hypotheses that could be established, they are relatively parsimonious and have been suggested or supported by previous studies. Additional hypotheses that use the abundance of reproductive female and adult crab and other plausible temporal lags among variables were evaluated and are presented in the online Supplemental materials 1<sup>1</sup>. In each graph, nodes represented ecosystem factors, and links connecting nodes indicated dependencies (or lack thereof) among the variables. 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 influenced 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 allowed for uncertainty in

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2019-0439>.

network structure by estimating the probability of each hypothesized link in the graph. Conditioning on the network structure, we computed posterior 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 the recruitment index in the first hypothesis (Fig. 1) was computed by correlating two variables after removing the effects of wind, temperature, salinity, habitat, and predation for both adult and juvenile blue crab indices. To help identify the statistically significant and strong associations between pairs of variables, we conducted model averaging and computed 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 estimation using GGMs

We evaluated the support for alternative networks using GGMs in which the copula-transformed latent variables were assumed to be multivariate Gaussian. For the network structure, we considered a noninformative prior. We assumed a G-Wishart prior for the precision matrix of the latent Gaussian variables (Roverato 2002). We applied a Markov chain Monte Carlo (MCMC) method to simulate both the latent Gaussian variables and the structure of the network. Specifically, the MCMC algorithm iteratively explored each of the hundreds of proposed links in a network space to obtain an estimate of the network. Given the network estimate, we estimated the corresponding parameters of the local distributions associated with each variable after the copula transformation. Model fitting was performed using R (R Core Team 2019) and the graphical analysis package BDgraph (Mohammadi et al. 2017). Owing to the high dimensionality of the graph space, ten parallel MCMC chains were run for 7 million iterations with the initial 3 million discarded in each chain as burn-in. Each chain was thinned by 5000 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 Brooks, Gelman, and Robin tests (Brooks and Gelman 1998). The 8000 post-burn-in iterations were used for posterior inference. The R code used to fit the GGMs is available in the online Supplemental materials<sup>1</sup>.

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 space was also fit to the data, representing a noninformative 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. Owing to the intractable extended likelihood (Hoff 2007), we approximated the DIC using the copula-transformed values of the recruitment indices. We also estimated the significance of the differences among DIC based on a 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 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 (Mallick 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 conditions. We then compared the cumulative probability distributions for the blue crab recruitment index between these two conditions. We computed the difference in the cumulative probabilities ( $\Delta p$ , posterior estimate and 90% credible interval) for networks of age-0 abundance. 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. Because of 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 recruitment and considering the uncertainty about the hypothesized networks.

### Simulation study

We performed a simulation study to evaluate the properties of GGM in estimating the network structure. We compared the performance of GGMs with nongraphical approaches of SEM or MARS. We focused on the dissolved oxygen pathways to reduce the computational burden of repeatedly enumerating the graphical space from the original network with all 41 nodes. Ten nodes were included in the simulation study: juvenile and contemporary adult abundance indices, the predator index, three indices of dissolved oxygen (mean summer bottom water concentration, hypoxic volume in July and August), and NAO in March, July, and November. The pathways represent 75% of the significant terms directly associated with blue crab abundances in the full network.

As a basis for the simulation, a total of 1080 samples of latent Gaussian variables were simulated from the posterior distributions of the fitted GGM model. Links with 90% posterior intervals excluding zero were considered the simulation truth for the purpose of identifying “significant” links. We applied three methods to each simulated data set: (i) GGM with the original G-Wishart prior on the graphs, (ii) SEM, and (iii) MARS. Candidate models for SEM were built from all nine possible combinations of the dissolved oxygen pathways from the three oxygen and three NAO variables and for all ( $2^4 = 32$ ) possible subsets of four links between juvenile abundance, adult abundance, predator abundance, dissolved oxygen (mean summer concentration, hypoxic volume in July, August), and NAO (March, July, and November). Model selection for SEM was conducted using Bayesian information criterion (BIC). First, an SEM with the minimum BIC was selected. Second, multiple SEMs within Occam’s window ( $\Delta_{\text{BIC}} = 3$ ) were selected. This window represented an approximate Bayes factor of  $\exp(3/2) \approx 4.5$  (Madigan and Raftery 1994). Coefficients were estimated using Bayesian model averaging (Bollen et al. 2014). Third, an SEM with the true network based on the fitted GGM was estimated to compare the inference between rank partial correlation coefficients. SEM coefficients with  $z$  statistics beyond 1.64 in magnitude were considered statistically significant. Lastly, a MARS approach was applied to estimate the links using R package earth (Milborrow 2019). Sensitivity (chance of

**Table 2.** Classification rates of Gaussian Graphical Model (GGM).

	Sensitivity	Specificity
GGM	0.85	0.94
SEM-GGM	0.46	1.00
SEM-BIC	0.25	0.92
SEM-BMA	0.17	0.93
MARS	0.06	0.98

**Note:** Sensitivity is ratio of true positive and all simulated links and varies from 0 to 1; specificity is the ratio of true negative and all simulated non-links and also varies from 0 to 1. True link was simulated base on the 90% posterior confidence interval of partial rank correlation coefficients of the fitted GGM model. SEM-GGM: structural equation modeling with best paths identified by GGM; SEM-BIC: SEM with best model identified by Bayesian information criterion; SEM-BMA: SEM inference based on Bayesian model averaging using Bayesian information criterion; MARS: Multivariate Adaptive Regression Splines.

detecting a true relationship) and specificity (chance of not detecting a false relationship) were computed for each method.

## Results

We compared the performance of GGM, SEM, and MARS in a simulation study. The sensitivity of GGMs, at 85%, was substantially higher than the other modeling approaches examined (Table 2). When provided with the correctly specified network structure, SEM achieved lower sensitivity at 46%. When the network structure was estimated using BIC, SEM resulted in an even lower sensitivity (<25%). MARS also had low sensitivity (6%). Even when the network structure was known, SEM was not as efficient in estimating the significance of the coefficients. All approaches obtained high specificity (>90%).

We examined the performance of GGMs using a noninformative fully connected graph, containing 820 links (Table 3; H0). Only three links were statistically significant. No significant links were identified between ecosystem factor variables. The fits for the fully connected graph were worse than that for any of the hypotheses (Table 3). GGMs were fit to three graphs representing three alternative hypotheses (Fig. 1) with up to 390 links, modeling over 700 potential pathways of ecosystem impacts on blue crab recruitment. All models converged to networks with approximately 120–195 links (Table 3). Of the links in the converged networks, ~40 links were statistically significant. The fitted model representing the first hypothesis (Fig. 1a) was associated with the best fit, the least complexity, and the lowest DIC; (Table 3). The DIC for this model was significantly lower than other hypotheses based on leave-one-out information criterion (Plummer 2008; Vehtari et al. 2017).

### Pathway and link strength

Figure 3 shows the conditional associations between the latent ecosystem processes generating the observed data for the most parsimonious model (H1; Table 3). Conditional rank association is represented by an edge between two nodes if the 90% credible interval for the corresponding regression parameter does not contain zero. Seven significant pathways were identified in the recruitment-level network (Table 2; five shown in Fig. 3). The pathway with the highest average link strength included the June and July NAO, DO-hypoxic volume, and contemporary 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. Lagged 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-

**Table 3.** Deviance information criteria (DIC) focused on age-0 abundance index of Chesapeake Bay-wide catch per unit effort using Winter Dredge Survey data.

Deviance	Hypotheses			
	H0	H1	H2	H3 (= H1 + H2)
Dbar	22.4	<b>20.1</b>	23.3	22.6
pD	14.1	<b>2.4</b>	7.6	7.9
DIC	36.5	<b>22.5</b>	30.9	30.5
$\Delta_{100}$	39.0	—	8.3	10.1
$SE_{\Delta}$	8.6	—	3.0	3.0
N links possible	820	355	273	390
N links in converged model	—	180	130	195
N significant links	3	38	35	39
N significant pathway	0	7	1	4

**Note:** Dbar and pD denote Gaussian Graphical Model fit and complexity, respectively. Bold font defines the most parsimonious model according to DIC.  $\Delta_{100}$  and  $SE_{\Delta}$  denote the difference in the leave-one-out information criterion (and its standard error) between each model and the model with the lowest DIC. Three rows indicated the number of links possible envisioned in the hypothesis, the number of links in the converged model, and the number of those links whose parameters were significantly different from 0. The final row indicates the number of unique influence pathways involving at least one variable that influences age-0 crab recruitment.

hypoxia pathway indicated that higher summer hypoxic volume was associated with lower adult crab abundance and consequently lower recruitment. Contemporary age-1+ crab abundance was the only variable estimated to have a direct and positive effect on recruitment.

Fits to other plausible hypotheses are provided in the online Supplemental materials 1<sup>1</sup>. No alternative models had fits with lower DIC than H1 presented here. The relationship to reproductive age-1+ crab abundance was evaluated. No significant links between reproductive age-1+ crab and age-0 crab was found, but a joint effect for reproductive age-1+ crab was found (Fig. S4, Supplemental materials 1<sup>1</sup>).

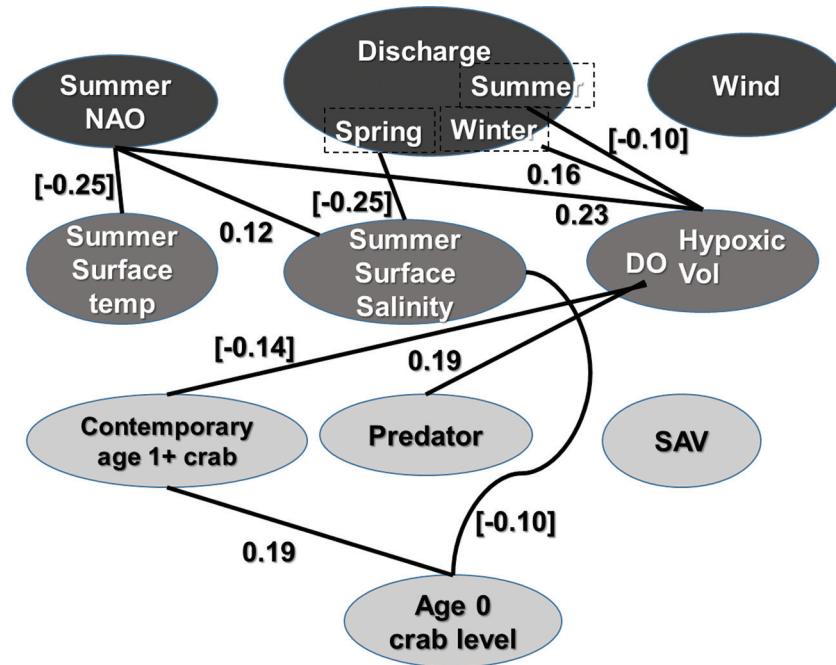
### Environmental impact ranking

Figure 4 shows the cumulative distribution functions (CDF) of recruitment conditional on each ecosystem variable being above average or not. The joint effect of each variable is represented by the separation between the two CDFs. The variable with the strongest joint effect on the probability of recruitment level was the contemporary age-1+ crab abundance, which had a  $\Delta p = -0.20$  (90% credible interval =  $-0.27, -0.13$ ), indicating that recruitment is larger when contemporary age-1+ abundance 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. 4). The cumulative probabilities between above average and below average wind were negative during years with large recruitment (CPUE > ~75 million); thus, stronger recruitments were observed with above average wind. For NAO and discharge, the cumulative probabilities were nearly identical based on the 90% credible interval bands overlapping zero. For three water quality variables, no significant differences were found. Among the three biological variables, recruitment was consistently larger when spawning stock size was above average (Fig. 4), while SAV abundance had a negative joint effect on recruitment during years when CPUE exceeded ~70 million. The cumulative probabilities were nearly identical between above average and below average predation.

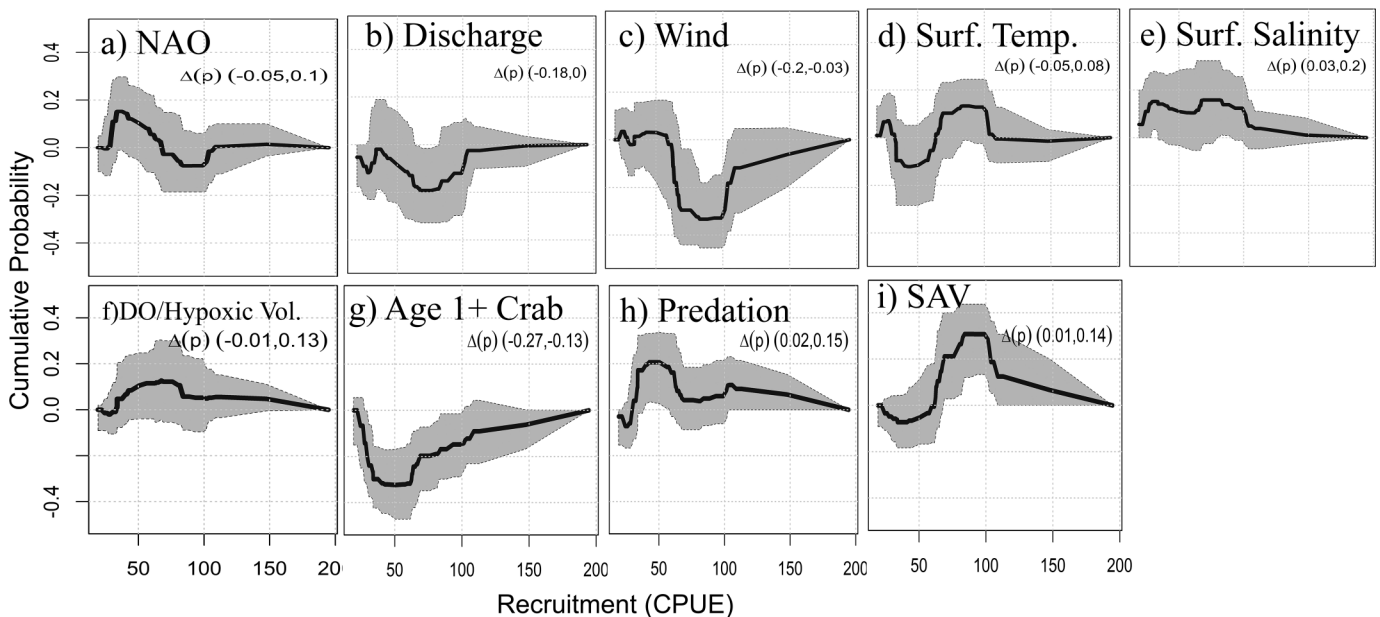
## Discussion

We applied GGMs to explore the impacts of abiotic and biotic variables on blue crab recruitment. Climate variability, water quality, and predator-prey dynamics were significant elements

**Fig. 3.** Graph of the Gaussian Graphical Model analysis using estimated Chesapeake Bay-wide catch per unit effort as recruitment level. Ovals represent variables, and links indicate dependencies among variables within the network. Numbers next to each link are the posterior partial rank correlation coefficients, and brackets [ ] denotes negative numbers.



**Fig. 4.** Cumulative probability distributions of blue crab recruitment from the most parsimonious network, conditional on each variable in the network. The curves indicate the difference between cumulative probability for recruitment given that the environmental variable is greater than average and when the environmental variable is less than average. Shading denotes 90% credible intervals. The  $\Delta p$  gives the difference in cumulative probability (posterior estimate and 90% credible interval) of the differences.



in the most parsimonious models for blue crab recruitment. The abundance of contemporary age-1+ blue crab had significant direct impacts on the recruitment index. Significant ecosystem factors included phase of the NAO in summer and spring, the Susquehanna River discharge in summer and winter, and the hypoxic volume. Given that the Bay blue crab recruit in the autumn of a year and 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 managing harvests may be warranted.

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). But to our knowledge, this is the first application of GGMs in a fisheries context. 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 multivariate analysis of variance (ANOVA), 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 (Friedman et al. 2008; Fu and Zhou 2013; Han and Zhong 2016; Ni et al. 2017; Yin and Li 2011). Finally, using monotonic transformations, GGMs can analyze non-Gaussian networks such that the assumption of multivariate normality is less restrictive in GGMs than is the case in other analytical frameworks.

The simulation study suggests that GGM achieved nominal probabilities (i.e.,  $p \geq 0.9$ ) of correctly identifying links and non-links in the simulated network. In contrast, the sensitivity of other approaches, as implemented herein, did not achieve this nominal level, even provided with the true network structure. The BIC-based SEM procedure did not fully explore the graphical space of all networks. Given the small sample size and large model uncertainty, the BIC-based SEM was not efficient in recovering the network structure. Spurious links were included in the Bayesian model averaging process, reducing the significance of the true links and sensitivity of the learning algorithm. Small sample size also limits the capability of MARS to estimate links from a simulated network (Ayyıldız et al. 2017). This study highlights the advantage of a graphical learning algorithm over non-graphical approaches in exploring graphical space with limited samples.

Our GGM results revealed important pathways of direct and indirect effects on blue crab recruitment. There were significant rank correlations between contemporary age-1+ crab abundance and recruitment. These findings are consistent with the results of earlier analyses that indicate the presence of a significant stock-recruitment relationship for blue crab in the Bay (Applegate 1983; Fogarty and Lipcius 2007; Lipcius and Van Engel 1990). However, we did not find a significant link between age-1+ abundance in the previous year and recruitment (Supplemental materials 1<sup>1</sup>). This might suggest the stock-recruitment relationship is weaker than if it had a similar effect in both analyses (lagged and unlagged age-1+). Several factors may account for these conflicting results. First, none of the indices we used are direct estimates of either the adult reproductive population or a direct estimate of recruits. Some crabs characterized as not being reproductive in the annual WDS may mature and spawn during the next summer some 6–8 months later (Miller et al. 2011). Thus, the estimate of age-1+ crabs in the contemporary year in which recruitment was estimated may be a more reliable index of the reproductive population. Lipcius and Van Engel (1990) noted the challenge of correctly indexing stock and recruitment for the Bay blue crab previously. An alternative explanation of the positive correlations between contemporary age-1+ female abundance and age-0 recruits is correlated catchabilities in the survey. Regardless, our results indicate the importance of maintaining the current focus on sustaining blue crab spawning stock biomass as a central management objective. This conclusion provides support for the continued application of female abundance and exploitation rate reference points that have been used to manage the fishery since 2008 and were updated in 2011 (Miller et al. 2011).

Based on our findings, the extent to which ecosystem factors affect recruitment in blue crab is more equivocal. In the Bay, Applegate (1983) and Tang (1985) indicated important roles for ecosystem effects on recruitment. Colton et al. (2014) indicated a role for a synoptic index of the Gulf Stream on blue crab recruitment. Other authors noted that these complex stock-recruitment relationships explained a low fraction of the variation in

the data (Lipcius and Van Engel 1990). Environmental effects on blue crab recruitment have been reported in other regions. Guillore (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 broad-scale climatic variables in determining blue crab abundance in the Gulf of Mexico. Our results further the case for a major role for environmental factors in affecting the blue crab recruitment, even though they were weaker than the direct effect of contemporary stock biomass. Climatic factors, water quality variables, and biotic factors were significant determinants of blue crab recruitment. For example, large-scale climatic patterns were shown to influence 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 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 understand stock performance be explored further.

Water quality variables, particularly dissolved oxygen levels, were shown to influence the blue crab recruitment. Hypoxia has been shown to affect the distribution of blue crab at a scale of tens of kilometres 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. 2003a, 2003b; Eggleston et al. 2005). In a modeling study, Aumann et al. (2006) illustrated how these behavioral changes may integrate to affect 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 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 Bay 1 or 2 years later is warranted.

We proposed an empirical framework to rank potential ecosystem influences and identified dissolved oxygen as having significant impact on blue crab recruitment through contemporary and reproductive adult abundance. The importance of developing an ecosystem-based context for understanding and managing blue crab was highlighted by the continuing uncertainty over the fate of the 2011 year class, which, despite appearing to be strong during the winter of 2011–2012, failed to survive to sustain a fishery in 2012. Our results were used to investigate the connections between ecosystem factors and past blue crab recruitment events that raised important management and stakeholder questions. We are planning to evaluate ecosystem impacts on blue crab productivity by integrating the stock-recruitment curve estimated in the stock assessment with the GGM model results. Finally, we can apply the GGM framework to probabilistically forecast the recruitment index. Given the findings herein, we can build a recruitment forecasting system based upon an existing hypoxia forecasting system in the Bay to support ecosystem-based management of blue crab (Testa et al. 2017).

We suggest that consideration of particular ecosystem components may be useful for 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 of blue crab is general and can be applied readily to other species such as striped bass and Atlantic menhaden should adequate survey data become available. 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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## References

- Applegate, A.J. 1983. An environmental model predicting the relative recruitment success of the blue crab, *Callinectes sapidus* (Rathbun), in Chesapeake Bay, Virginia. M.S., School of Marine Science, College of William and Mary, Williamsburg, Va.
- Aumann, C.A., Eby, L.A., and Fagan, W.F. 2006. How transient patches affect population dynamics: The case of hypoxia and blue crabs. *Ecol. Monogr.* **76**(3): 415–438. doi:10.1890/0012-9615(2006)076[0415:HTPAPD]2.0.CO;2.
- Ayyıldız, E., Ağraz, M., and Purutçuoğlu, V. 2017. MARS as an alternative approach of Gaussian graphical model for biochemical networks. *J. Appl. Stat.* **44**(16): 2858–2876. doi:10.1080/02664763.2016.1266465.
- Bahner, L. 2006. User guide for the Chesapeake Bay and tidal tributary interpolator. Available from [ftp://ftp.chesapeakebay.net/Monitoring/LHernandez/Vol3D46/Vol3D461\\_Distribution/](ftp://ftp.chesapeakebay.net/Monitoring/LHernandez/Vol3D46/Vol3D461_Distribution/) [accessed 8 January 2019].
- Banerjee, O., Ghaoui, L.E., and d'Aspremont, A. 2008. Model selection through sparse maximum likelihood estimation for multivariate Gaussian or binary data. *J. Mach. Learn. Res.* **9**(Mar): 485–516.
- Bauer, L.J., and Miller, T.J. 2010a. Temperature, salinity and size-dependent winter mortality of juvenile blue crab (*Callinectes sapidus*). *Estuar. Coasts*, **33**: 668–677. doi:10.1007/s12237-010-9277-2.
- Bauer, L.J., and Miller, T.J. 2010b. Spatial and temporal variability in winter mortality of the blue crab (*Callinectes sapidus*) in the Chesapeake Bay. *Estuar. Coasts*, **33**: 678–687. doi:10.1007/s12237-009-9237-x.
- Bell, G.W., Eggleston, D.B., and Wolcott, T.G. 2003a. Behavioral responses of free ranging blue crabs to episodic hypoxia. II. Feeding. *Mar. Ecol. Prog. Ser.* **259**: 227–235. doi:10.3354/meps259227.
- Bell, G.W., Eggleston, D.B., and Wolcott, T.G. 2003b. Behavioral responses of free-ranging blue crabs to episodic hypoxia. I. Movement. *Mar. Ecol. Prog. Ser.* **259**: 215–225. doi:10.3354/meps259215.
- Bollen, K.A., Harden, J.J., Ray, S., and Zavisca, J. 2014. BIC and alternative Bayesian information criteria in the selection of structural equation models. *Struct. Equation Model.* **21**(1): 1–19. doi:10.1080/10705511.2014.856691. PMID:31360054.
- Bonzek, C.F., Garland, J., Gauthier, D.J., and Latour, R.J. 2019. Annual report — 2018 Data collection and analysis in support of single and multispecies stock assessments in Chesapeake Bay: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Virginia Institute of Marine Science, College of William and Mary.
- Brooks, S.P., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* **7**(4): 434–455.
- Buchheister, A., Miller, T.J., and Houde, E.D. 2017. Evaluating ecosystem-based reference points for Atlantic menhaden. *Mar. Coast. Fish.* **9**(1): 457–478. doi:10.1080/19425120.2017.1360420.
- Carscadden, J.E., Frank, K.T., and Leggett, W.C. 2000. Evaluation of an environment–recruitment model for capelin (*Mallotus villosus*). *ICES J. Mar. Sci.* **57**(2): 412–418. doi:10.1006/jmsc.1999.0526.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., and Niquen, M. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, **299**(5604): 217–221. doi:10.1126/science.1075880.
- Chen, J., Thompson, M.E., and Wu, C. 2004. Estimation of fish abundance indices based on scientific research trawl surveys. *Biometrics*, **60**(1): 116–123. doi:10.1111/j.0006-341X.2004.00162.x.
- Chesapeake Fishery Ecosystem Plan Technical Advisory Panel. 2006. Fishery ecosystem planning for Chesapeake Bay. American Fisheries Society, Bethesda, Md.
- Colton, A.R., Wilberg, M.J., Coles, V.J., and Miller, T.J. 2014. An evaluation of the synchronization in the dynamics of the blue crab (*Callinectes sapidus*) populations in the western Atlantic. *Fish. Oceanogr.* **23**(2): 132–146. doi:10.1111/fog.12048.
- Cooper, G.F. 1990. The computational complexity of probabilistic inference using Bayesian belief networks. *Artif. Intell.* **42**(2–3): 393–405. doi:10.1016/0004-3702(90)90060-D.
- Crowder, L.B., Hazen, E.L., Avissar, N., Bjorkland, R., Latanich, C., and Ogburn, M.B. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. *Annu. Rev. Ecol. Evol. Syst.* **39**: 259–278. doi:10.1146/annurev.ecolsys.39.110707.173406.
- Eby, L.A., and Crowder, L.B. 2002. Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds. *Can. J. Fish. Aquat. Sci.* **59**(6): 952–965. doi:10.1139/f02-067.
- Eggleston, D.B., Bell, G.W., and Amavisca, A.D. 2005. Interactive effects of episodic hypoxia and cannibalism on juvenile blue crab mortality. *J. Exp. Mar. Biol. Ecol.* **325**(1): 18–26. doi:10.1016/j.jembe.2005.04.023.
- Etherington, L.L., Eggleston, D.B., and Stockhausen, W.T. 2003. Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. *Bull. Mar. Sci.* **72**(2): 371–391.
- Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S.R., Park, H., and Shao, C. 2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecol. Process.* **5**(1): 19. doi:10.1186/s13717-016-0063-3.
- Fogarty, M.J., and Lipcius, R.N. 2007. Population dynamics and fisheries. In *The Blue Crab, Callinectes sapidus*. Edited by V.S. Kennedy and L.E. Cronin. Maryland Sea Grant College, College Park, Md. pp. 711–755.
- Friedman, J.H. 1991. Multivariate adaptive regression splines. *Ann. Stat.* **19**: 1–67. doi:10.1214/aos/1176347973.
- Friedman, J., Hastie, T., and Tibshirani, R. 2008. Sparse inverse covariance estimation with the graphical lasso. *Biostatistics*, **9**(3): 432–441. doi:10.1093/biostatistics/kxm045.
- Friedman, J., Hastie, T., and Tibshirani, R. 2010. Regularization paths for generalized linear models via coordinate descent. *J. Stat. Soft.* **33**(1): 1. doi:10.18637/jss.v033.i01.
- Fu, C.H., Gaichas, S., Link, J.S., Bundy, A., Boldt, J.L., Cook, A.M., et al. 2012. Relative importance of fisheries, trophodynamic and environmental drivers in a series of marine ecosystems. *Mar. Ecol. Prog. Ser.* **459**: 169–184. doi:10.3354/meps09805.
- Fu, F., and Zhou, Q. 2013. Learning sparse causal Gaussian networks with experimental intervention: regularization and coordinate descent. *J. Am. Stat. Assoc.* **108**(501): 288–300. doi:10.1080/01621459.2012.754359.
- Glandon, H.L., Kilbourne, K.H., Schif, J., and Miller, T.J. 2018. Counteractive effects of increased temperature and pCO<sub>2</sub> on the thickness and chemistry of the carapace of juvenile blue crab, *Callinectes sapidus*, from the Patuxent River, Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* **498**: 39–45. doi:10.1016/j.jembe.2017.11.005.
- Glandon, H.L., Kilbourne, K.H., and Miller, T.J. 2019. Winter is (not) coming: Warming temperatures will affect the overwinter behavior and survival of blue crab. *PLoS ONE*, **14**(7): e0219555. doi:10.1371/journal.pone.0219555.
- Grace, J.B., Anderson, T.M., Olff, H., and Scheiner, S.M. 2010. On the specification of structural equation models for ecological systems. *Ecol. Monogr.* **80**(1): 67–87. doi:10.1890/09-0464.1.
- Grace, J.B., Schoolmaster, D.R., Jr., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., and Schweiger, E.W. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**(8): 1–44. doi:10.1890/ES12-00048.1.
- Guillory, V. 2000. Relationship of blue crab abundance to river discharge and salinity. In *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies*, Vol. 54. pp. 213–220.
- Han, S.W., and Zhong, H. 2016. Estimation of sparse directed acyclic graphs for multivariate counts data. *Biometrics*, **72**(3): 791–803. doi:10.1111/biom.12467.
- Hoff, P.D. 2007. Extending the rank likelihood for semiparametric copula estimation. *Ann. Appl. Stat.* **1**: 265–283.
- Hovel, K.A., and Lipcius, R.N. 2002. Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *J. Exp. Mar. Biol. Ecol.* **271**(1): 75–98. doi:10.1016/S0022-0981(02)00043-6.
- Hurt, P.R., Libby, L.M., Pandolfi, L.J., Levine, L.H., and Van Engel, W.A. 1979. Periodicities in blue-crab population of Chesapeake Bay. *Clim. Change*, **2**(1): 75–78. doi:10.1007/BF00138228.
- Jensen, O.P., and Miller, T.J. 2005. Geostatistical analysis of the abundance and winter distribution patterns of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Trans. Am. Fish. Soc.* **134**(6): 1582–1598. doi:10.1577/T04-218.1.
- Jia, B., Xu, S., Xiao, G., Lamba, V., and Liang, F. 2017. Learning gene regulatory networks from next generation sequencing data. *Biometrics*, **73**(4): 1221–1230. doi:10.1111/biom.12682.
- Johnson, D.R. 1995. Wind forced surface currents at the entrance to Chesapeake Bay: Their effect on blue crab larval dispersion and post-larval recruitment. *Bull. Mar. Sci.* **57**(3): 726–738.
- Johnston, C.A., and Lipcius, R.N. 2012. Exotic macroalgae *Gracilariaria vermiculophylla* provides superior nursery habitat for native blue crab in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **467**: 137–146. doi:10.3354/meps09935.
- Kennedy, V.S., Oesterling, M., and Van Engel, W.A. 2007. History of blue crab fisheries on the U.S. Atlantic and Gulf Coasts. In *The Blue Crab, Callinectes sapidus*. Edited by V.S. Kennedy and L.E. Cronin. Maryland Sea Grant College, College Park, Md. pp. 655–710.
- Kimmel, D.G., and Newell, R.I.E. 2007. The influence of climate variation on eastern oyster (*Crassostrea virginica*) juvenile abundance in Chesapeake Bay. *Limnol. Oceanogr.* **52**(3): 959–965. doi:10.4319/lo.2007.52.3.0959.
- Kimmel, D.G., and Roman, M.R. 2004. Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. *Mar. Ecol. Prog. Ser.* **267**: 71–83. doi:10.3354/meps267071.
- Kimmel, D.G., Miller, W.D., and Roman, M.R. 2006. Regional scale climatic forcing of Chesapeake Bay zooplankton dynamics. *Estuar. Coasts*, **29**(3): 375–387. doi:10.1007/BF02784987.

- Koller, D., and Friedman, N. 2009. Probabilistic graphical models: principles and techniques. MIT Press, Cambridge, Mass.
- Liang, D., Nesslage, G., Wilberg, M.J., and Miller, T.J. 2017. Bayesian calibration of blue crab (*Callinectes sapidus*) abundance indices based on probability surveys. *J. Agric. Biol. Environ. Stat.* **22**(4): 481–497. doi:10.1007/s13253-017-0295-4.
- Link, J.S. 2010. Ecosystem-based fisheries management: confronting trade-offs. Cambridge University Press, New York.
- Lipcius, R.N., and Van Engel, W.A. 1990. Blue crab population dynamics in Chesapeake Bay — variation in abundance (York River, 1972–1988) and stock–recruit functions. *Bull. Mar. Sci.* **46**(1): 180–194.
- Liu, H., Lafferty, J., and Wasserman, L. 2009. The nonparanormal: Semiparametric estimation of high dimensional undirected graphs. *J. Mach. Learn. Res.* **10**(Oct): 2295–2328.
- Ma, H., Townsend, G., Zhang, X., Sigrist, M., and Christensen, V. 2010. Using a fisheries ecosystem model with a water quality model to explore trophic and habitat impacts of a fisheries stock: A case study of the blue crab population in the Chesapeake Bay. *Ecol. Modell.* **221**: 997–1004. doi:10.1016/j.ecolmodel.2009.01.026.
- Madigan, D., and Raftery, A.E. 1994. Model selection and accounting for model uncertainty in graphical models using Occam's window. *J. Am. Stat. Assoc.* **89**(428): 1535–1546. doi:10.1080/01621459.1994.10476894.
- Mallick, M.J., Cox, S.P., Peterman, R.M., Wainwright, T.C., and Peterson, W.T. 2015. Accounting for multiple pathways in the connections among climate variability, ocean processes, and coho salmon recruitment in the Northern California Current. *Can. J. Fish. Aquat. Sci.* **72**(10): 1552–1564. doi:10.1139/cjfas-2014-0509.
- Maryland Sea Grant. 2010. Ecosystem-based management in Chesapeake Bay: Blue crab background and issue briefs. Maryland Sea Grant, College Park, Md.
- Maunder, M.N., and Watters, G.M. 2003. A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example. *Fish. Bull. (NOAA)*, **101**(1): 89–99.
- McConaughy, J.R., Johnson, D.F., Provenzano, A.J., and Maris, R.C. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. *J. Crustac. Biol.* **3**(4): 582–591. doi:10.2307/1547953.
- Meinshausen, N., and Bühlmann, P. 2006. High-dimensional graphs and variable selection with the lasso. *Ann. Stat.* **34**(3): 1436–1462. doi:10.1214/009053606000000281.
- Methratta, E.T., and Link, J.S. 2006. Evaluation of quantitative indicators for marine fish communities. *Ecol. Indic.* **6**(3): 575–588. doi:10.1016/j.ecolind.2005.08.022.
- Milborrow, S. 2019. Derived from mda:mars by Trevor Hastie and Rob Tibshirani. Uses Alan Miller's Fortran utilities with Thomas Lumley's leaps wrapper. (2019). earth: multivariate adaptive regression splines. R package version 5.1.2. Available from <https://CRAN.R-project.org/package=earth>.
- Miller, T.J., Wilberg, M.J., Colton, A.R., Davis, G.R., Sharov, A., Lipcius, R.N., et al. 2011. Stock assessment of blue crab in Chesapeake Bay, 2011. University of Maryland Center for Environmental Science Chesapeake Biological Laboratory TS-614-611, Solomons, Md.
- Mohammadi, A., Abegaz, F., van den Heuvel, E., and Wit, E.C. 2017. Bayesian modelling of Dupuytren disease by using Gaussian copula graphical models. *J. R. Stat. Soc.* **66**(3): 629–645.
- Ni, Y., Stingo, F.C., and Baladandayuthapani, V. 2015. Bayesian nonlinear model selection for gene regulatory networks. *Biometrics*, **71**(3): 585–595. doi:10.1111/biom.12309.
- Ni, Y., Stingo, F.C., and Baladandayuthapani, V. 2017. Sparse multi-dimensional graphical models: A unified Bayesian framework. *J. Am. Stat. Assoc.* **112**(518): 779–793. doi:10.1080/01621459.2016.1167694.
- Nye, J.A., Bundy, A., Shackell, N., Friedland, K.D., and Link, J.S. 2010. Coherent trends in contiguous survey time-series of major ecological and commercial fish species in the Gulf of Maine ecosystem. *ICES J. Mar. Sci.* **67**(1): 26–40. doi:10.1093/icesjms/fsp216.
- Orth, R.J., and van Montfrans, J. 1987. Utilizations of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus* I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* **41**: 283–294. doi:10.3354/meps041283.
- Orth, R.J., Dennison, W.C., Lefcheck, J.S., Gurbisz, C., Hannam, M., Keisman, J., et al. 2017. Submersed aquatic vegetation in Chesapeake Bay: sentinel species in a changing world. *Bioscience*, **67**(8): 698–712. doi:10.1093/biosci/bix058.
- Overton, A.S., Margraf, F.J., and May, E.B. 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. *Trans. Am. Fish. Soc.* **138**(4): 915–926. doi:10.1577/T07-261.1.
- Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T.E., et al. 2012. Little fish: big impacts. Lenfest Ocean Program, Washington, D.C.
- Plummer, M. 2008. Penalized loss functions for Bayesian model comparison. *Biostatistics*, **9**(3): 523–539. doi:10.1093/biostatistics/kxm049.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Roman, M.R., and Boicourt, W.C. 1999. Dispersion and recruitment of crab larvae in the Chesapeake Bay plume: Physical and biological controls. *Estuaries*, **22**(3A): 563–574. doi:10.2307/1353044.
- Roverato, A. 2002. Hyper inverse Wishart distribution for non-decomposable graphs and its application to Bayesian inference for Gaussian graphical models. *Scand. J. Stat.* **29**(3): 391–411. doi:10.1111/1467-9469.00297.
- Rue, H., and Held, L. 2005. Gaussian Markov random fields: theory and applications. CRC Press, Boca Raton, Fla.
- Sanchez-Rubio, G., Perry, H.M., Biesiot, P.M., Johnson, D.R., and Lipcius, R.N. 2011. Climate-related hydrological regimes and their effects on abundance of juvenile blue crabs (*Callinectes sapidus*) in the northcentral Gulf of Mexico. *Fish. B.-Noaa*, **109**(2): 139–146.
- Scutari, M., and Denis, J.B. 2014. Bayesian networks with examples in R: texts in statistical science. CRC Press, Boca Raton, Fla.
- Sharov, A.F., Volstad, J.H., Davis, G.R., Davis, B.K., Lipcius, R.N., and Montane, M.M. 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Bull. Mar. Sci.* **72**(2): 543–565.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and Van Der Linde, A. 2002. Bayesian measures of model complexity and fit. *J. R. Stat. Soc. B. Stat. Methodol.* **64**(4): 583–639. doi:10.1111/1467-9868.00353.
- Tang, Q. 1985. Modification of the ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue-crab fishery in Chesapeake Bay. *Fish. Res.* **3**(1): 13–21. doi:10.1016/0165-7836(85)90004-9.
- Testa, J.M., Clark, J.B., Dennison, W.C., Donovan, E.C., Fisher, A.W., Ni, W.F., et al. 2017. Ecological forecasting and the science of hypoxia in Chesapeake Bay. *Bioscience*, **67**(7): 614–626. doi:10.1093/biosci/bix048.
- van Montfrans, J., Epifanio, C.E., Knott, D.M., Lipcius, R.N., Mense, D.J., Metcalf, K.S., et al. 1995. Settlement of blue crab postlarvae in Western North Atlantic Estuaries. *Bull. Mar. Sci.* **57**(3): 834–854.
- Varis, O. 1995. Belief networks for modeling and assessment of environmental change. *Environmetrics*, **6**(5): 439–444. doi:10.1002/env.3170060504.
- Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**(5): 1413–1432. doi:10.1007/s11222-016-9696-4.
- Voorman, A., Shojaie, A., and Witten, D. 2014. Graph estimation with joint additive models. *Biometrika*, **101**(1): 85–101. doi:10.1093/biomet/ast053.
- Walter, J., III, Overton, A., Ferry, K., and Mather, M. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. *Fish. Manage. Ecol.* **10**(5): 349–360. doi:10.1046/j.1365-2400.2003.00373.x.
- Wang, H. 2012. Bayesian graphical lasso models and efficient posterior computation. *Bayesian Anal.* **7**(4): 867–886. doi:10.1214/12-BA729.
- Wang, H. 2015. Scaling it up: Stochastic search structure learning in graphical models. *Bayesian Anal.* **10**(2): 351–377. doi:10.1214/14-BA916.
- Wang, T., Ren, Z., Ding, Y., Fang, Z., Sun, Z., MacDonald, M.L., et al. 2016. FastGGM: An efficient algorithm for the inference of Gaussian graphical model in biological networks. *PLoS Comput. Biol.* **12**(2): e1004755. doi:10.1371/journal.pcbi.1004755.
- Wood, R.J., and Austin, H.M. 2009. Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, USA. *Can. J. Fish. Aquat. Sci.* **66**(3): 496–508. doi:10.1139/F09-013.
- Yin, J.X., and Li, H.Z. 2011. A sparse conditional Gaussian graphical model for analysis of genetical genomics data. *Ann. Appl. Stat.* **5**(4): 2630–2650. doi:10.1214/11-AOAS494.
- Yuan, M., and Lin, Y. 2007. Model selection and estimation in the Gaussian graphical model. *Biometrika*, **94**(1): 19–35. doi:10.1093/biomet/asm018.