

Ecosystem-based forecasts of recruitment in two menhaden species

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Abstract

Gulf (*Brevoortia patronus*, Clupeidae) and Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae) support large fisheries that have shown substantial variability over several decades, in part, due to dependence on annual recruitment. Nevertheless, traditional stock–recruitment relationships lack predictive power for these stocks. Current management of Atlantic menhaden explicitly treats recruitment as a random process. However, traditional methods for understanding recruitment variability carry the very specific hypothesis that the effect of adult biomass on subsequent recruitment occurs independently of other ecosystem factors such as food availability and predation. Here, we evaluate the predictability of menhaden recruitment using a model-free approach that is not restricted by these strong assumptions. We find that menhaden recruitment is predictable, but only when allowing for interdependence of stock with other ecological factors. Moreover, while the analysis confirms the presence of environmental effects, the environment alone does not readily account for the complexity of menhaden recruitment dynamics. The findings set the stage for revisiting recruitment prediction in management and serve as an instructive example in the ongoing debate about how to best treat and understand recruitment variability across species and fisheries.

KEYWORDS

ecosystem-based management, empirical dynamic modelling, nonparametric forecasting, recruitment dynamics

1 | INTRODUCTION

Gulf and Atlantic menhaden have both supported large fisheries over the past several decades. US landings of menhaden from 2011 to 2015 total 7.7 billion lbs., making them the second largest US fishery by weight only to Alaskan pollock (*Gadus chalcogrammus*, Gadidae), and the average annual catch is valued at over \$100 million (source: NOAA Commercial Fisheries Statistics). These fisheries also experience a great deal of catch variability. This is unsurprising given that menhaden, like most forage fish species, are strongly recruitment driven. That is, the youngest adult age class (new recruits) constitute most of the commercial catch, and so variability in recruitment directly translates to variability in catch.

Here, we take a model-free approach to understanding and predicting the year-to-year changes in menhaden recruitment, which remain a significant sticking point for management. Current practice for setting catch recommendations of Atlantic menhaden use the median of historical recruitment—in essence treating recruitment as fundamentally unpredictable. For Gulf menhaden, a stock–recruitment curve is specified but highly uncertain. Due to the recruitment-driven nature of these fisheries, the inability to accurately predict recruitment is a substantial limitation for management and risk evaluation.

Moreover, recent discussions of menhaden management have centred on the role that these species play in their ecosystems as both species occupying key middle trophic levels that support piscivorous fish such as striped bass (*Morone saxatilis*, Moronidae) and red drum (*Sciaenops ocellatus*, Sciaenidae). The Atlantic Menhaden Management Board has expressed interest in maintaining a forage base for piscivorous species while also maintaining commercial fishing interests, while the Gulf Menhaden Fishery Management Plan goals include management based on ecosystem science (VanderKooy & Smith, 2015). While considering an ecosystem-based perspective is important for effective management of menhaden, it is also a tall order given key uncertainties for each species, such as recruitment dynamics.

More broadly, recent work has questioned the ultimate predictability or randomness of recruitment (Schindler & Hilborn, 2015; Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015). Menhaden present a useful test case for this debate, in that there are empirical measurements of recruitment for both species. Thus, the relationship between stock and recruitment can be studied in a much cleaner way than other cases where recruitment measures are ultimately derived from observations of the stock, for example through stock assessments (Brooks & Deroba, 2015; Storch, Glaser, Ye, & Rosenberg, 2017).

Yet, while these exceptional data exist for menhaden, the dynamics are still treated as largely random. This current understanding hinges on the lack of success of the traditional parametric modelling approaches. The models, for example the Ricker and Beverton–Holt stock–recruitment curves treat recruitment as a univariate function of the stock size. While poor fits of fisheries data to these stock–recruitment curves are far from unusual (Subbey,

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Devine, Schaarschmidt, & Nash, 2014), the stock–recruitment curve model fits for menhaden are exceptionally poor and are not used in projections for management (Quinn & Deriso, 1999). This lack of explanatory power is true whether deriving recruitment in a traditional stock assessment of adult data (SEDAR, 2013, 2015) or for the empirical measures of recruitment ala Figure 1b,d.

Multiple reasons have been given for the failure to fit parametric models and the apparent randomness of the stock–recruitment relationship. Measurement error is an obvious place to look. For menhaden, there are particular problems stemming from the fact that observational programmes responsible for measuring menhaden juveniles are largely designed around other species (e.g., striped bass). Strong dependence on stochastic environmental drivers is also a common explanation, with studies across both species identifying a wide array of processes that—at least at one time or another—affect recruitment, including longshore wind patterns (Quinlan, Blanton, Miller, & Werner, 1999), winter storms (Checkley, Raman, Maillet, & Mason, 1988) and river flow (Govoni, 1997; Sanchez-Rubio & Perry, 2015; Vaughan, Govoni, & Shertzer, 2011). However, attempts to incorporate environmental information into recruitment forecasts via the traditional “environmental Ricker” (Nelson, Ingham, & Schaaf, 1977) have not met with much success (Myers, 1998).

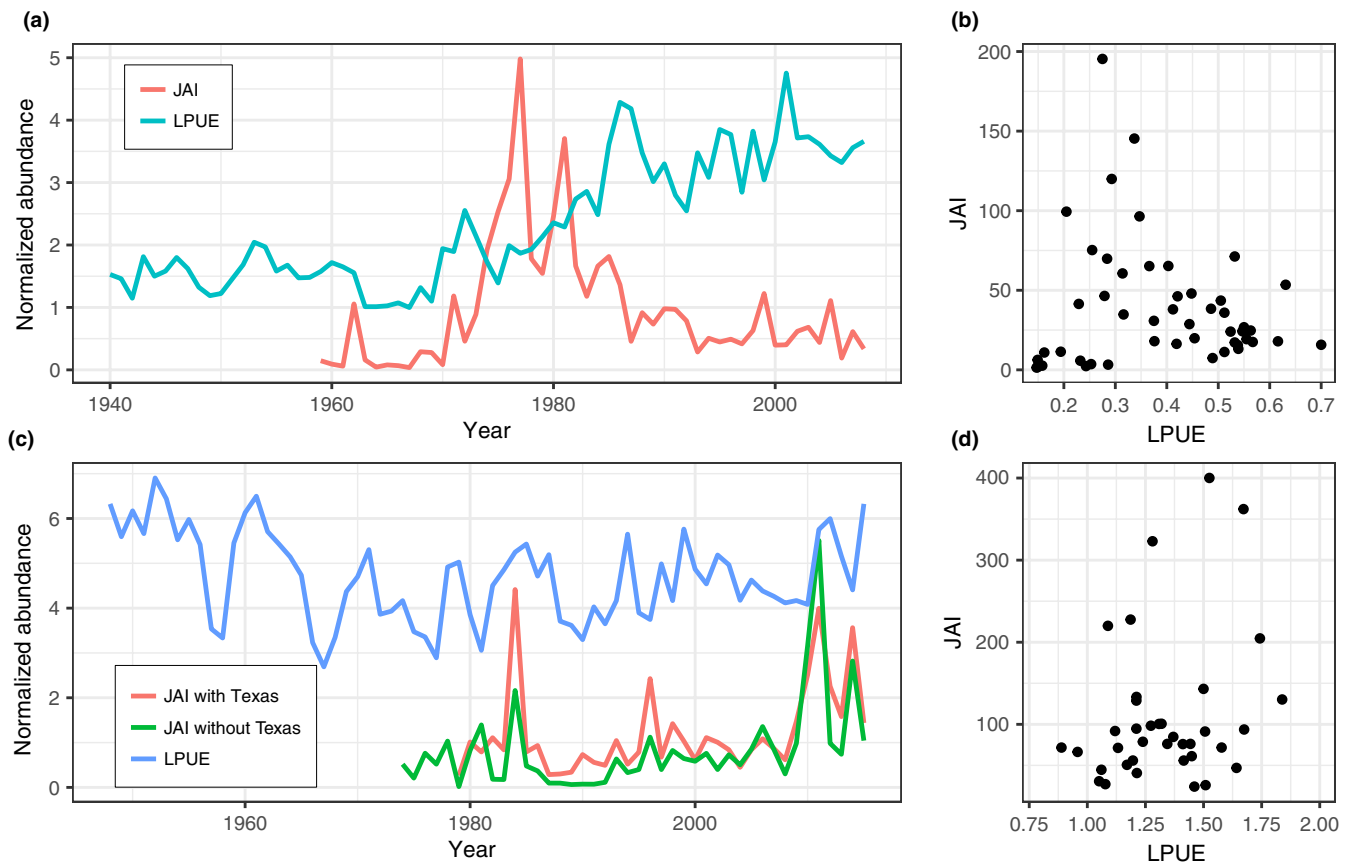


FIGURE 1 Normalized time-series observations for Atlantic (top) and Gulf (bottom) menhaden species. Time series (a, c) are shown for Juvenile Abundance Indices (JAI—a proxy for recruitment) and Landing per Unit Effort (LPUE—an indicator of adult spawning biomass). Traditional single-species management treats recruitment as a univariate function of stock size. However, plotting the data together shows (b, d) statistical fits are extremely poor, giving very little evidence for a univariate relationship

Less well acknowledged in fisheries circles is the potential for problems to lie with the basic equation-based modelling approach itself. Mechanistic models can be very appealing. For example, benchmarks like maximum sustainable yield can be explicitly derived from the model structure. However, these easy inferences are only valid if the model structure is correct and properly parameterized. In fact, fitting model parameters to population time series can be surprisingly difficult (Perretti, Munch, & Sugihara, 2013). More fundamentally, the functional forms and structure of a parametric model encapsulate very specific hypotheses about dynamics, and studies typically take these on as tacit assumptions that are not critically evaluated or quantitatively tested. The widely used Beverton–Holt and Ricker stock–recruitment curves capture very basic, reasonable mechanisms, but also carry very specific assumptions about dynamics—for example that the population experiences a static growth rate and natural mortality rate and exists as a single stock that is independent of the rest of the ecosystem. Yet, these assumptions can be difficult to reconcile with current knowledge. Recent work on Atlantic menhaden, for example, shows clear evidence that growth rates depend on the population density (Schueller & Williams, 2017).

Consequently, while these assumptions make for manageable and expedient models, the reality that populations are embedded in

complex ecosystems can greatly limit their insight. In this paper, we take an alternative approach, empirical dynamic modelling (EDM) (Ye, Beamish, et al., 2015), to re-examine the notion that menhaden recruitment variability is random and attempt to develop predictive models by treating recruitment as an ecosystem-dependent process. The key to EDM is to view time-series data as evolving through time.

As an illustration, Figure 2 shows simulated data of a fish population. In panel (a), a scatterplot of stock vs. recruitment (with the appropriate reproductive delay) does not show any clear relationship; a single curve fit through the data would leave much of the variance unexplained. However, this assumes that the effect of stock on recruitment is static and can be treated as independent of context. If we take the same data and “connect the dots” (Figure 2b) by drawing lines through consecutive points in time, it is evident that the state of recruitment and stock follows similar trajectories many different times through the observation period. That is, by considering the temporal nature of these data instead of treating them as static, there is evidence of deterministic processes at work. However, this still treats stock as the only factor explaining recruitment.

What happens if we consider other factors? This might seem hard to do, as we have only been given stock and recruitment data.

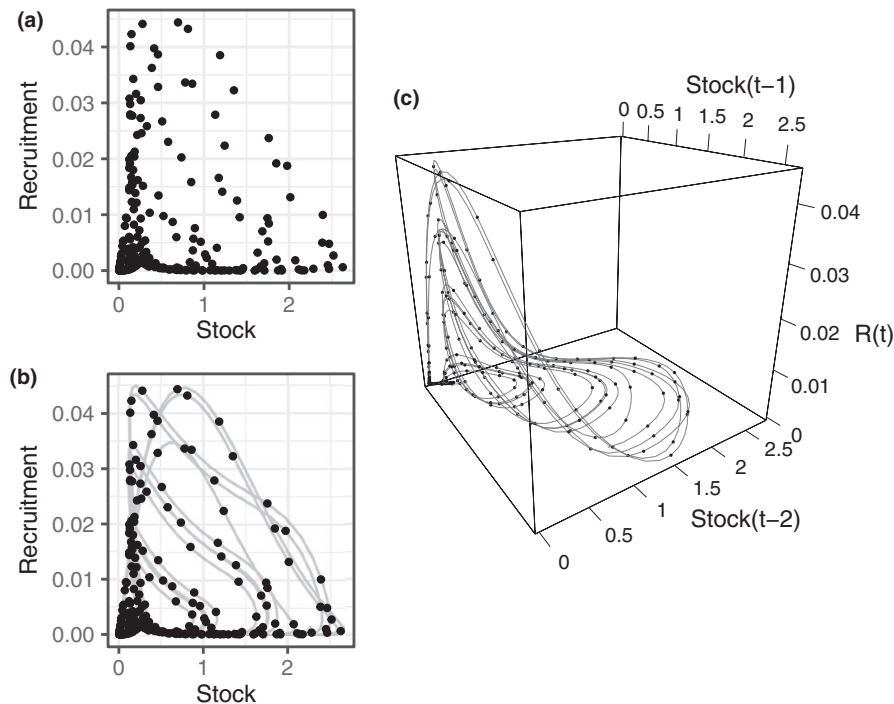


FIGURE 2 Model illustration of stock–recruitment relationships with multivariate dynamics. Stock–recruitment relationships can appear very messy when important ecosystem dynamics are ignored. In this model example, the stock–recruitment relationship looks extremely noisy (or non-existent) if one tries to understand recruitment as a univariate function of stock (a), independent of time and ecosystem. Population data are fundamentally dynamic; however, they occur as a sequence. (b) Connecting the dots shows that the behaviour is not totally random, but there is reoccurring behaviour. If the trajectories are expanded into three dimensions using a time-lagged coordinate of Stock (c), the pattern is fully resolved as a dynamic attractor. What appeared to be a scatter of random noise in (a) can be resolved as a completely deterministic flow of trajectories

The time-delay embedding theorem of Takens (1981) offers a solution: using time lags of measured variables in place of unmeasured variables. In other words, instead of considering recruitment as a function of stock size, we can model recruitment as a function of current stock size and stock size at a 1-year lag (Figure 2c). Doing so “untangles” the trajectories and allows recruitment to be uniquely defined and modelled from the time series of stock size, even in the case at hand where the data actually arise from a continuous-time Ricker model with a third species that preys on the juveniles (Supporting Information).

This set of untangled trajectories constitutes the dynamic attractor, which can be studied in its own right to understand and predict system dynamics in much the same way as model equations. This is the crux of EDM. While detailed description of the methods is provided later in the Methods section, the essential approach (Figure 3) is to use historical trajectories (blue) most analogous to the current state (magenta) to predict future dynamics (red). Note that this only works because the multidimensional dynamics have been properly unfolded. If we tried to do this in the 2D representation in panel B, for example akin to a Loess fit (Cleveland & Devlin, 1988), the prediction of the future values would be very poor because the different states of the system are poorly resolved. While we only needed to include one more dimension here to resolve the states, the approach is not limited to three dimensions, just our ability to neatly visualize them in a manuscript plot.

In this way, the EDM approach can reflect multivariate state dependence (unlike an autoregressive or multivariate autoregressive model), while being entirely equation free. Moreover, the ability to use time lag variables in place of explicit measurements of interacting variables makes the approach eminently practical, because ecosystem dynamics can be allowed and accommodated for even when the other variables are not identified, measured or exactly understood mechanistically. Variations on this simple nearest neighbour forecasting have been used to test for the presence of multidimensional (Sugihara & May, 1990) and nonlinear (Sugihara, 1994) dynamics, but also to probe mechanistic relationships between variables (Deyle, May, Munch, & Sugihara, 2016; Sugihara et al., 2012), understand the role of stochastic drivers (Dixon, Milicich, & Sugihara, 1999), and make true out-of-sample forecasts (McGowan et al., 2017).

Our immediate goal is to develop predictive models for menhaden recruitment. In so doing, we pose the following hypothesis: that the apparent unpredictability of menhaden recruitment is a consequence of ecosystem effects on menhaden dynamics. We test if ecosystem factors had a key impact on menhaden and if an ecosystem perspective can lead to recruitment predictability not possible in the single-species framework. We further explicitly look at basic environmental drivers to see if they can account for the ecosystem effects or if there is evidence of unmeasured biotic factors like prey availability or predation that are key to the recruitment dynamics.

2 | METHODS

2.1 | Atlantic menhaden

A juvenile abundance index (JAI; young of year or age-0 recruitment) was compiled for Atlantic menhaden during 1959–2013 (SEDAR, 2015). The index is composed of 16 fishery-independent data sets from Georgia to Rhode Island. Each data set was standardized using the criterion outlined for the stock assessment (SEDAR, 2015). Individual indices were combined into a coast-wide index using hierarchical modelling (Conn, 2010). Indices were able to be combined because they had similar age-0 selectivity.

Landings per unit effort (LPUE) was the total commercial reduction landings by year divided by the vessel-weeks per year for the fleet (SEDAR, 2015). Reduction landings were reported as daily vessel unloads by the companies and were converted into kilograms (SEDAR, 2015). Effort was vessel-weeks, which was defined as a vessel fishing at a minimum 1 day of a week (Nicholson, 1971; SEDAR, 2015).

2.2 | Gulf menhaden

A JAI (young of year or age-0 recruitment) was compiled for Gulf menhaden during 1996–2015 (Schueller, 2016). The index was composed of three fishery-independent data sets from Louisiana to Alabama for the months of December–September. Each data set was standardized using the criterion outlined for the stock assessment (SEDAR, 2013). Individual indices were combined into a coast-wide index using hierarchical modelling (Conn, 2010). Indices were able to be combined because they had similar age-0 selectivity.

An additional Gulf menhaden JAI index was considered in this analysis. The additional index included data from Texas, as well as the data from the original index considered during the stock assessment. Texas data were not included in the stock assessment due to concerns related to correct species identification (SEDAR, 2013). The Texas data were included here to determine if the recruitment dynamics were different with the addition of spatial and temporal coverage. However, data up to 1978 were constituted from very few survey stations and hence were excluded before any analysis was done.

Landings per unit efforts were the total landings by year divided by the vessel-ton-weeks (VTW) per year for the Gulf menhaden fishery fleet. A VTW was net tonnage of a given vessel fishing at a minimum 1 day in a given week (SEDAR, 2013). The total effort for a year was the sum of VTW across vessels and weeks in a fishing season. The unit of VTW was correlated with numbers of trips and number of sets over time; thus, all three metrics measured effort similarly over time (SEDAR, 2013). VTWs were used as that effort metric provided the longest time series.

For this study, LPUE was treated as an index of adult abundance over time. Historically, LPUE has been used as an indicator of adult abundance over time in stock assessment models. However, LPUE has not always been a reliable indicator of stock size due to

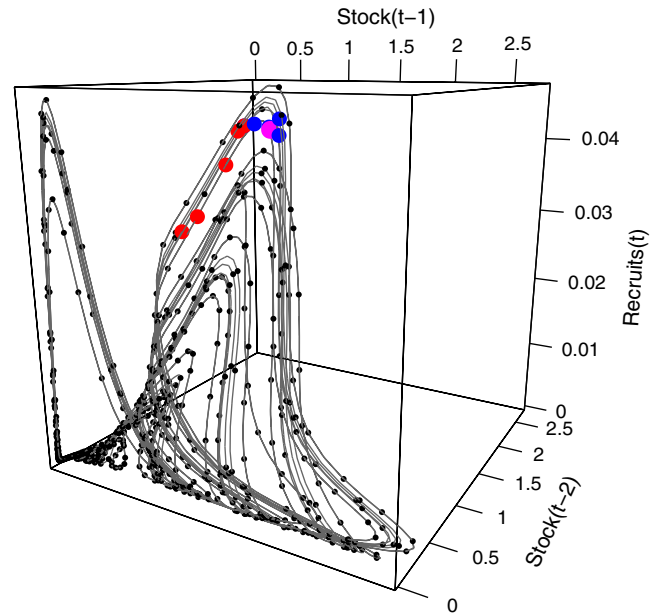


FIGURE 3 Illustration of basic EDM with model data. For this model, the attractor can be completely unfolded in three dimensions by taking stock, $S(t)$, recruitment, $R(t)$ and a 1 year lag of stock, $S(t - 1)$, as the three axes. When the dynamic attractor is fully unfolded in this way, the dynamics can be predicted and studied with very simple nonparametric methods, such as nearest neighbour forecasts. Here, the dynamics at the target point (magenta point) can be understood by looking at the behaviour of analogous historical states, that is points on the attractor that are nearest in the three-dimensional state space and thus most similar (the blue points). Good predictions can be made by a simple weighted average the evolution of these nearest neighbours (the red points)

hyperstability in some fishing fleets. Specifically, as abundance becomes very low, the fishery is able to continue harvesting regardless, or as abundance increases and is high, the fishery can become saturated and can only harvest a limited amount of fish. For the menhaden fishery, hyperstability can be a concern both at low and high abundances. The menhaden fishery uses spotter pilots to locate schools of fish; thus, when abundances are low, the pilots are still able to locate schools with some efficiency. When abundance is high, the menhaden fleet has a limited number of vessels fishing with a limited hold capacity, and the reduction facilities processing the catch have a maximum processing capacity. Regardless, LPUE for the menhaden species appears to capture the dynamics of the adult populations adequately. LPUEs track age classes or cohorts over time through the fishery. Correlations between landings and adult indices used in the respective stock assessments lend support that LPUE is an indicator of adult abundance. Finally, the current analysis supports the conclusion that LPUE indicates adult abundance.

2.3 | Environmental variables

Sea surface temperature and sea level pressure data are derived from EERST v3b (Smith, Reynolds, Peterson, & Lawrimore, 2008),

retrieved 14 February 2015. While these data are given on a $2^\circ \times 2^\circ$ grid, we compute a single summary index by performing a PCA analysis on the annual averages of each grid over a regional bounding box (for the grid centre points) and taking the first EOF. For the Atlantic, the bounding box is $\{66^\circ\text{W}, 82^\circ\text{W}\} \{24^\circ\text{N}, 44^\circ\text{N}\}$; for the Gulf of Mexico, it is $\{80^\circ\text{W}, 96^\circ\text{W}\} \{20^\circ\text{N}, 30^\circ\text{N}\}$. In both cases, the first EOF captures a great deal of the variability at individual grid sites over the population ranges.

River discharge data are derived from USGS NWIS, retrieved 3 March 2015. These data are provided for individual geo-located stations. For the Gulf, we use stations with coverage from 1 January 1964 to 31 December 2014 that are located in Texas, Louisiana, Mississippi, Alabama, Georgia or Florida and are within 60 nautical miles of shoreline. For the Atlantic, we use stations with coverage from 1 January 1950 to 31 December 2013 that are located in North Carolina, Virginia, Maryland, Delaware, Pennsylvania, New Jersey, New York, Connecticut or Rhode Island and are within 60 nautical miles of shoreline. As with the gridded SLP and SST measures, we compute a single summary index with a PCA analysis. However, the individual stations are first averaged annually and the stations are weighted in the PCA by their local density (as the stations are not uniformly distributed).

$$w_i = \sum_j e^{-\|\text{station}_i, \text{station}_j\|}$$

As above, the first EOF of the river discharge data captures a great deal of the variability in individual stations.

2.4 | EDM theory

Figure 2 in the introduction illustrated the basis of EDM: reimagining time-series data as a sequence of points (trajectory) in a multidimensional Cartesian space that then traces out the evolution of the system over time, that is the dynamic attractor. All EDM analysis in this paper started with that premise.

Formally, the attractor was reconstructed by defining a state space as a set of time-series variables and their lags, and thus, reinterpreting the time series as a sequence of points in this space, $\mathbf{x}(t_1) = \langle x_1(t_1), x_2(t_1), x_3(t_1), \dots \rangle$, $\mathbf{x}(t_2) = \langle x_1(t_2), x_2(t_2), x_3(t_2), \dots \rangle$, etc. If many system variables are observed, it may be possible to simply use each observation variable as one of the state-space coordinates. However, even if only a single variable is observed, an attractor can still be reconstructed using time lags of the observed variable as proxies for the other system variables (Takens, 1981). If some variables were observed and some were not, a mixture of unlagged and lagged variables is also admissible (Deyle & Sugihara, 2011).

The number of coordinate variables used is called the embedding dimension, denoted E . If too few coordinates are used, there will not be enough information to resolve distinct ecosystem states. This is exhibited by the simulated data in Figure 2b, where the state space is just two dimensions. The trajectories are tangled, because there is a third variable to account for, predators. If predators are abundant, the dynamics can be very different than if predators are

scarce. Thus, the point (stock, recruitment) could correspond to a time when the population is growing or contracting, depending on the third variable. Once a third dimension is included (either the predator abundance explicitly or a lag of stock), the trajectories are cleanly resolved. Of course, real systems may require more than three dimensions, so the embedding dimension must be determined in the analysis (essentially fit like a parameter).

When envisaged as an attractor in state space, the dynamics of the system boil down to the multivariate function that maps one time point to the next:

$$F(\mathbf{x}(t)) = \mathbf{x}(t+1).$$

Again, the vector $\mathbf{x}(t)$ is the encapsulation of the data in a particular state space. It could be an explicit embedding of the data where each coordinate is a different time-series variable— $\mathbf{x}(t) = \langle x_1(t), x_2(t), x_3(t) \dots x_E(t) \rangle$; it could be a univariate embedding of the data using time lags as the different coordinates— $\mathbf{x}(t) = \langle x_1(t), x_1(t-1), x_1(t-2), \dots, x_1(t-(E-1)) \rangle$; or it could be a mixed embedding that uses a few different variables and lags to fill in the rest— $\mathbf{x}(t) = \langle x_1(t), x_2(t), x_3(t), x_3(t-1) \dots, x_3(t-(E-3)) \rangle$.

Now in traditional modelling approaches, the function F is described by the parametric model equations. However, the function F can also be treated empirically from the data using simple, nonparametric approaches.

Simplex projection is a very simple way to approximate the attractor dynamics. It boils down to the simple principle that similar system states will evolve similarly in time. Formally, the similarity of two time points is judged by the Euclidian distance between them in the reconstructed state space, that is $\|\mathbf{x}, \mathbf{x}'\| = ((x_1 - x'_1)^2 + (x_2 - x'_2)^2 + \dots + (x_E - x'_E)^2)^{1/2}$.

The simplex projection prediction for a state $\mathbf{x}(t^*)$, then, is a weighted average of the $E+1$ historical time points that have the shortest Euclidian distance to $\mathbf{x}(t)$, that is:

$$\mathbf{x}(t^*+1) = F(\mathbf{x}(t^*)) \approx \sum_{i=1}^{E+1} \mathbf{x}(t_i+1) e^{\|\mathbf{x}(t^*), \mathbf{x}(t_i)\|}$$

Note that the only parameter for simplex projection is the embedding dimension.

Another simple approach to modelling the attractor dynamics is to use the fact that any smooth function can be approximated by a local linear function over a small enough neighbourhood. S-maps accomplish this by performing a weighted linear regression where historical points on the attractor are given an exponentially decaying weight based on their distance from the target. Explicitly, local linear model is the matrix \mathbf{C} that solves,

$$\mathbf{b} = \mathbf{AC},$$

where

$$B_j = w(\|\mathbf{x}(t^*), \mathbf{x}(t_j)\|) \mathbf{x}(t_j+1).$$

$$A_{ij} = w(\|\mathbf{x}(t^*), \mathbf{x}(t_j)\|) x_j(t_j).$$

$$w(d) = e^{-\alpha d/\bar{d}}$$

Here, \bar{d} is the average distance between points on the attractor. The strength of the local weighting is controlled by the parameter θ . Note that if $\theta = 0$, the regression becomes just a global linear map, that is S-map with $\theta = 0$ is just a standard VAR model over the embedding coordinates.

Note too that the S-map weighting is based on proximity in the multidimensional state space, not proximity in time. This is a key difference between it and MARSS or DLM methods. The weighting of S-maps addresses the fact that the system dynamics change on the manifold due to the inherent underlying nonlinearity/state-dependence. MARSS and DLM instead treat changes to the dynamics as random drift processes in time. Thus, they are a rather indirect way to deal with multivariate state-dependence at best, but can also give very wrong answers in the presence of state-dependence (Deyle et al., 2016).

Applying simplex projection and S-map to a time series can be an immediate way to address prediction, for example of population data. However, the ability to make forecasts from data can also be a means to an end, for example detecting causal influence (Sugihara et al., 2012).

2.5 | EDM analysis: univariate

Basic univariate analysis consists of sequential application of simplex and S-maps. First, simplex forecast skill over the historic time series is measured as a function of the embedding dimension E , that is the number of lag coordinates used to unfold the dynamic attractor (Sugihara & May, 1990). Forecasts are made using leave-one-out cross-validation, that is the target time point is not used in the attractor reconstruction. The forecast skill is measured using mean absolute error (MAE) and the Pearson's correlation between observed and predicted values (ρ). Pearson's correlation is more sensitive to performance at the extremes of the time series, which can be a boon for measuring nonlinear processes but also makes it less robust to observation error than MAE. For the LPUE time series, the predictive skill is measured on the first differences in LPUE from t to $t + 1$, that is $\Delta\text{LPUE}(t) = \text{LPUE}(t + 1) - \text{LPUE}(t)$. This makes it easier to distinguish meaningful attractor-based prediction from the trivial statistical prediction one gets from the autocorrelation.

Analysis then proceeds to S-maps. The embedding dimension is fixed based on the simplex results, and the nonlinear S-map parameter θ is varied from 0 to 5. As with simplex projection, forecast skill is measured either using ρ or MAE. The improvement in forecast skill for $\theta > 0$ over the linear S-map with $\theta = 0$ is also of particular interest, that is $\Delta\rho = \rho - \rho(\theta = 0)$.

Parametric statistics for the statistical significance of EDM results cannot be readily derived. Instead, statistical significance of EDM results can be established using appropriately designed surrogate tests. Here, we employ phase-randomized surrogates (Ebisuzaki, 1997) that preserve the basic statistical properties of the time series (e.g., autocorrelation), but otherwise randomizes the time series. The same analysis performed for the real-time series

are performed on 500 realizations of the surrogate time series to generate null distributions for the S-map predictability (ρ) and the nonlinear forecast improvement ($\Delta\rho$).

2.6 | EDM analysis: convergent cross-mapping

In the case of convergent cross-mapping (CCM), attractor predictability can be a way to measure interactions between time-series variables. If x and y belong to the same system, then the system states can be recovered with univariate embeddings of either x or y , and the attractor reconstructed from x can be used to predict values of y . Using simplex projection, this boils down to:

1. Finding the historical states closest to the target time t^* on the x manifold, that is the time points $t_1, t_2, \dots, t_{(E+1)}$ so that $\mathbf{x}(t_1)$ has the smallest distance of historical states to $\mathbf{x}(t^*)$, $\mathbf{x}(t_2)$ the next smallest, etc.
2. Predicting $y(t^*)$ based on a weighted average of the observed y values at these historical analogues, that is

$$y(t+tp) = F(x(t)) \approx \sum_{i=1}^{E+1} y(t_i+tp).$$

Note that the prediction time tp is included. For normal application of CCM, this is set at $tp = 0$. However, for stochastic drivers that act with time delays, the driven variable x will only contain information about past values of the drivers y , and so CCM may only be measurable at negative time lag, $tp < 0$ (Ye, Beamish, et al., 2015; Ye, Deyle, Gilarranz, & Sugihara, 2015).

Note too that as with simplex projection for basic univariate forecasting, CCM has a parameter, E , the embedding dimension of the predictor manifold. For CCM with prediction lag tp , E is selected that maximizes CCM prediction at lag $tp - 1$. This reduces the chance of false positives (Deyle et al., 2016).

If y can be predicted from states of x , this means that information about y has been encoded in variable x , and therefore that y had a causal influence on x . This is general to systems with identifiable deterministic dynamics (e.g., demonstrated with univariate EDM analysis) and robust to realistic amounts of observational noise (Sugihara et al., 2012). The generality of EDM makes CCM convergent cross-mapping a test for causation that does not rely on any assumptions about separability of different variables (i.e., cross-correlation or GAMs) or functional form (sequential f-testing e.g., to detect environmental effects).

2.7 | EDM analysis: predicting recruitment from stock

Predicting recruitment from stock is possible with only a small adjustment to CCM in the prediction time. That is, instead of predicting contemporaneous or lag values ($tp < 0$) of the JAI from lags of LPUE, we predict future JAI ($tp = 1$ year). Again, these forecasts have a single parameter, E . As with univariate simplex projection, this is fit by

maximizing the forecast skill, ρ . However, the prediction skill as a function of E is also of interest in addressing the question of whether the effect of recruitment must be treated in an ecosystem context or not (i.e., cannot be treated as a univariate function of stock).

2.8 | EDM analysis: including climate drivers in predictions

The final analysis is akin to that above, but instead of prediction $JAI(t+1)$ from $\langle LPUE(t), LPUE(t-1), \dots, LPUE(t-E-1) \rangle$, the embedding also includes a lag of environment. That is, $JAI(t+1)$ is predicted from $\langle Env(t), LPUE(t), LPUE(t-1), \dots, LPUE(t-E-2) \rangle$. Additionally, the lags of LPUE and Env are normalized to have standard deviation of 0 so that the distance calculations are not affected by the units of scaling of the variables.

3 | RESULTS

3.1 | Question 1: Do recruitment/year-to-year abundance changes have predictable dynamics?

We begin by testing for predictable dynamics in the JAI and LPUE time series for both Atlantic and Gulf menhaden (see Methods). The first column of Figure 4a,d,g,j shows forecast skill, ρ , as a function of the embedding dimension (number of lags in the simplex model) for each of the four biological time series. For each time series, we select the embedding dimension, E , that maximizes the simplex ρ for all subsequent analyses (Glaser et al., 2014; Sugihara & May, 1990). Nonlinearity is tested by using S-maps and measuring ρ as a function of the nonlinear parameter θ . The second column of Figure 4b,e,h,k shows S-map ρ as a function of θ , and the third column (c,f,i,l) shows the improvement in ρ over the linear S-map, that is the change in ρ compared to ρ at $\theta = 0$.

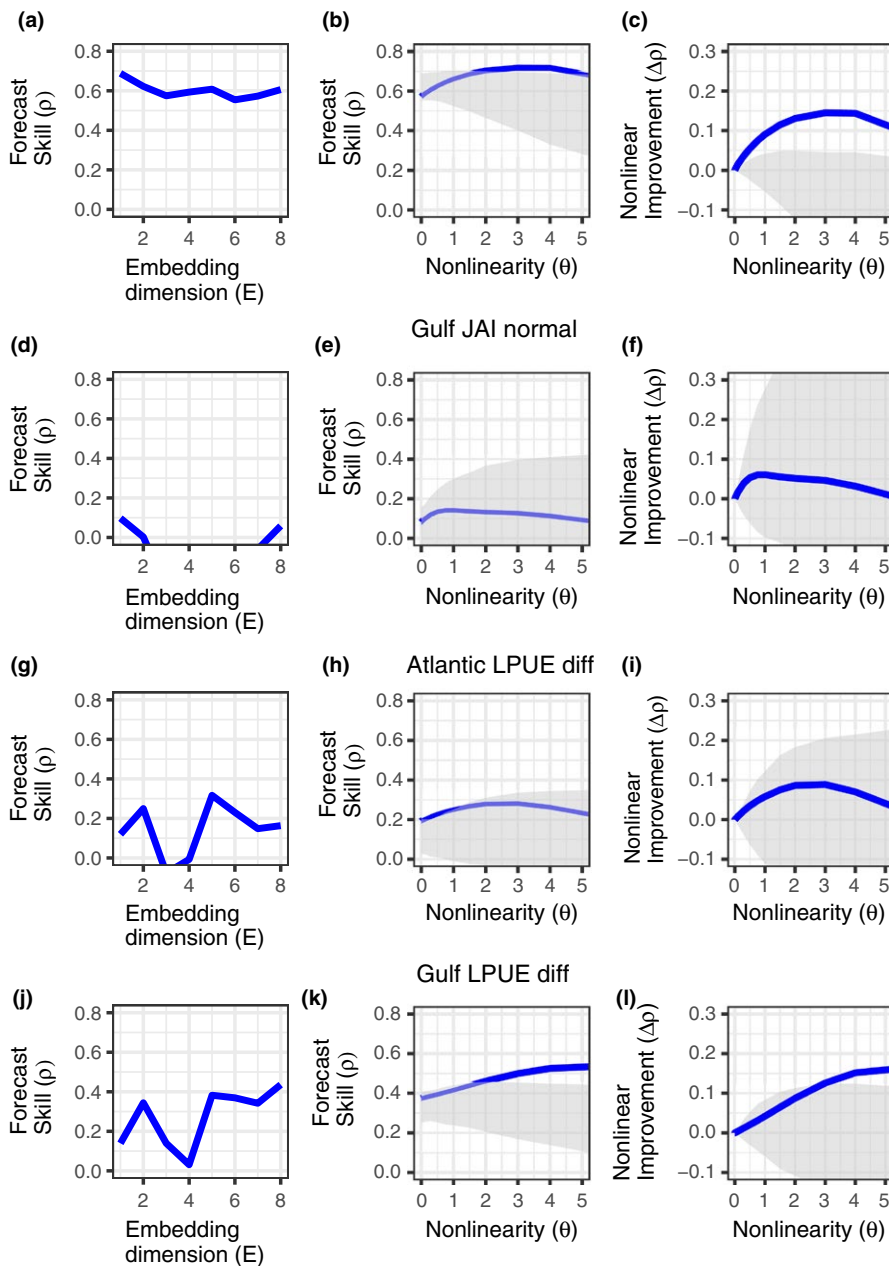


FIGURE 4 Univariate EDM analysis of Atlantic and Gulf menhaden. The left column (a,d,g,j) shows forecast skill (ρ) as a function of embedding dimension (E) using simplex projection. Atlantic JAI, Atlantic LPUE and Gulf LPUE all show signs of low-dimensional attractor dynamics. The centre (b,e,h,k) column shows forecast skill (ρ) as a function of the nonlinear parameter θ for S-map analysis, where $\theta = 0$ corresponds to a global linear model (i.e., a MAR) and larger θ correspond to increasingly nonlinear models. The rightmost column (c,f,i,l) shows the same analysis, but explicitly looking at the improvement, $\Delta\rho$, in nonlinear S-map ($\theta > 0$) forecast skill over the linear S-map ($\theta = 0$). Grey regions show the 0.05 and 0.95 quantiles of the null distributions

Atlantic JAI and Gulf LPUE time series show clear statistically significant predictability. More importantly, forecast skill increases with θ indicating the presence of deterministic nonlinear behaviour ($p < .05$), and that any environmental effects may be convolved with stock–recruitment dynamics. The nonlinear signal is less strong for Atlantic LPUE ($p < .2$) and Gulf JAI. In the latter case, baseline predictability is very low, indicating that the time series itself may not be very predictable.

Overall, year-to-year changes in both Gulf and Atlantic menhaden abundance show predictable nonlinear dynamics. However, for the Gulf, this is only recoverable from LPUE. The apparent lack of signal in the Gulf JAI time series could be due to (i) limited time-series length, (ii) too much uncertainty or incompleteness of the measurements or (iii) strong stochastic forcing.

3.2 | Question 2: Is there evidence of interaction between stock and recruitment?

Next, we look for interactions between stock and recruitment by using convergent cross-mapping (CCM). Essentially, if stock and recruitment are dynamically related to each other, there should be a

correspondence (mapping) between the attractors reconstructed from each that can be used predictively. Namely, if stock has a dynamic effect on recruitment, then the recruitment time series contains the signature of the stock dynamics, and so it should be possible to predict stock by cross-mapping from recruitment. As expected, CCM identifies clear and strong coupling between the JAI and LPUE time series of each species. In the Atlantic (Figure 5a), there is evidence of causation in both directions: stock affects recruitment, recruitment affects stock. For the Gulf (Figure 5b,c), there is evidence that stock affects recruitment, indicated by cross-mapping from JAI to LPUE. LPUE, however, cannot predict JAI at 0 time lag. Additionally, the effect of stock on recruitment is much clearer when Texas data are included ($\rho(L_{\max}) = 0.5x$) rather than excluded ($\rho(L_{\max}) = 0.2x$). That is to say, the JAI appears to contain much more information about the stock dynamics when it is constructed with Texas data. This justifies focusing on the JAI with Texas in the remaining analysis.

The CCM results for Gulf JAI contravene the idea that weak univariate predictability of recruitment is due to observation error, as the time series has clearly recoverable information about adult biomass. The CCM results are more consistent with low univariate

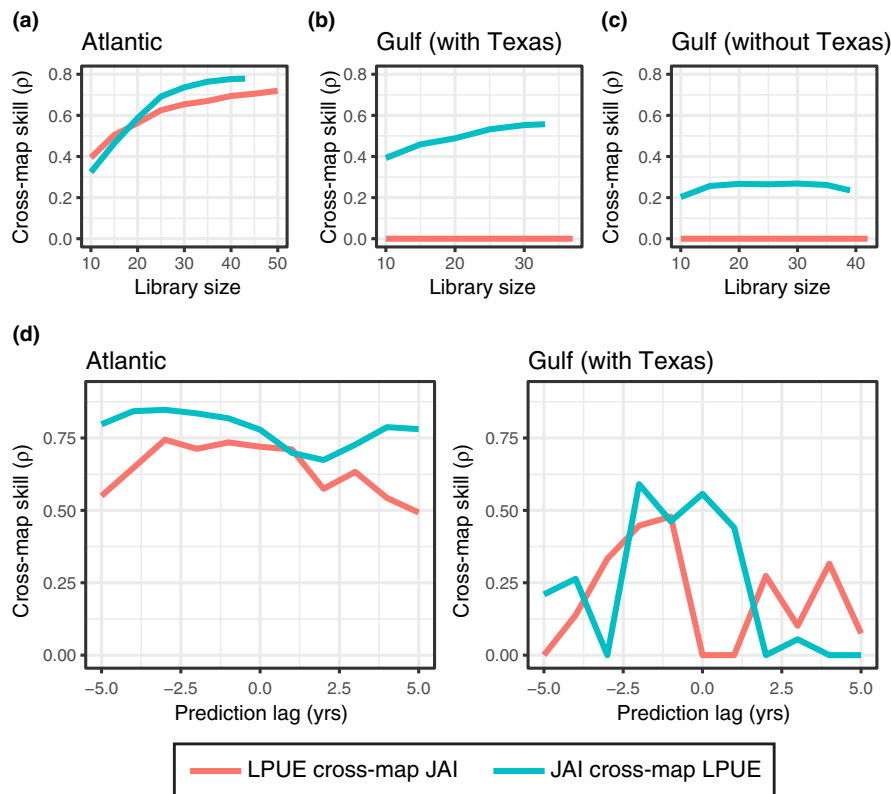


FIGURE 5 Measuring effects between stock and recruitment using CCM. Convergent cross-map results are shown between empirical indicators of recruitment (JAI) and stock size (LPUE). In the Atlantic (a), stock and recruitment show strong mutual cross-map indicating that despite poor parametric stock–recruitment fits, there is a deterministic effect of stock on recruitment (and vice versa). In the Gulf (b,c), recruitment can cross-map stock, which again indicates there is a deterministic effect of stock on recruitment. This effect is substantially stronger when using JAI time series that include Texas juvenile survey data (b) than when it is left out (c). However, stock cannot cross-map recruitment. This is better understood by looking at cross-map (ρ) skill as a function of prediction lag (d,e). Stock does cross-map of past values of recruitment in the Gulf, suggesting that there is the expected effect of recruitment on stock, but that recruitment in the Gulf has important exogenous drivers

predictability being a symptom of strong stochastic forcing. In this case, it would be difficult to predict current JAI from past LPUE, as the LPUE time series cannot contain current information about any stochastic driver. However, it would still contain information about past states of JAI, so lag prediction should be possible. Performing a lagged CCM analysis bears out this point exactly (Figure 5d,e). While LPUE cannot cross-map JAI with a zero prediction lag in the Gulf (Figure 5b), LPUE cross-maps past values of JAI (from 1 to 3 years) with comparable predictability to the other direction (Figure 5e).

3.3 | Question 3: Can recruitment be predicted from stock?

In the previous analysis (Figure 5), recruitment of Atlantic menhaden is modelled using a lag coordinate embedding of stock size. However, this is essentially a “nowcast,” where the recruitment in year t is estimated using stock size up to time t . Figure 6a shows forecast skill for predicting next year’s recruitment, the JAI at time $(t + 1)$, using simplex projection and varying the number of lags of LPUE. For both the Atlantic and the Gulf, prediction skill (ρ and MAE) increases substantially when including multiple lags of LPUE. This indicates that recruitment is not a function of stock size *alone* (per a traditional stock–recruitment curve), as then a single lag of LPUE would be sufficient for prediction. Optimum prediction requires multiple lags, suggesting that there are additional ecosystem factors that influence recruitment. Forecast skill is compared to the constant predictor (dashed lines), that is predicting that recruitment next year will be the same as the recruitment in the current year. This is an important baseline to establish for ecological forecasting to establish if the analysis is achieving meaningful prediction beyond just the serial autocorrelation present in the time series. Note that although ρ for Gulf menhaden is lower than that for the constant predictor, MAE is better.

3.4 | Question 4: Are there synoptic climate drivers?

Given evidence that the effect of stock on recruitment cannot be understood without additional variables, a logical next step is to identify potential climatic drivers. As environmental effects may not show up immediately in recruitment, we allow up to a 5-year lag in the CCM analysis (Ye, Deyle, et al., 2015). Figure 7 shows the strength of cross-mapping to regional sea surface temperature (SST, in green), sea level pressure (SLP, in red) and river discharge (in blue). For the Atlantic, SST shows to be the best indicator of environmental effects on recruitment, whereas SLP appears to be the best indicator of effects on recruitment in the Gulf.

3.5 | Question 5: Do environmental drivers explain ecosystem effects?

Having found CCM evidence for climatic drivers, it makes sense to revisit the EDM predictions of JAI from LPUE and explicitly account for climate in the model. In the Atlantic, explicitly including SST with

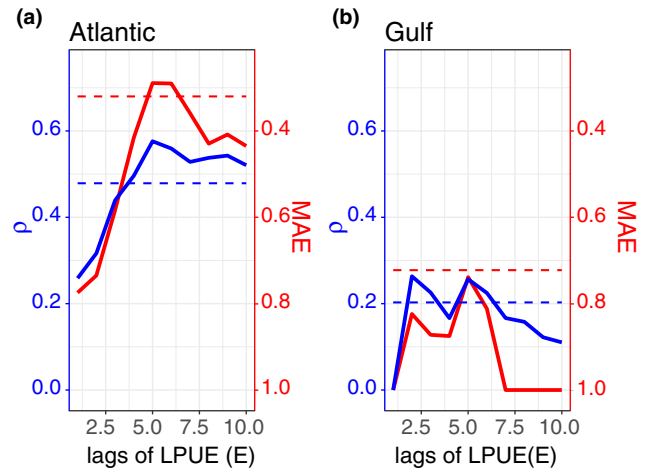


FIGURE 6 Predicting recruitment from stock in Atlantic (left) and Gulf (right) menhaden. EDM forecast skill (ρ) and error (MAE) are shown as a function of the number of lags of stock being used to predict recruitment (forecast skill in red, error in blue). The Atlantic shows strong evidence of predictability, but only when multiple lags of Stock are used, that is when the dynamics are treated as multivariate. Prediction is weaker in the Gulf, but also suggests multivariate dynamics. For comparison, the skill and error of the constant predictor (i.e., predict that $JAI(t + 1) = JAI(t)$) are included as dashed lines. Note that MAE direction is reversed to correspond with the direction of ρ

lags of LPUE actually does slightly worse (though not significantly so) than forecasts based on just LPUE (Figure 8a). Moreover, the same number of lags of LPUE (5) is required for optimal prediction. Thus, while SST appears to causally affect the population dynamics, the LPUE time series itself already contains sufficient information about the SST effect. This means it is unlikely that SST has a strong, direct stochastic effect on recruitment in the Atlantic.

The picture is different for the Gulf (Figure 8b). For Gulf menhaden, including SLP (following Figure 7d) with LPUE gives substantially better forecast skill than predicting menhaden from LPUE alone. However, multiple lags of LPUE are still required to get the best predictability even when SLP is explicitly included. Thus, while SLP shows evidence of direct stochastic effect on recruitment (as lags of LPUE are not sufficient to account for it), there appears to still be additional, unidentified ecosystem effects.

4 | DISCUSSION

The above analysis shows that menhaden recruitment is predictable. However, in contrast to the standard approach of identifying a simple stock–recruit relationship, there are clear signs that recruitment is driven nonlinearly by ecosystem interactions. For Atlantic menhaden, the multivariate modelling results indicate that ecosystem dynamics can be described using lags of stock size. In contrast, for Gulf menhaden, including sea level pressure directly into the models is required for good forecasting. Although we caution against overinterpreting these results, they suggest differences between the

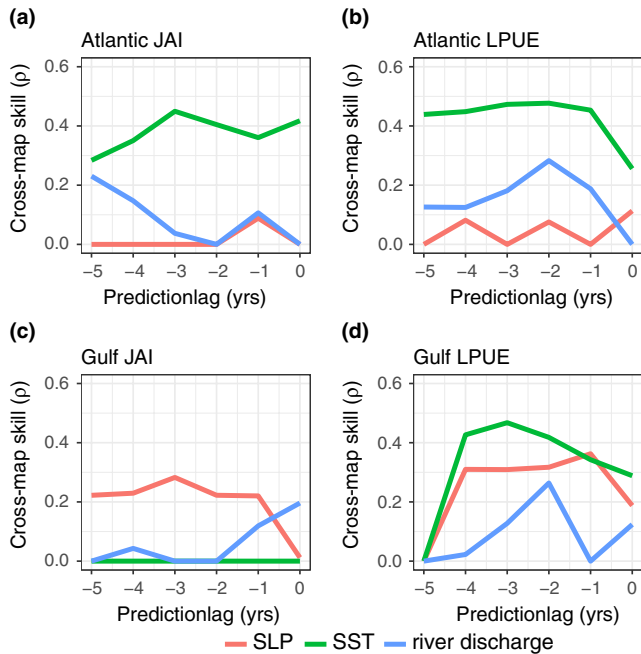


FIGURE 7 Convergent cross-mapping (CCM) analysis of environmental drivers. As environmental drivers may act with time lags, CCM analysis is done with a variable time lag. Here, cross-map skill (ρ) is shown as a function in the prediction time between menhaden time series and regional summaries of three environmental measurements: sea level pressure (SLP), sea surface temperature (SST) and river discharge. Generally, SST shows the strongest effect, although SLP appears to be more important for Gulf recruitment (JAI)

species in the strength of the environmental forcing, as well as in how much of the relevant environmental effect is captured in the tested variables.

Indeed, the results pertaining to environmental drivers in the Atlantic might seem to run counter to other studies (Buchheister, Miller, Houde, Secor, & Latour, 2016). While our analysis shows that SST influences Atlantic menhaden, it does not need to be directly accounted for to achieve accurate predictions of recruitment. Note, however, that we analyse all Atlantic menhaden as a single population, in contrast to Buchheister et al., who looked explicitly at spatial differences in recruitment. In combination with what is already known about Atlantic menhaden larval dispersal (Quinlan et al., 1999), a reasonable hypothesis is that environmental drivers have a stronger effect on local recruitment variability than on aggregate recruitment, for example in determining the particular estuary to which larvae recruit (Light & Able, 2003). While this question may not be relevant to the basic management questions for Atlantic menhaden, local recruitment is an important consideration for understanding interactions with other, spatially isolated species, such as striped bass. This invites future work to synthesize the insights of EDM here into ecosystem effects with the spatial insights of Buchheister et al. (2016).

The results for Gulf menhaden agree with previous analysis showing that environmental drivers are important for understanding recruitment variability. Previous studies have focused on the effect

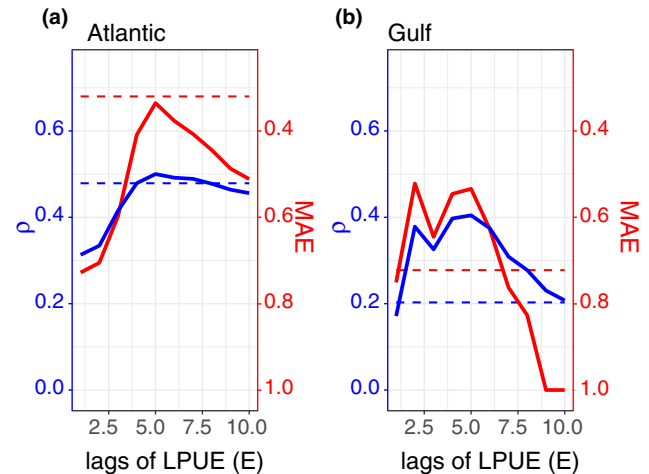


FIGURE 8 Predicting recruitment from stock and environment in Atlantic (left) and Gulf (right) menhaden. The analysis shown in Fig. 6 is repeated with key environmental drivers included with lags of stock, with forecast skill (ρ) and error (MAE) shown in red and blue, respectively. In the Atlantic, incorporating SST does not improve prediction over using just lags of stock. In the Gulf, incorporating SLP leads to substantial improvement. In either case, optimal prediction is still achieved when multiple lags of LPUE are included, suggesting that there are additional ecosystem factors besides synoptic measures of climate that are important to menhaden recruitment. The skill and error of the constant predictor (i.e., predict that $JAI(t+1) = JAI(t)$) are included as dashed lines. MAE direction is reversed to correspond with the direction of ρ

of Mississippi and Atchafalaya river outflow (Govoni, 1997; Vaughan et al., 2011) on recruitment. These analyses, however, were based on stock assessments including adult landings data with assumptions such as the natural mortality of menhaden being constant across all years (i.e., independent of ecosystem processes). The CCM analysis here shows an effect of SLP on both recruits and year-to-year changes in adults, with marginally significant evidence of an effect of river discharge on adult LPUE only.

More generally, this case-study is instructive to larger questions about prediction and management. Several recent publications (Hilborn et al., 2017; Szuwalski & Hilborn, 2015) have questioned management approaches due to a failure to find quantitative evidence for interaction between stock size and recruitment. The studies at the core of these debates (Gilbert, 1997; Szuwalski et al., 2015; Vert-pre, Amoroso, Jensen, & Hilborn, 2013), however, relied on the traditional parametric stock-recruitment curves and simple linear correlations that carry a large number of embedded assumptions. In fact, those methods would suggest that stock has no effect on recruitment in menhaden. Rather than immediately concluding stock size does not need to be maintained for future productivity, the analyses here show that a clear predictive effect of stock on recruitment exists. One simply must remove assumptions about separability and independence and allow for the reality that ecology interplays with the reproductive dynamics of these populations.

These results join several other recent studies that forge inroads into adapting the EDM approach to practical fisheries management (Harford, Karnauskas, Walter, & Liu, 2017; Liu, Karnauskas, Zhang, Linton, & Porch, 2017; Ye, Beamish, et al., 2015). However, real forecast skill is invaluable to proactive management; without it, management can only be reactive. So, while the number of success cases with EDM grows, studies continue to find trouble with using classical fisheries models predictively. There is still a somewhat open question of the best way to translate the baseline forecasting ability demonstrated in these papers into improved management, but the demonstrated predictability clearly outlines a usefulness for EDM approaches. The ability to predict the near-term growth potential of the stock is a valuable piece for moving forward with management, ecosystem-based or not. The most immediate opportunity perhaps being to use EDM forecasts of recruitment to improve the next-year projections of stock that are used to set harvest limits. This could be valuable not only for these menhaden species, but other recruitment-driven fisheries or populations with highly variable recruitment.

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