

Predicting nonlinear dynamics of short-lived penaeid shrimp species in the Gulf of Mexico

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Abstract

Predicting the dynamics of harvested species is essential for assessing stock status and establishing index-based management strategies. However, conventional approaches for short-lived species predict dynamics poorly, possibly because unobserved interactions with other species and abiotic factors are often treated as noise. Alternatively, the empirical dynamic modeling (EDM) approach, which uses the time delays of the observed states to compensate for unobserved interactions, may improve the predictions for short-lived species. We test this idea using time series data of two federally managed, short-lived penaeid shrimp species, whose abundances were surveyed over 30 years (1987–2018) across the US Gulf of Mexico. We show that (i) abundance dynamics of these annual shrimp stocks are well-predicted by EDM, (ii) the dynamics are spatially similar across most of the gulf, and (iii) the stock dynamics are characterized by nonlinear density-dependent interaction and vary with temperature. Our findings suggest that EDM may be more responsive than single-species, catch-at-age models in assessing the stock dynamics for short-lived penaeid shrimp species.

Key words: penaeid shrimp fisheries, short-lived species, nonlinear time-series forecasting, dynamic correlation, spatial synchrony, Gulf of Mexico fisheries management

Introduction

Dynamics of short-lived marine species are notoriously difficult to predict, often exhibiting large fluctuations in population size and increased sensitivity to environmental variability compared with longer-lived stocks (Hsieh et al. 2006; Essington et al. 2015; Pinsky and Byler 2015). This high variability in abundance is often attributed to stochastic environmental processes underlying recruitment (Somarakis et al. 2019; Siple et al. 2021). However, interactions with other species (e.g., predation and competition), depending on abiotic environmental conditions, can also give rise to apparent stochasticity when these species interactions are not considered (Munch et al. 2020).

In the Gulf of Mexico (GOM), penaeid shrimps are short-lived, annual stocks that pose several challenges to fisheries management (see Gulf of Mexico penaeid shrimp fisheries management history below). In addition to their high variability in abundance, one major limitation of applying more advanced, stock assessment models to evaluate the stock dynamics for these annual stocks is the lag time in acquiring and processing the necessary fisheries data to populate, for instance, an integrated, catch-at-age assessment model (i.e., Stock Synthesis, SS; Maunder and Punt 2013; Methot and Wet-

zel 2013). Specifically, processing and receiving landings and catch-at-age data from various state partners in the southeastern USA tends to lag behind the ability to process fisheries independent survey data. This logistical delay represents nearly two generations (ca. 2 years) for these shrimp species. Consequently, the stock assessment model outputs and management advice are out of date because the projections are based on previously assumed model structure, rather than informed by data or the inherent predictability of data. Other approaches, such as surplus production models, stock-recruitment analyses, and virtual population analyses, also depend on data that take time to acquire and result in a substantial lag for these shrimp stocks. The time lag from data collection to management may represent a common issue of stock assessment for both short-lived and long-lived marine species. But this issue is particularly pressing for volatile annual species, like penaeid shrimp in GOM, a predictive rather than retrospective assessment tool is warranted.

There may be a variety of factors that can affect the dynamics of the GOM penaeid shrimp stocks. Penaeid shrimps are broadcast spawners—adults spawn year-round in offshore waters, and then postlarval recruits (~10 mm in length) settle in shallow estuarine waters throughout the northwestern

GOM (Nance and Nichols 1988). Postlarval recruits grow to reach subadult size (~70 mm) in just a few months, and then migrate to offshore waters to spawn and repeat this annual lifecycle. During postlarval to subadult stages, individuals are highly susceptible to variable environmental conditions in shallow water estuaries—temperature, salinity, and dissolved oxygen have all been correlated with stock productivity previously (Zein-Eldin and Griffith 1967; Barrett and Gillespie 1973; Keiser and Aldrich 1976; Minello et al. 2003). Importantly, penaeid shrimps are often forage species (Fujiwara et al. 2016) and may be strongly influenced by interactions with other species embedded in a dynamic food web. Disease dynamics caused by parasitic ciliates may also affect penaeid shrimp dynamics (Swinford and Anderson 2021; Tuckey et al. 2021).

Because we often lack direct estimates of the abovementioned effects on GOM penaeid shrimp dynamics, it is common to treat these hidden interactions as process noise (Sugihara et al. 2011; Best and Punt 2020; Munch et al. 2020). Modern SS models compensate by modeling these hidden effects as time-varying parameters (Maunder and Punt 2013; Methot and Wetzel 2013). Although an important advance, this approach still treats variation in vital rates (e.g., natural mortality, fecundity, and somatic growth) as random, ignoring the possibility that they reflect nonlinear, state-dependent dynamics (Sugihara et al. 2011). Treating nonrandom effects, such as unobserved species interactions, as random effects might be appropriate when the goal is to filter noise for state estimation (Ziebarth et al. 2010); however, this approach may mischaracterize population variability and produce poor out-of-sample predictions (Sugihara et al. 2011; Perretti et al. 2013; Munch et al. 2020). Not accounting for nonlinear feedbacks can potentially lead to inaccurate estimation of harvest benchmarks (Glaser et al. 2014; Fogarty et al. 2016) and suboptimal management (Brias and Munch 2021). An ideal approach to managing GOM penaeid shrimp fisheries (see GOM penaeid shrimp fisheries management history below) would be an assessment tool that could, at least implicitly, account for these nonlinear, state dependent dynamics.

Empirical dynamic modeling (EDM) provides an equation-free framework to tackle the prediction problem when the underlying dynamics are nonlinear and dependent on unobserved variables (Sugihara and May 1990; Chang et al. 2017; Munch et al. 2020). EDM approximates dynamics based on Takens' embedding theorem (Takens 1981) using lags of the observed states to account for hidden/unobserved state variables (Schaffer 1985). Consequently, EDM may extract more of the deterministic signal from indices of abundance. This was found to be the case for menhaden in GOM (Deyle et al. 2018), salmon in Fraser River (Ye et al. 2015), and sardine in Gulf of California (Giron-Nava et al. 2021). In a global meta-analysis, EDM predicted recruitment more accurately than traditional stock-recruitment models in 90% of 185 cases analyzed (Munch et al. 2018). However, applications of EDM for the purpose of making fishery management decisions remains limited (but see Deyle et al. 2018).

Unfortunately, few managed fish stocks have time series of biomass, catch, and (or) effort that extend back more than

40 years. To make better use of short time series (e.g., less than 30 observations), Munch et al. (2017) proposed a hierarchical Bayesian framework for EDM. This approach uses Gaussian process regression (hereinafter, GP-EDM) to combine data from multiple stocks and improve forecast performance. This method also produces an estimate of dynamic (i.e., model) similarity among populations or sites. Recently, Rogers and Munch (2020) applied hierarchical GP-EDM to blue crab abundance, finding that local dynamics were similar throughout the US east coast, even though the time series were only weakly correlated. By identifying sub-regions with similar dynamics, GP-EDM may also provide information useful for spatial fisheries management (Schindler et al. 2010; Takashina and Mougi 2015; Engen et al. 2018).

Here, we aim to provide a proof of concept for use of GP-EDM to assess annual penaeid shrimp dynamics in the US GOM as an index-based approach for fisheries management. Specifically, we (i) predict the temporal dynamics of two penaeid shrimp species, brown shrimp and white shrimp, across federally managed statistical zones, (ii) develop a “gulf-scale” abundance index, (iii) compare correlations between observed abundance fluctuations versus predictive intrinsic dynamics of a paired statistical zones, and (iv) demonstrate nonlinear, state-dependent interactions in GOM shrimp dynamics.

GOM penaeid shrimp fishery management history

The Gulf of Mexico Fishery Management Council (GMFMC) considers annual stock status determination criteria (SDC) for several federally harvested shrimp stocks, including three penaeid species: brown, white and pink shrimp (*Farfantepenaeus aztecus*, *Litopenaeus setiferus*, and *Farfantepenaeus duorarum*, respectively). In 2012, integrated SS models were developed, deemed to produced best scientific information available by the Gulf Scientific and Statistical Committee (SSC), and used to estimate SDC by the GMFMC. In 2019, an assessment model review found several technical concerns among these three penaeid shrimp SS models (e.g., conflicting indices, convergence issues, and residual patterns), prompting the GMFMC to initiate a Southeast Data, Assessment, and Review (SEDAR) research track process for all three stocks. Compared to an operational assessment (updating an existing model with current data inputs), the SEDAR research track process allows for consideration of new data inputs and (or) modeling types.

An initial goal of the SEDAR research track process is to define all available model inputs (e.g., time series of catch and catch-per-unit-effort (CPUE)) and (based on those available data inputs, limitations, and assumptions, as well as information on the biology and ecology of the stock) to define an appropriate assessment tool given data availability. Preliminary findings of the research track process showed that data limitations (e.g., lack of recruitment information) prohibits the use of an advanced stock assessment model to estimate SDC for these shrimp stocks. Given technical concerns and data limitations exist, consideration of an index-based approach for these shrimp species is warranted—particularly if an index-based method could implicitly account for en-

vironmental or other “unobserved” ecological interactions that likely drive annual penaeid shrimp stock dynamics but that lack time series of observational data (i.e., EDM). Further, interim analyses—stock “health checks” that simply update a representative index of stock abundance (fishery independent CPUE)—are now annually considered by the GMFMC for updating management for several federally managed finfish species.

Materials and methods

SEAMAP and GMFMC

Our analyses focused on two of the three federally managed penaeid shrimp species in the GOM, brown shrimp and white shrimp. Previously, SS models (Methot and Wetzel 2013) were annually updated with time series data of fishery catch and effort (CPUE) (1984–2018), fishery size composition data (1984–2018), and fishery-independent CPUE and length composition time series data from both the Southeast Area Monitoring and Assessment Program (SEAMAP) (1987–2018) and the west-Louisiana inshore trawl survey (1984–2018) (Masi 2018). Benchmarks from the last assessment update for these two penaeid shrimp stocks were presented to the SSC and GMFMC in 2020 (also see Gulf of Mexico penaeid shrimp fisheries management history), using 2018 terminal year input data (Masi 2018).

In the present study, we used fishery-independent data from the SEAMAP Summer Groundfish Trawl Survey across statistical zones 9–21 (Fig. 1). This was because GOM penaeid shrimp fisheries management required that all managed shrimp statistical zones, where target species have occurred (zones 9–21), should be included into the analysis. To align the time series length of shrimp statistical zone, the shorter time series data from zones 9, 10, and 12 were combined into the adjacent zone 11 that comprised full length of time series, and zone 13 was merged into the adjacent zone 14.

We focused on summer-season CPUE data of brown shrimp and white shrimp at an interannual scale, because they were well-represented for the duration of the SEAMAP survey. We did not include pink shrimp for analysis because the available data were too limited in space and time to use EDM. In each statistical zone, CPUE was estimated using all tows for brown shrimp and tows at stations <25 fathom deep (1 fathom = 1.828 m) for white shrimp. Additionally, we considered important environmental variables potentially driving shrimp dynamics including bottom temperature, bottom dissolved oxygen, and bottom salinity. Long-term (i.e., 1987–2018) averages were used to impute the missing values (total $n < 10$) of environmental variables in each of our representative GOM shrimp statistical zones. The timeframe of environmental variables was aligned with the timeframe of CPUE data for EDM analyses of shrimp dynamics.

Gaussian process empirical dynamic modeling

We used GP regression (Williams and Rasmussen 2006) combined with EDM to recover nonlinear dynamics and environmental drivers, as well as predict CPUE time series (see

Munch et al. 2017 for details). We begin with describing the method for a single time series and then introduce the hierarchical approach.

Let x_t and T_t represent the CPUE and environmental variable (e.g., temperature) at time t . We model x_t as a function of lags of CPUE (x_{t-1}, \dots, x_{t-L}) and environmental variable (T_{t-1}, \dots, T_{t-K}), where $L + K = m$ is the maximum number of lags used. Here, we set $m = 4$ to facilitate finding a parsimonious model. We used GP regression to approximate this function (Munch et al. 2017; Rogers and Munch 2020). Gathering all inputs into a vector, $\mathbf{X}_{t-m} = \{\text{CPUE}_{t-1}, \dots, \text{CPUE}_{t-L}, T_{t-1}, \dots, T_{t-K}\}$, the hierarchical Bayesian model was formulated as follows:

$$\begin{aligned} P(x_t | f, \mathbf{X}_{t-m}, V_e) &\sim N(f(\mathbf{X}_{t-m}), V_e) \\ (1) \quad P(f | \theta) &\sim \text{GP}(0, \Sigma) \\ P(\theta) &\sim \text{hyperparameter priors} \end{aligned}$$

where, in the first layer of eq. 1, $P(x_t | f, \mathbf{X}_{t-m}, V_e)$ represents the probability density of observing CPUE at next time step (year ahead) given the input data, function approximation, and parameters. Specifically, x_t represents the univariate output variable, which is CPUE at next time step, f is the delay embedding map that we are trying to estimate, and V_e represents process noise. In the second layer of eq. 1, $P(f | \theta)$ represents the probability density of function approximation given the parameters, where the unknown function f is assigned a GP prior, essentially following a multivariate normal distribution with mean zero denoted by GP. The covariance function, Σ , is a tensor product of squared exponential covariances with pointwise variance τ^2 and inverse length scales ϕ_i . Specifically, $\Sigma(\mathbf{X}_t, \mathbf{X}_s) = \tau^2 \prod_{i=1}^m \exp[-\phi_i(x_{t-i} - x_{s-i})^2]$, where \mathbf{X}_t and \mathbf{X}_s are delay coordinate vectors for years. The third layer of eq. 1, $P(\theta)$ is the prior specification for the hyperparameters $\theta = \{\phi_1, \dots, \phi_m, V_e, \tau^2\}$. Sparsity in the fitted model was encouraged by assigning a half-normal prior for ϕ_i , such that f has on average one local extremum over the range of the data and uninformative lags drop out of the model (i.e., $\phi \rightarrow 0$). Flat priors were used for V_e and τ^2 . See Munch et al. (2017) and supplementary material for more details on prior specification.

We used the maximum a posteriori (MAP) estimate approach to obtain parameter estimates and to simultaneously predict the CPUE time series in each zone. Collecting the next states in a column vector $\mathbf{y} = \{x_{t+m}, \dots, x_T\}^T$ and all the pairwise covariances in Σ_{stack} , the log marginal posterior is

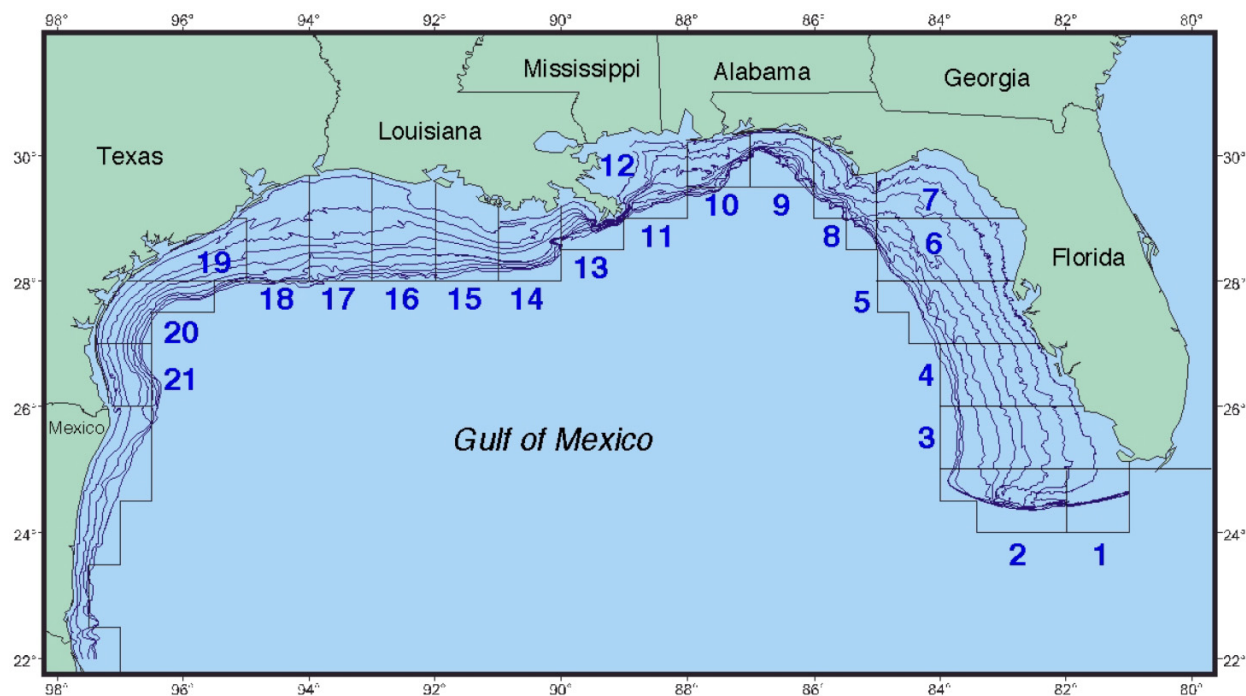
$$\begin{aligned} (2) \quad \ln P(\varphi, \tau, V_e | \mathbf{y}, \mathbf{X}) &= \text{const} - \frac{1}{2} \ln |\Sigma + V_e \mathbf{I}| \\ &\quad - \frac{1}{2} \mathbf{y}^T (\Sigma + V_e \mathbf{I})^{-1} \mathbf{y} - \frac{1}{2} \ln P(\theta) \end{aligned}$$

where \mathbf{I} is the identity matrix and Σ is the covariance matrix constructed by applying the covariance function, $\Sigma(\mathbf{X}_t, \mathbf{X}_s)$, to all pairs of inputs.

Spatially structured GP-EDM

We extended non-spatial GP-EDM mentioned above to simultaneously account for state-dependent dynamics across

Fig. 1. Shrimp statistical zones (five fathom increments; 1 fathom = 1.828 m) in the US Gulf of Mexico.



the statistical zones. Specifically, the spatially structured GP-EDM included an additional layer of covariance structure between the embedding maps (shadow manifolds) estimated for each statistical zone. This was formulated following (Munch et al. 2017; Rogers and Munch 2020):

$$\begin{aligned}
 P(x_{i,t} | f_i, X_{i,t-m}, V_e) &\sim N(f_i(X_{i,t-m}), V_{i,e}) \\
 P(f_i | \theta) &\sim GP(\mu, (1 - \rho) \Sigma) \\
 P(\mu | \theta) &\sim GP(0, \rho \Sigma) \\
 P(\theta) &\sim \text{hyperparameterpriors}
 \end{aligned}
 \tag{3}$$

where the notation in eq. 3 is as defined previously, except for an additional spatial covariance structure between statistical zones. μ represents the gulf-wide mean function scaled to have a zero mean and unit covariance between statistical zones. The hierarchical structure partitions variability in the dynamics into within- and between-zone components and the additional parameter ρ , termed the “dynamic correlation” (Rogers and Munch 2020), measures the similarity in the shape of f across sites (Munch et al. 2017; Rogers and Munch 2020) (see Supplementary Material for details of spatial covariance kernel). That is, the dynamical correlation measures the similarity between reconstructed state space to leverage the spatial structure of the stocks. This is a marked contrast to the commonly used “synchrony correlation” that measures Pearson correlation coefficient between observed time series. The dynamical correlation may provide the unique information about spatial dynamics that may not be detectable from synchrony correlation. Specifically, for two time series x_t and y_t , with dynamics $x_{t+1} = f(x_t)$ and $y_{t+1} = g(y_t)$ the dynamic correlation measures $\text{corr}[f(s), g(s)]$ over states s , rather than

$\text{corr}[x_t, y_t]$ over times t . Thus, the dynamic correlation provides information on the similarity of the dynamics irrespective of whether populations are correlated through time. As above, we obtain the MAP estimates of the hyperparameters by maximizing the log marginal posterior.

Predicting CPUE time series

We used the GP-EDM estimates to predict the conditional posterior mean and variance for year-ahead CPUE time series of brown shrimp and white shrimp across statistical zones. The posterior mean and covariance for year-ahead predictions, conditional on GP-EDM estimates and data, is multivariate normal with mean and covariance given by

$$\begin{aligned}
 m(X') &= \Sigma(X', X) [\Sigma(X, X) + V_e I]^{-1} y \\
 v(X') &= \Sigma(X', X') - \Sigma(X', X) [\Sigma(X, X) + V_e I]^{-1} \Sigma(X, X)
 \end{aligned}
 \tag{4}$$

where m and v represent the posterior mean and covariance, respectively, and X' represents the in-sample or out-of-sample delay coordinate vectors (inputs) for predictions. After obtaining the CPUE predictions for stocks in each statistical zone, the arithmetic mean of the within-zone predictions was used as a “gulf-scale” abundance index. We also computed the area-weighted average as an alternative gulf-scale abundance index.

The CPUE data were log-transformed and scaled to zero mean and unit variance prior to GP-EDM estimation. To measure model performance, predictive correlation (r) (i.e., the Pearson correlation coefficient between observed CPUE and GP-EDM predicted posterior mean) was computed for both zone-specific and gulf-scale predictions. Note that, GP-EDM

predictions were transformed back to the original scale of CPUE for computing r .

Comparing dynamic correlation with synchrony correlation

We compared the spatial synchrony correlations in temporal CPUE dynamics between GOM shrimp statistical zones for both brown shrimp and white shrimp and contrasted this with the dynamic correlation estimates for all pairs of statistical zones. Spatial synchrony was determined by the Pearson correlation coefficient in observed CPUE through time between all pairs of statistical zones.

Visualizing state dependence

To illustrate how density dependence varies across statistical zones and changes with temperature, we plotted the conditional posterior mean for the relationship between current CPUE and next CPUE, holding CPUE at earlier time lags fixed at the average and sea bottom temperature at low (25% quantile) and high (75% quantile) levels in each statistical zone.

Results

Using GP-EDM, we produced year-ahead predictions of brown shrimp and white shrimp in the US GOM. We found that the stock dynamics of both species were generally well predicted across statistical zones (Figs. 2 and 3). At the scale of individual statistical zones, the average prediction accuracy was slightly higher for brown shrimp than white shrimp (predictive $r = 0.86$ and $r = 0.75$, respectively; Figs. 2J and 3J). Notably, GP-EDM captured both the cyclic-like dynamic behavior for brown shrimp (~3–5 years period cycles in statistical zones 19, 20, and 21; Fig. 2G–2I) and more episodic dynamic behavior for white shrimp in the same statistical zones (Figs. 3G–3I). Leave-one-out (LOO) out-of-sample year-ahead predictions were comparable with somewhat lower year-ahead prediction accuracy than the in-sample predictions (predictive $r = 0.71$ and $r = 0.5$ for brown shrimp and white shrimp, respectively; Figs. S2 and S3).

Year-ahead predictions for gulf-wide CPUE were constructed by averaging the year-ahead predictions within statistical zones. At this scale, GP-EDM produced in-sample predictions for both species (predictive $r = 0.89$ and $r = 0.85$ for brown shrimp and white shrimp, respectively; Figs. 2K and 3K) and reasonable LOO predictions (predictive $r = 0.75$ and $r = 0.56$ for brown shrimp and white shrimp; Figs. S2 and S3). The simple-averaged gulf-wide CPUE abundance index is highly correlated (Pearson $r = 0.98$) with the averaged abundance index weighted by the area of statistical zones.

We evaluated models that included bottom temperature, salinity, and dissolved oxygen as well as prior CPUE. We found that the best model included only the previous year's bottom temperature as well as the previous three and two years of CPUE for brown shrimp and white shrimp, respectively (Table 1; Fig. S1). However, the most important variable differs between these two shrimp species: for brown shrimp, lag-3 CPUE is the most relevant, whereas lag-2 CPUE and bot-

tom temperature are of similar importance for white shrimp (Fig. S1).

For brown shrimp and white shrimp, respectively, spatial similarity in intrinsic dynamics (as measured by the dynamic correlation) was generally higher than the synchrony correlation in the CPUE time series (Fig. 4). When the synchrony correlation was strong between a pair of statistical zones, the dynamic correlation also tended to be strong. However, when the synchrony correlation was weak between a pair of statistical zones, the dynamic correlation may be either strong or weak (Fig. 4). The spatial similarity in dynamic correlations tended to be higher around the western GOM (zones 19, 20, and 21; see Fig. 1). In contrast, the spatial similarity in synchrony correlations were relatively lower in the west and higher around Louisiana (zones 14, 15, and 16; see Fig. 1). Interestingly, a geographical break between zones 11 and 14 appeared in both dynamic and synchrony correlations, which coincided with the Mississippi River outflow.

The GP-EDM models for both brown shrimp and white shrimp exhibited density dependence that interacted with bottom temperature (Figs. 5 and 6). Specifically, the functional form of lag-1 density dependence clearly differed with the bottom temperature at low or high levels (25% and 75% quantiles in each statistical zone, blue and red curves, respectively; Figs. 5 and 6). Although the lag-1 density dependence varied across statistical zones, increasing bottom temperature appeared to increase the slope of density dependence at low CPUE levels or to increase carrying capacity at high CPUE levels (Figs. 5 and 6). By contrast, shrimp population dynamics in statistical zone 11 (where CPUE is merged with zones 9, 10, and 12 of the east Mississippi River outflow; see Fig. 1) showed almost no effect of increasing bottom temperature and limited evidence for density dependence.

Discussion

Our results show that penaeid shrimp multistock dynamics in the US GOM are robustly captured through GP-EDM. Considering the substantial variability observed in annual penaeid shrimp abundance (fishery-independent CPUE), our results suggest that a responsive, index-based management approach may be a more appropriate tool for assessing annual stock dynamics. Extending this model to include shrimp catch would allow EDM to be used to evaluate harvest policy for GOM penaeid shrimp, an important area for future research (Brias and Munch 2021; Giron-Nava et al. 2021).

The forecast skill of GP-EDM at a low embedding dimension ($E \sim 3$ to 4) suggests a relatively small number of effective state variables governing the dynamics of GOM penaeid shrimps (Figs. 2 and 3; Table 1; Fig. S1). This is surprising, since vital rates in penaeid shrimps can vary substantially at different life stages, such as offshore spawning, development of pelagic larvae, and migration to coastal estuaries during post-larval stages (van de Kerk et al. 2016). In contrast, our results suggest that these demographic processes are well summarized by a few aggregate drivers, whose effects are recorded in the time-delayed observations of shrimp abundance. Moreover, differences in magnitude of length-scale parameters for time delays (Fig. S1) signals the “nonlinear-

Fig. 2. Gaussian process empirical dynamic modeling (GP-EDM) applied to annual catch-per-unit-effort (CPUE) dynamics of brown shrimp across statistical zones in the US Gulf of Mexico (GOM). (A–I) Statistical zone-scale abundance time series. Dashed and solid lines represent observed and predicted CPUE, respectively. Shaded area represents 95% prediction interval. (J) Overall predictive power of GP-EDM on brown shrimp CPUE across statistical zones. Solid line represents the 1:1 relationship. (K) Gulf-scale (averaged) CPUE time series (abundance index). Dashed and solid line represents observed and predicted average CPUE, respectively.

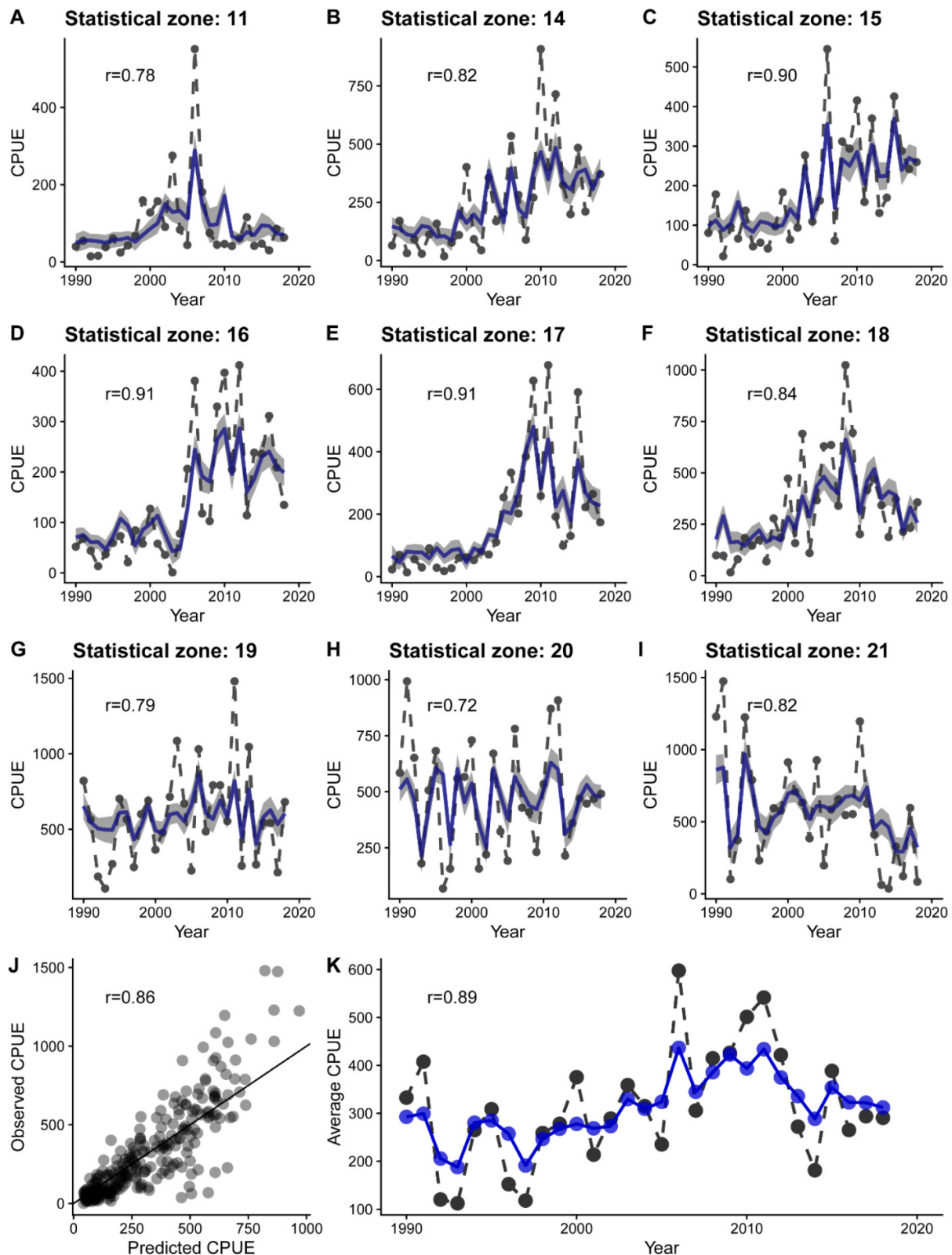


Fig. 3. Gaussian process empirical dynamic modeling (GP-EDM) applied to annual catch-per-unit-effort (CPUE) dynamics of white shrimp across statistical zones in the US Gulf of Mexico (GOM). (A–I) Statistical zone-scale abundance time series. Dashed and solid lines represent observed and predicted CPUE, respectively. Shaded area represents 95% prediction interval. (J) Overall predictive power of GP-EDM on white shrimp CPUE across statistical zones. Solid line represents the 1:1 relationship. (K) Gulf-scale (averaged) CPUE time series (abundance index). Dashed and solid line represents observed and predicted average CPUE, respectively.

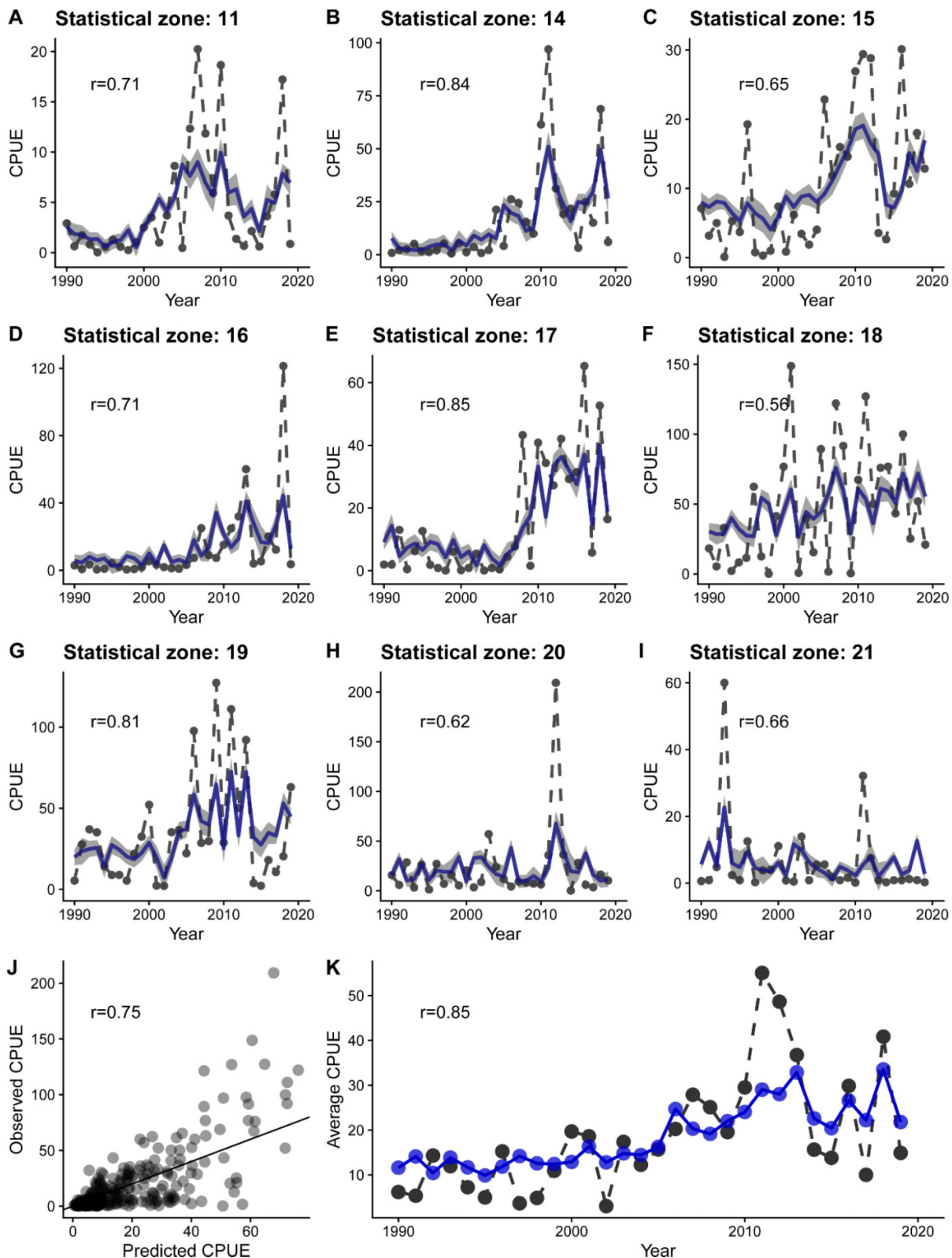


Table 1. Model selection of predictive Gaussian process empirical dynamic modeling (GP-EDM) for Gulf of Mexico (GOM) brown shrimp and white shrimp.

Candidate variables	ARD selected variables	Zone-scale r	Gulf-scale r
Brown shrimp			
CPUE	CPUE($t - 1$), CPUE($t - 2$), CPUE($t - 3$), CPUE($t - 4$)	0.82 (0.69)	0.84 (0.67)
CPUE + T + DO + S	CPUE($t - 1$), CPUE($t - 2$), CPUE($t - 3$), T($t - 1$)	0.86 (0.71)	0.88 (0.75)
White shrimp			
CPUE	CPUE($t - 1$), CPUE($t - 2$)	0.6 (0.5)	0.73 (0.37)
CPUE + T + DO + S	CPUE($t - 1$), CPUE($t - 2$), T($t - 1$)	0.75 (0.5)	0.81 (0.56)

Note: For candidate variables, “CPUE” represents possible abundance time lags, while “CPUE + T + DO + S” represents possible combinations of abundance and environmental time lags as defined in the Materials and methods section. “ARD selected variables” represents the variables selected in the best predictive GP-EDM model, which has nonzero inverse length-scale coefficient. Predictive r and LOO r (in parentheses) are computed at statistical zone and gulf-wide scales. Note that the number of ARD selected variables is equivalent to the embedding dimension (E) in EDM and GP-EDM. CPUE, catch-per-unit-effort; DO, dissolved oxygen; LOO, leave-one-out; S, salinity; T, bottom temperature.

Fig. 4. Intrinsic dynamic correlation versus synchrony correlation of two GOM penaeid shrimp species between statistical zones. (A and C) Dynamical correlation of brown shrimp and white shrimp, respectively. (B and D) Synchrony correlation of brown shrimp and white shrimp, respectively. Geographic map of statistical zones as in Fig. 1.

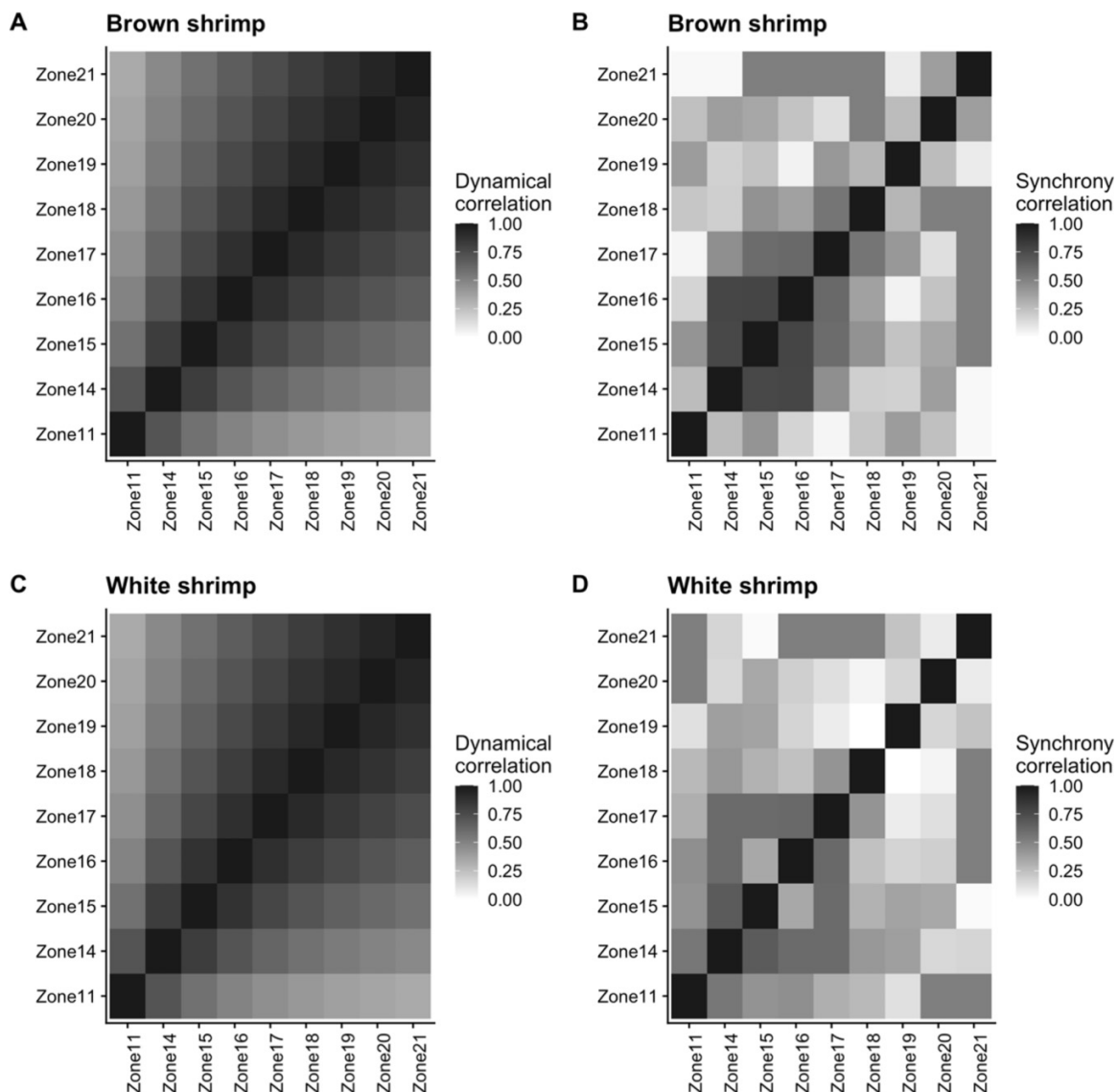
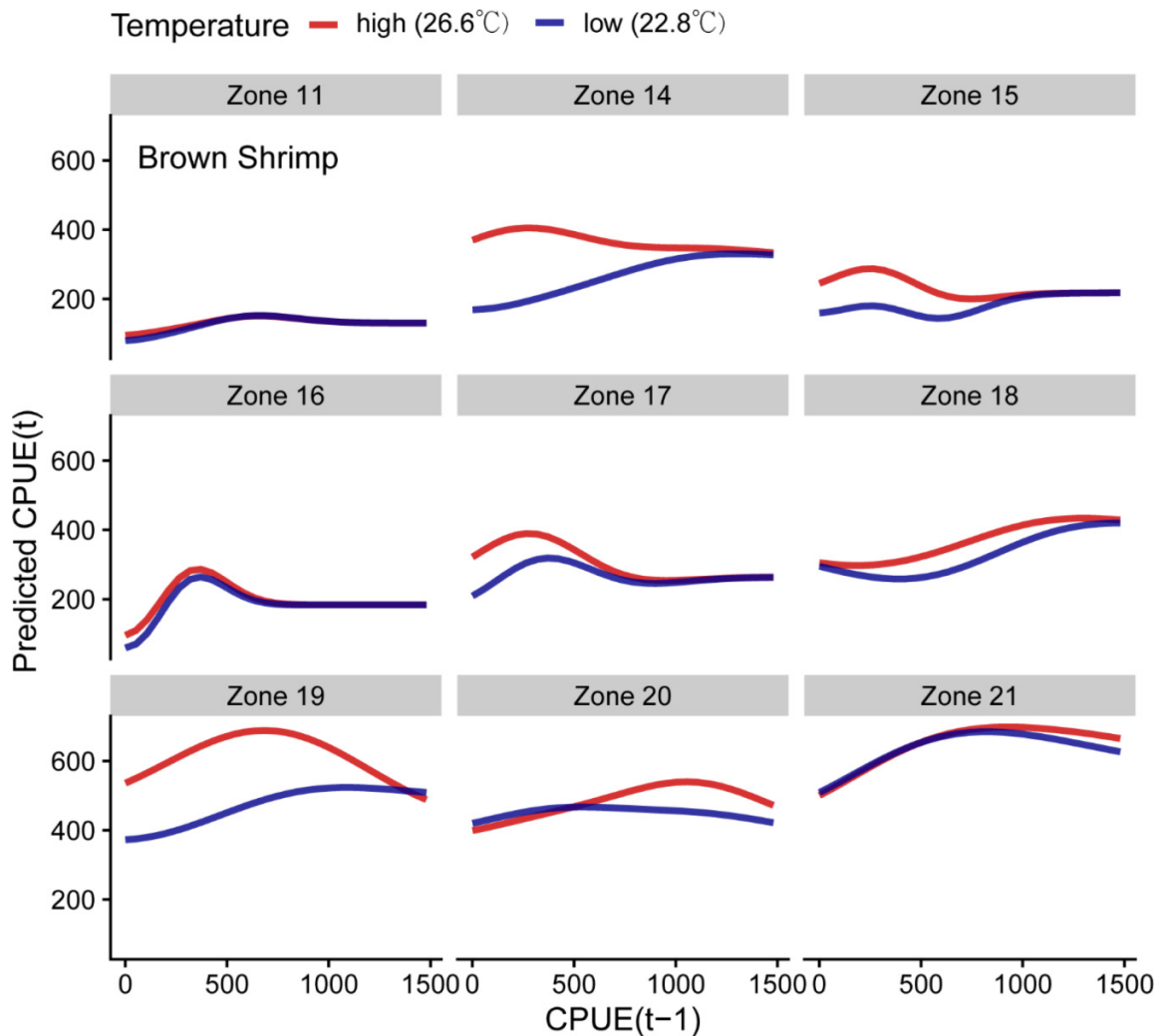


Fig. 5. Density dependence in brown shrimp dynamics varies depending on statistical zone and bottom temperature. Y-axis represents the catch-per-unit-effort (CPUE) predicted by Gaussian process empirical dynamic modeling (GP-EDM) and X-axis represents the CPUE at previous time step. Red and blue color represents the bottom temperature at a high and low level (25% and 75% quantile), respectively, in each statistical zone. Other state variables are fixed at mean levels for visualization. Geographic map of statistical zones as in Fig. 1.



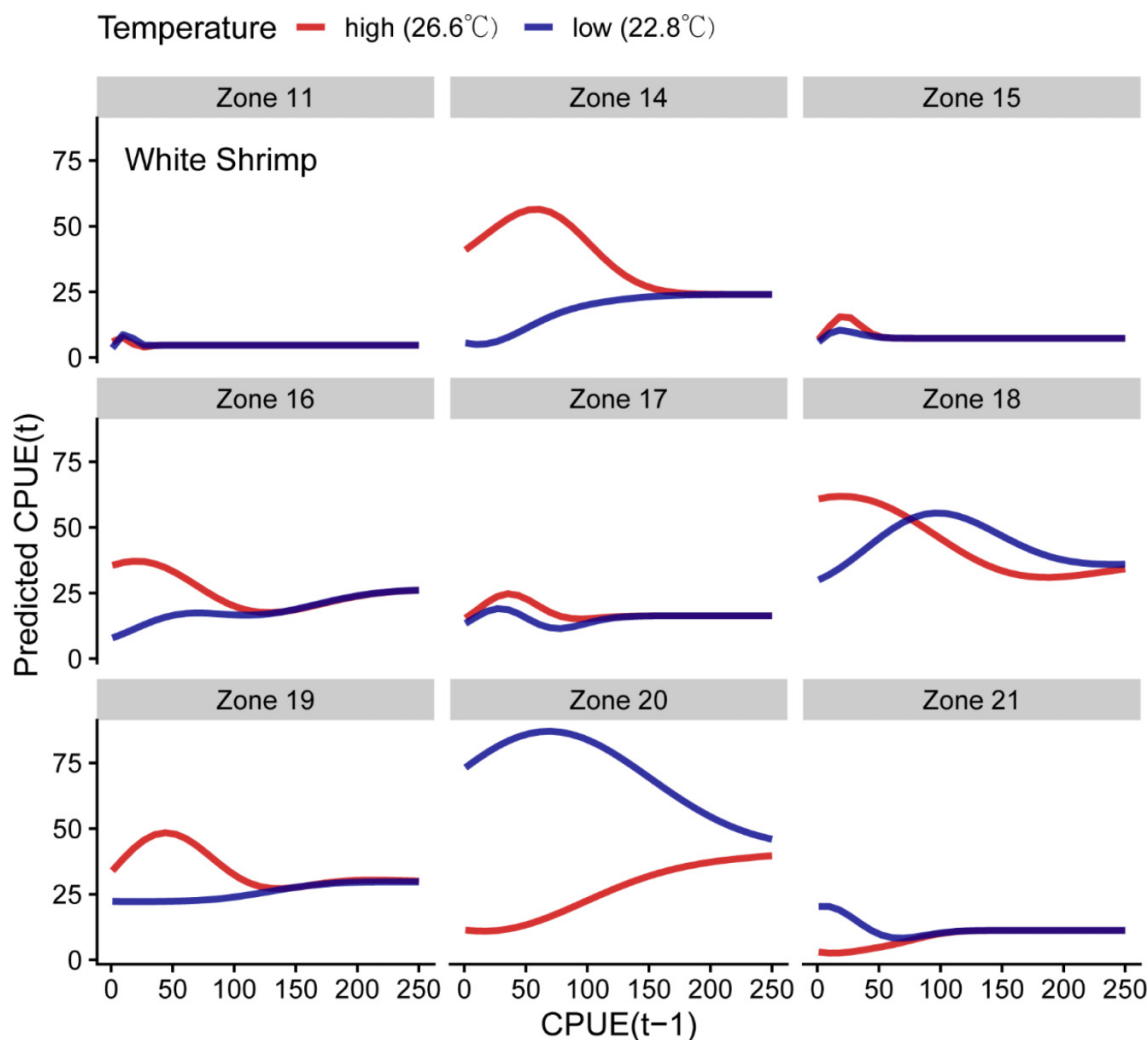
ity” in time series observations of annual shrimp dynamics (Munch et al. 2017), which cannot be captured by traditional linear stochastic approaches such as autoregressive models (Hsieh et al. 2008; Munch et al. 2020). Such nonlinearity, captured by GP-EDM, in GOM shrimp dynamics might be due to unobserved interactions with other species and from environmentally mediated density dependence in various life stages.

Note that, white shrimp appears to be overestimated early in the CPUE time series across statistical zones. This may be because the CPUE is lower and less variable early in the time series and is higher in both mean and variability later. This suggests that an EDM model that allows for non-stationarity over time (e.g., Munch et al. 2017) might be also worth investigations. There might be several reasons resulting in the nonstationarity of CPUE time series, such as a trophodynamic shift in predator abundance (e.g., red snapper) and the downward trend around 2012 influenced by the *Deepwater Horizon*

oil spill; however, there are no data available to understand these potential drivers.

Although it is widely recognized that temperature can influence the population dynamics of marine fauna, the effects of temperature and density are often modelled independently. For GOM penaeid shrimp, GP-EDM indicates that bottom temperature and density interact nonlinearly. The conditional mean plots (Figs. 5 and 6) suggest that density dependence exhibits a roughly Ricker-like functional form. However, this shape varies across spatial areas and depends strongly on bottom temperature, such that the slope at low abundance increases with bottom temperature. These results are broadly consistent with those of Ye et al. (2015) who showed that temperature and abundance interact strongly in the dynamics of Pacific salmon. Our results therefore suggest that harvest benchmarks for GOM penaeid shrimp could be determined in part, albeit nonlinearly, based on bottom temperature in the previous year.

Fig. 6. Density dependence in white shrimp dynamics varies depending on statistical zone and bottom temperature. Y-axis represents the catch-per-unit-effort (CPUE) predicted by Gaussian process empirical dynamic modeling (GP-EDM) and X-axis represents the CPUE at previous time step. Red and blue color represents the bottom temperature at a high and low level (25% and 75% quantile), respectively, in each statistical zone. Other state variables are fixed at mean levels for visualization. Geographic map of statistical zones as in Fig. 1.



Interestingly, there seems to be a break in both dynamic and synchrony correlations near areas of Mississippi River outflow (between zones 11 and 14; Fig. 4), implying spatial heterogeneity and geographically distinct subpopulation dynamics in this area. This suggests that a spatial approach to setting management targets might be more appropriate than a single gulf-wide target (Takashina and Mougi 2015), and might have implications for managements that rely on portfolio effect mechanisms and synchrony indicators (Schindler et al. 2010; Carlson and Satterthwaite 2011). Note that, our EDM results have implicitly accounted for dispersal, and parameter estimation and predictions are robust to assumptions about immigration/emigration process or source-sink dynamics in space. In fact, spatially structured simulations with substantial dispersal showed that the hierarchical approach used here is optimal when there is relatively little spatial variation in the local dynamics (Johnson et al. 2021).

Although we have focused here on GP-EDM as a potential replacement for age-structured (size-structured) assessment models in annual, short-lived species such as GOM penaeid shrimp, it may be more valuable to consider GP-EDM and modern assessment methods as complementary processes. For instance, GP-EDM may benefit from leveraging the information incorporated into traditional assessment models, such as age-specific or size-related vital rates. Another potential improvement would be to consider age-structured (size-structured) dynamics when age-specific (e.g., catch-at-age) or size class time series are available or can be extracted from traditional assessment models. Extending the hierarchical GP-EDM approach to incorporate these life-history data structure is an important area for future research and will be a useful addition to traditional assessment models for fisheries forecasting.

Overall, our gulf-scale, year-ahead GP-EDM forecasts (both in-sample and out-of-sample next time step predictions) pro-

vide a predictive index that is based on fishery-independent data, and, therefore, can be updated in almost real time for timely and effective management. This may address concerns of previous stock assessment approaches raised by the GOM Fisheries Management Council. By incorporating landings (catch) into the GP-EDM model, it is possible to estimate steady-state yields and provide harvest benchmarks (e.g., maximum yield at equilibrium abundance/biomass) as was done previously with Gulf of California sardines (Giron-Nava et al. 2021). However, considering the substantial temporal variability of GOM penaeid shrimp, a more responsive, state-dependent approach may be more appropriate. Such policies can be derived using empirical dynamic programming or reinforcement learning approaches, an active research area in optimal control theory and operations research (Brias and Munch 2021). Applying empirical dynamic programming/reinforcement learning to derive harvest benchmarks for GOM penaeid shrimp is an important next step.

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Data availability

SEAMAP data analyzed during this study are available from the Gulf States Marine Fisheries Commission.

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C-HT, SBM, MDM, and AGP devised the research program. C-HT and SBM performed analysis with help from MDM and AGP. C-HT and SBM wrote the first draft of manuscript, and all authors were involved in interpreting the results and contributed to the final draft of manuscript.

Competing interests

The authors declare no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2022-0029>.

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