Fisheries Research 187 (2017) 31–40

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Full length article

Forecasting dynamics of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico

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ARTICLE INFO

Article history:
Received 23 June 2016
Received in revised form 27 October 2016
Accepted 4 November 2016
Handled by Dr. B Arara
Available online 15 November 2016

Keywords:
Population dynamics
Stock structures
Nonlinear forecasting
Red snapper (*Lutjanus campechanus*)

ABSTRACT

Understanding dynamics and stock structures of fish is particularly relevant to assessments and management of marine living resources. Using the nonparametric, nonlinear time series (NLTS) approach, we modeled dynamics of red snapper (*Lutjanus campechanus*) represented by time series of two fisheries-independent abundance indices and two fisheries-dependent abundance indices in the eastern and western portions of the U.S. Gulf of Mexico (Gulf). Further, we examined regional dynamics of red snapper in the two areas and explored the utility of NLTS models in generating short term forecasts. Overall, red snapper in the eastern Gulf and western Gulf displayed distinct patterns in terms of the Gulf-wide ecosystem indicators, which likely implies different underlying regional dynamics of the species. Moreover, dynamic features of red snapper differed between the two regions. Specifically, the system dimension (mean $\pm$ SE), i.e., the number of potential processes affecting the underlying dynamics of the species, was higher in the western Gulf (5.5 ± 1.32) than in the eastern Gulf (3.75 ± 1.44). The NLTS models exhibited significant skill (i.e., a measure of the goodness of fit (ρ) between observations and predictions) in forecasting red snapper abundance indices. The forecast skill (one year ahead) was 0.48 ± 0.01 for indices representing the eastern Gulf and 0.33 ± 0.05 for indices representing the western Gulf. The average dimension and forecast skill was 3 ± 1.43 and 0.37 ± 0.01 for fisheries-dependent indices, and 6.25 ± 1.32 and 0.45 ± 0.05 for fisheries-independent indices. These findings have implications for the Gulf red snapper fisheries in that the NLTS approach shows potential for forecasting stock abundance indices, and provides new information regarding the appropriate spatial scale for management of the species. Moreover, the ecosystem considerations in this study can be further explored to forecast the dynamics of red snapper for better assessments and management of the species.

1. Introduction

Red snapper (*Lutjanus campechanus*) is widely distributed in the Gulf of Mexico (hereafter Gulf) and is arguably the Gulf's signature reef fish. It can reach 100 cm in length and is one of the top predators in the region, occupying a wide range of habitats from depths of 10 to over 150 m. It is also brightly colored and highly prized as table fare, making it a favorite target of commercial and recreational anglers.

The fishery for red snapper began in the early 1840s (Collins, 1887) with a few small vessels selling to local markets, but grew rapidly during the 1870s when expansions of the railway system opened up the lucrative markets along the eastern seaboard. Signs of serial overfishing were evident as early as the 1880s (Stearns, 1883; Collins, 1885) and by the 1950s most of the snapper banks in the eastern Gulf were considered to be impoverished (Camber, 1955). By the 1970s fishermen were also raising concerns about declines in the western Gulf, which they attributed to a combination of increases in the number of snapper vessels and the bycatch of juvenile snapper by the burgeoning offshore shrimp fishery (Moe, 1963; Lyles, 1965; Bradley and Bryan, 1975). At the same time, the mass production of fiberglass boats with improved motors and navigational equipment fueled a rapid increase in offshore recreational fishing from negligible levels prior to the 1950s (Ellis et al., 1958) to over half of the total Gulf red snapper landings today. The increased fishing pressure caused red snapper populations to continue to decline through the 1980s, during which time egg production is

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http://dx.doi.org/10.1016/j.fishres.2016.11.002
0165-7836/

Table 1
Time series of red snapper (*Lutjanus campechanus*) abundance indices in the U.S. Gulf of Mexico.

Data Type	Index	Eastern Gulf		Western Gulf	
		Period	Length (yr)	Period	Length (yr)
Fisheries-dependent	Recreational headboat	1986–2013	28	1986–2013	28
	Recreational private/charter	1981–2013	33	1981–2013	33
Fisheries-independent	SEAMAP Groundfish survey summer	1982–2013	32	1982–2013	32
	SEAMAP Groundfish survey fall	1972–2013	42	1972–2013	42

estimated to have dropped to less than five percent of the unfished level (Porch, 2007; Calay et al., 2015).

A variety of management measures were implemented in the late 1980s both to curb overfishing and to rebuild red snapper, including limits on the total allowable catch, the length of fish that can be kept, and the type of gear that can be used. Shrimp vessels were also required to install devices in their trawl nets to reduce bycatch of juvenile red snapper. These early measures led to some small increases in the number of red snapper, but substantial gains were not evident until after 2006 when the recreational and commercial catch limits were nearly cut in half and offshore shrimp trawling was reduced by about 75%.

The most recent assessment estimated that the number of red snapper age two and older has increased since the low point in the 1980s (Calay et al., 2015). However the rapid rise in red snapper abundance has actually contributed to making the fishery more controversial than before, especially in the eastern Gulf where most of the recreational fishing occurs. The expansion of the red snapper population into more of its historical range, including shallower waters near human population centers, has made it increasingly easy for the recreational sector to meet its total allowable catch and the open fishing season for red snapper has become progressively shorter. At the same time, several states have responded to the shortened federal seasons by instituting longer seasons in their waters, forcing federal regulators to further shorten the season in federal waters in order to ensure the total allowable recreational catch is not exceeded. Not surprisingly, the outcry from recreational anglers has been deafening and the management of Gulf red snapper has become one of the most controversial fishery issues in the U.S. today.

Managing the complex mix of fisheries for red snapper is further challenged by the uncertain population structures of red snapper in the Gulf area. Several studies have suggested that it is actually a collection of metapopulations that are interconnected genetically, but may be demographically independent over time scales relevant to management (Gold and Saillant, 2007; Patterson, 2007). To some extent this view is reflected in recent stock assessments, which have operated under the assumption that the populations east and west of the Mississippi River delta are demographically distinct (Ortiz and Cass-Calay, 2004; Porch, 2007). Most federal management measures, on the other hand, have been set on a Gulf-wide basis. The latest stock assessment (Calay et al., 2015) suggests the population in the Gulf as a whole is rebuilding on schedule, but that the Gulf-wide management measures may have had the unintended consequence of allowing proportionately higher harvest rates in the east (where most recreational fishing occurs) than in the west. Thus, most of the rebuilding appears to have occurred in the west, and at the expense of the east. This perception has helped fuel calls for more regionally based management, but it is important to remember that the results are predicated on the fundamental assumption made by the assessment model that the eastern and western populations are in fact, demographically distinct. While several studies of life history traits and otolith microchemistry are not inconsistent with this assertion (Fischer et al., 2004; Patterson et al., 2008; Woods et al., 2003), the results have not been conclusive.

One line of evidence that has sometimes been used to argue for demographically distinct "stocks" has been the existence of spatially distinct temporal trends in fishery or survey catch per unit effort data, which in theory, implies that there may be relatively little mixing between the populations in question. The primary difficulty with this approach is that index trends can be driven by a number of factors that are unrelated to the abundance trends of the population. In principle, the effects of these other drivers can be filtered out by treating them as covariates in a statistical model; however, such an approach requires that the main drivers have been identified and measured. In the case of red snapper, however, the factors driving index trends are not clear, and few potential covariates have been measured. In such cases, nonparametric, nonlinear time series (NLTS) models (Sugihara and May, 1990; Sugihara, 1994) provide a more viable alternative. The potential of NLTS lies in its ability to generate accurate short term forecasts by capturing the hidden processes implicitly expressed in the behavior of time series data without the need for mechanistic explanations (Anderson et al., 2008; Dixon et al., 1999; Deyle et al., 2013; Glaser et al., 2011, 2014; Liu et al., 2012, 2014; Ye et al., 2015).

This study applies NLTS methods to examine and forecast the behavior of four time series of abundance indices used in the latest stock assessments of red snapper. Specifically, we test the hypothesis that each time series exhibits dynamic similarity (e.g., dimensionality and predictability) and then examine whether the time series for the eastern and western Gulf are consistent in their response to Gulf-wide external ecosystem indicators. Substantially different dynamic features may imply that the stocks are distinct. Further, we examine the utility of the NLTS by generating short term forecasts of four time series of abundance indices of red snapper.

2. Methods

2.1. Time series of abundance indices

Time series of annual abundance indices (Table 1) were compiled through SEDAR (Southeast Data, Assessment and Review) process (SEDAR 31, 2013) and updated in 2015 (Calay et al., 2015). Here, we focused on the two fisheries-dependent and two fisheries-independent indices currently incorporated in stock assessments of the species, for which sufficient time series length was available (generally, around 30 years minimum). The two fishery-dependent abundance indices were the recreational headboat index based on the NMFS Southeast Region Headboat Survey, and the recreational private/charter index which is based on the Marine Recreational Fisheries Statistics Survey and the Marine Recreational Information Program (Matter, 2012). The fishery-independent abundance indices are based on the Southeast Area Monitoring and Assessment Program (SEAMAP) groundfish survey, a semi-annual trawl survey with a stratified random sampling design (Pollack et al., 2012). The fishery-independent survey captures predominantly age classes 0 and 1 and to a lesser extent age 2 red snapper (Pollack et al., 2012), whereas the fishery-dependent abundance index obviously represents age classes that have recruited to the fishery; selectivity of red snapper as estimated in the stock assessment model is predominantly individuals age 2–7 (Calay et al., 2015). To examine the spatial patterns in dynamics of red snapper we selected parallel time series available in both the eastern and western Gulf separated by the Mississippi River delta. Prior to analyses, time series were first-differenced ($\Delta x = x_t - x_{t-1}$) and standardized (mean = 0, standard deviation (SD) = 1) to remove trends and normalize data. To avoid over-differencing, unit root KPSS stationary test (Kwiatkowski et al., 1992) was conducted for each series.

2.2. NLTS models

The dynamics of any deterministic system, as opposed to strictly stochastic ones, can be reduced to a subset of key driving variables (often called dimensions of system state space) and their interactions. The evolution of the system through time, as defined by those dimensions, describes the geometry (i.e., attractor) of system state space (Lorenz, 1963). Theoretically, if system state space can be reconstructed, prediction about future behavior of the system becomes feasible. In reality, the original state space and its attractor are not directly observed. However, each observed time series can be viewed as a series of projections of the attractor onto one axis of the system state space through time. These observed time series contain information of system dynamics and can be used to rebuild a phase space mathematically equivalent to the original state space using lagged coordinate embedding techniques (Takens, 1981).

Generally, to reconstruct an E dimensional phase space using lagged coordinate embedding techniques, each vector $\boldsymbol{X_t}$ of lagged observations,$\{x_t, x_{t-\tau}, x_{t-2\tau}, \ldots x_{t-(E-1)\tau}\}$, represents a point in the E dimensional space. Here, x is the variable of interest (e.g., species abundance or an environmental factor), E is the embedding dimension, the discrete time interval $t \in [1,2, \ldots, N,]$, and the time lag $\tau = 1$. The embedding dimension (E) is the minimum number of lagged variables needed to unfold the attractor so that trajectories do not overlap. Model prediction is evaluated using out-of-sample validation. When analyzing a single time series, if the time series is of sufficient length, it is divided evenly into library halves to build the NLTS models and prediction halves to generate forecasts. When time series are short, cross-validation is used whereby only one vector is retained in the prediction set. This forecast protocol is rigorous to avoid either model overfitting or arbitrary fits to the data.

Simplex projection (Sugihara and May, 1990) and sequentially weighted global linear maps (S-map, Sugihara, 1994) are two fundamental models to the NLTS forecasting. Both approaches hinge on the idea that a prediction y_{t+1} from an historical point $\boldsymbol{Y}_t\{y_t, y_{t-\tau}, y_{t-2\tau}, \ldots y_{t-(E-1)\tau}\}$should be similar to observations x_{t+1} with similar histories $\boldsymbol{X}_t$. Simplex projection is typically used to generate forecasts and to determine the dimensionality E of a given time series. The only free parameter is E, which in this case is allowed to vary from 1 to a maximum value of 10 due to the constraints imposed by the finite lengths of the time series. The best value of E to be chosen gives the highest Pearson correlation (ρ) or minimum forecasting mean absolute error (MAE) between the set of predictions and the corresponding library of observations. The projections, $y_{t+1,}$ are generated for a given value of E by first calculating the Euclidean distance from the point $\boldsymbol{Y}_t$ to each of the i observed points in the library $\{\boldsymbol{X_t}(i)\}$. The $E+1$ points with the shortest distance are selected to form the "simplex" around the point $\boldsymbol{Y}_t$. A prediction for the value of y_{t+1} can then be obtained from a weighted average of the projected simplex, i.e., from the collection of observations $\boldsymbol{x}_{t+1}$ corresponding to each of the selected points $\boldsymbol{X_t}(j)$:

$$\hat{y}_{t+1} = \sum_{j=0}^{E} w_j x_{t+1}(j) \tag{1}$$

where the weighting w_j is inversely proportional to the Euclidean distance between $\boldsymbol{Y}_t$ and $\boldsymbol{X}_t\ (j)$.

S-map is used to conduct forecasting and also identify nonlinearity in time series. In S-map, the forecast for prediction vectors in embedded space is predicted by the location of all library vectors (as opposed to only the nearest neighbors in simplex projection) with weighting factors given locally to library vectors nearest to prediction points. Again, the distances (in embedded space) from the library vectors to the prediction vectors are used to generate forecasts. Specifically, for the unknown forecast $\hat{y}_t$ of prediction vector $\boldsymbol{x}_t$, given library vectors $\{\boldsymbol{x}_i\}$ and setting $x_t(0) \equiv 1$ for the constant term is the solution of following equation,

$$\hat{y}_t = \sum_{j=0}^{E} c_t(j) x_t(j) \tag{2}$$

where E is the estimated embedding dimension and $\boldsymbol{c}$ is solved using singular value decomposition as:

$$\mathrm{b} = \mathrm{Ac} \tag{3}$$

the matrix A contains elements for the library (predictor) set:

$$A_{ij} = w(\|x_i - x_t\|) x_i(j) \tag{4}$$

and the vector b contains the elements for the prediction set:

$$b_i = w(\|x_i - x_t\|) y_i, \tag{5}$$

where w is a weighting function defined as

$$w(d) = e^{-\theta d / \bar{d}} \tag{6}$$

The quantity d is the Euclidean distance between any library vector ($\boldsymbol{x}_i$) and the prediction vector $\boldsymbol{x}_t$, and $\bar{d}$ is the mean across all library vectors $\{\boldsymbol{x}_i\}$,

$$\bar{d} = \frac{1}{n} \sum_{j=1}^{n} \|x_i - x_t\| \tag{7}$$

and the variable θ represents a nonlinear tuning parameter and weights the library vectors when generating a forecast. When θ = 0, S-map weights all library vectors equally and represents a global linear model (a vector autoregressive (AR) model of order E). Values of θ > 0 indicate the system is nonlinear and assign more weight to the neighborhood immediately surrounding the prediction vector. These nearby trajectories contain more similar recent information on the attractor, resulting in higher forecast skill if the system displays nonlinear behavior (Sugihara, 1994). By comparing the performance of locally weighted (nonlinear) forecasts to the global linear forecast, S-map can test for nonlinear dynamics. A significant decrease in forecasting mean absolute error (MAE) or significant increase in the forecast skills (ρ) of the S-map model is taken as evidence of nonlinear dynamics.

2.3. Modeling and analytical approach

First, under a linear assumption we compared dynamic similarity in time series between the eastern and western Gulf by conducting nonparametric Spearman's rank test. Then we modeled the time series using the NLTS approach, compared the dynamic features of red snapper in the two regions and generated short

Table 2
Time series abundance indices and environmental indicators for the nonlinear time series analysis of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico.

Data Type	Full Name of Time Series	Code
Abundance Indices	Recreational Headboat	HBT
	Recreational Private/Charter	RPC
	SEAMAP Groundfish Summer Survey	SMS
	SEAMAP Groundfish Fall Survey	SMF
Ecosystem Indicator	Pacific Decadal Oscillation	PDO
	Atlantic Multi-decadal Oscillation	AMO
	North Atlantic Oscillation	NAO
	GOM Mean Offshore SST	SST
	Mississippi River Fertilizer Index	FET
	Average Rainfall	ARF
	Mississippi River Water Discharge	MDH
	Area of the Hypoxic Zone	HYZ
	Number of Oil Rigs	ORS
	Number of Oil Spills	OSP
	Shrimp Abundance	SPA
	Menhaden Abundance	MHA
	Total Landings of Finfish	FFL
	Total Landings of Invertebrate	INV
	Commercial Fishing Revenues	REV

term forecasts. Where averages are presented, the standard error is provided (mean ± SE).

To examine dynamics of red snapper in response to the external forcing, we selected a set of ecologically meaningful Gulf-wide ecosystem indicators (Table 2). In the Gulf region, these ecosystem indicators potentially directly or indirectly influence the underlying dynamics of marine living resources (Karnauskas et al., 2015). Following the analytical approach recently applied to the ecosystem on the Northeast Atlantic Shelf (Liu et al., 2014), we examined dynamics of red snapper between the two regions assuming that abundance indices of a fish stock may show consistency in response to the Gulf-wide ecosystem indicators.

Specifically, we used simplex projection to identify a universal embedding dimension of the entire time series including four indices and 15 Gulf ecosystem indicators, after a random shuffling of these time series 500 times for the two regions separately. Using the universal dimension, we calculated pair-wise co-prediction coefficients among the 15 ecosystem components and four abundance indices (Liu et al., 2014). The overall similarity of the two 19 by 19 coefficient matrices was examined using Mantel tests (Mantel, 1967) to compare the consistency of the indices responding to the Gulf-wide ecosystem indicators between the two regions. To further quantify the consistency we considered the co-prediction skills (ρ_{co}) from predictors to predictees as attributes of predictors and conducted multivariate correlative tests ($\alpha = 0.05$) on these attributes to examine the dynamic coherence of predictors, i.e., predictors sharing similar trends of co-prediction skills to predictees result in evident and positive coherence (Liu et al., 2014).

One objective of this study is to explore the utility of NLTS models to forecast the short term dynamics of fish stocks. To be consistent and rigorous, we conducted S-map forecasts on the four abundance indices of the eastern and western Gulf at annual scales using cross-validation for a period 1980–2013. We further tested the NLTS skills for a near-term prediction by conducting out-of-sample forecast on a single point and compared performance of the NLTS models by regions and data types. Goodness of fit (ρ) between predictions and observations was used to evaluate the overall performance of the NLTS models, and MAE was used as a measure of forecast error.

Fisheries management often requires an estimate of the uncertainty surrounding each forecast. NLTS can generate point estimates, but currently there is no standard approach for estimating forecast uncertainty. Residuals represent the remaining uncertainty of model prediction and can be useful for estimating uncertainty of model forecasts. We estimated the NLTS prediction uncertainties over the time series using bootstrapping. First, we computed the original residuals of NLTS predictions as $\varepsilon_{i+1} = \Delta x_{(i+1)} - \Delta\hat{x}_{(i+1)}$($\Delta x_{(i+1)}$ and $\Delta\hat{x}_{(i+1)}$ represent first differenced and normalized data and their NLTS predictions respectively), and checked the assumption of iid (independent and identically distributed) of the residual series (Efron and Tibshirani, 1994). Then, we resampled (with replacements) the prediction residuals (ε'_{i+1}) and repeated 200 times. To retain the original dynamics of observations constant each time we substituted resampled residuals (ε'_{i+1}) for original residuals (ε_{i+1}) to calculate the bootstrapped predictions ($\Delta\hat{x}'_{(i+1)}$). Finally, we estimated prediction variance at each point of the first differenced and normalized indices (var($\Delta\hat{x}_{(i+1)}$)) using 200 bootstrapped predictions ($\Delta\hat{x}'_{(i+1)}$). We calculated the variance of abundance indices ($var(x_{obs(i)})$) at the original scale. In order to back-transform to the original scale, we first converted the first differenced and normalized predictions $\Delta\hat{x}_{(i+1)}$ to first-differenced quantities by using $\hat{x}_{diff(i+1)} = \Delta\hat{x}_{(i+1)} \times SD + \mu$ (SD and μ represent the standard deviation and mean of the first differenced time series respectively) and $var(\hat{x}_{diff(i+1)}) = SD^2 \times var(\Delta\hat{x}_{(i+1)})$ assuming constant SD and μ for a given time series. Then the predictions at the original scale were calculated as $\hat{x}_{i+1} = \hat{x}_{diff(i+1)} + x_{obs(i)}$ and the variance of back-transformed predictions was calculated as $var(\hat{x}_{i+1}) = var(\hat{x}_{diff(i+1)}) + var(x_{obs(i)})$ assuming that the two processes of the NLTS forecasts and estimation of abundance indices are independent.

3. Results

3.1. Dynamics of red snapper

Dynamics of red snapper represented by two fisheries-dependent indices and two fisheries-independent indices were distinct between the eastern and western Gulf when considered in a nonlinear perspective, but not necessarily from a linear framework (Fig. 1). Time series of indices between the two regions were correlated for recreational private charter ($r = 0.51$, $p = 0.003$, Spearman's rank test), and SEAMAP Groundfish fall survey ($r = 0.52$, $p < 0.001$), but not for SEAMAP Groundfish summer survey ($r = 0.30$, $p = 0.093$) and recreational headboat ($r = -0.01$, $p = 0.957$).

When using the nonlinear methods, dynamic features of red snapper tend to differ in the two regions (Table 3). By region, the average dimension was 5.5 ± 1.32 in the western Gulf and 3.75 ± 1.44 in the eastern Gulf, whereas the average prediction skill was 0.48 ± 0.01 in the eastern Gulf and 0.33 ± 0.05 in the western Gulf. For fisheries-dependent indices, the average dimension was 3.0 ± 1.43 and for fisheries-independent indices the average dimension was 6.25 ± 1.32; the forecast skill was 0.37 ± 0.01 for fisheries-dependent indices and 0.45 ± 0.05 for fisheries-independent indices.

3.2. Red snapper in response to the Gulf-wide ecosystem indicators

Red snapper in the eastern and western Gulf displayed significantly different patterns in response to the potential driving processes. The two matrices of co-prediction coefficients were significantly different between the two regions (Mantel test with $\alpha = 0.05$ after 1000 permutations). The patterns of dynamic consistency of red snapper regarding potential external forcing were distinct (Fig. 2), between the two regions after a multivariate correlative test ($\alpha = 0.05$). These ecosystem indicators may represent the underlying hidden processes driving the observed population behaviors of red snapper.

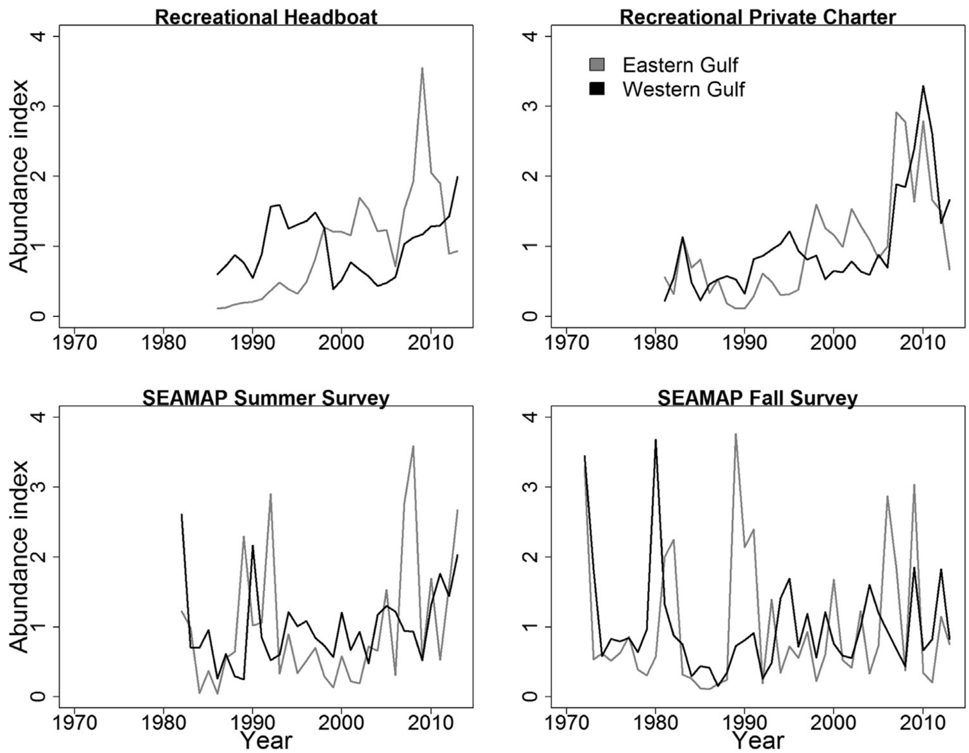

Fig. 1. Fisheries-dependent and fisheries-independent abundance indices of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico (black line: western Gulf, grey line: eastern Gulf).

3.3. NLTS forecast skill on indices of red snapper

Of four fisheries-independent indices, the S-map forecasts of three series were significant at a significant level of $\alpha = 0.05$ (Fig. 3), while the forecasts of two of four fisheries-dependent indices were significant (Fig. 4). Three indices, which did not exhibit significant forecasting ability were from the western Gulf, and contained either relatively few data points or high dimensionality. The absolute prediction errors were heavily skewed (Fig. 5), but not significantly different between the eastern and western Gulf for each data type (Wilcoxon test, $\alpha = 0.05$). The MAE of S-map forecasts of fisheries-dependent indices was 0.84 ± 0.17 and 0.81 ± 0.13 for recreational headboat, and 0.79 ± 0.14 and 0.94 ± 0.15 for recreational private charter in the eastern and western Gulf, respectively. The MAE of fisheries-independent indices was 0.72 ± 0.10 and 0.61 ± 0.07 for SEAMAP Groundfish summer survey, and 0.80 ± 0.10 and 0.60 ± 0.08 for SEAMAP Groundfish fall survey in the eastern and western Gulf, respectively.

The NLTS prediction uncertainty embraced the observations and predictions for fisheries-independent indices (Fig. 6), and fisheries-dependent indices (Fig. 7). For predictions of a single point, the forecast error measured as MAE for fisheries-independent indices was 0.88 ± 0.35 and less than 2.21 ± 0.79 of fisheries-dependent indices. Forecast MAE of fisheries-independent indices was 0.90 ± 0.31 in the eastern Gulf compared to 0.86 ± 0.79 in the western Gulf. Conversely, prediction accuracy of fisheries-dependent indices was higher in the western Gulf with MAE of 0.96 ± 0.65 compared to 3.47 ± 0.35 in the eastern Gulf.

4. Discussion

We modelled fisheries-dependent and fisheries-independent abundance indices of red snapper to examine the overall dynamical features of the population and to evaluate regional differences in population dynamics. The dimensionality of the system is broadly thought to represent forces affecting the processes, such as environmental drivers, regulations, or market needs. Our findings indicate that fisheries-independent indices, representing age classes that have not yet recruited to the fishery, display higher dimensionality than fisheries-dependent indices. This result is consistent with the

Table 3
Dynamic features of red snapper (*Lutjanus campechanus*) characterized using the nonlinear time series models in the U.S. Gulf of Mexico.

Data Type	Index	Eastern Gulf		Western Gulf	
		E[b]	rho[c]	E[b]	rho[c]
Fisheries-dependent	Recreational headboat	3	0.47	5	0.28
	Recreational private/charter	2[a]	0.49	2	0.24
Fisheries-independent	SEAMAP Groundfish survey summer	2	0.46	8	0.32
	SEAMAP Groundfish survey fall	8[a]	0.52	7	0.47

[a] Significant nonlinearity (randomization test of delta MAE of S-map forecast at $\alpha = 0.05$).
[b] Best dimension estimated using simplex projection model.
[c] S-map prediction conducted using the estimated best dimension by simplex projection model.

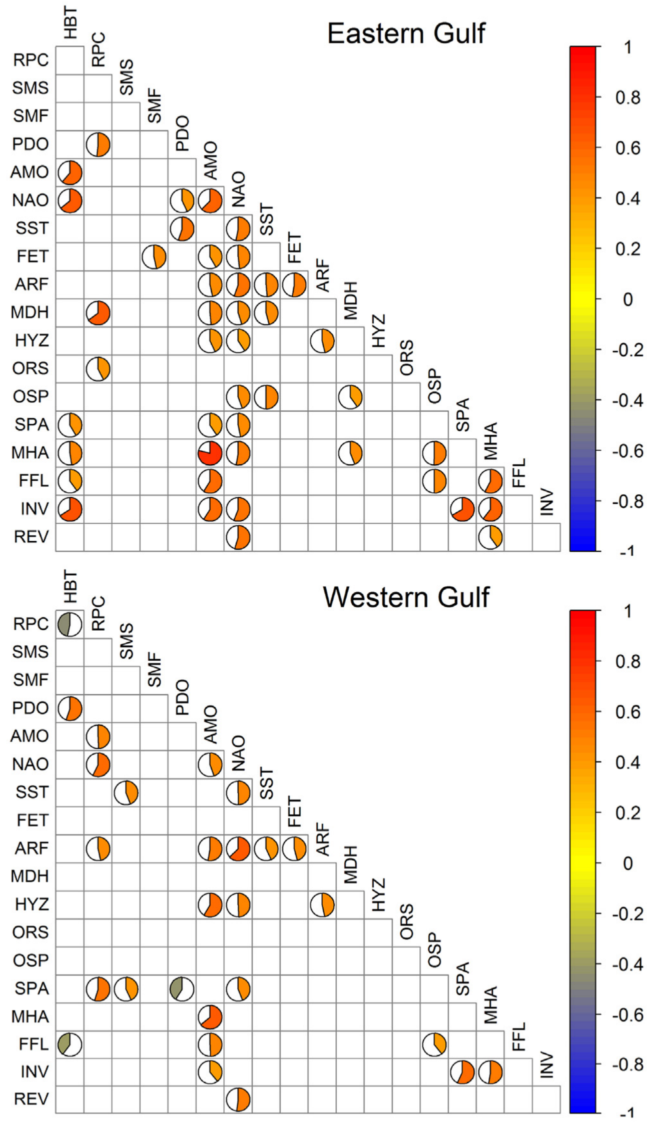

Fig. 2. Strength of dynamic response of red snapper (*Lutjanus campechanus*) to the Gulf-wide ecosystem indicators measured using nonlinear time series co-prediction (circle areas indicate correlation coefficients of multivariate correlative tests of co-prediction coefficients at a significant level of 0.05).

notion that fishing acts to simplify the processes controlling the dynamics of a species (Glaser et al., 2014), suggesting that indeed for red snapper, fishing has reduced the number of important processes controlling the population. Also of note, we found that on average, the embedding dimension for abundance indices of the eastern subpopulation was lower than that for the western subpopulation. Our findings suggest that heavy exploitation of red snapper, which occurred for several decades particularly in the eastern Gulf, may have simplified the processes controlling the population. The relatively low dimension and high predictability observed in the eastern Gulf may reflect the influence of human interventions on population behaviors of the species.

Fishing tends to intensify the nonlinear fluctuation in fish abundance (Anderson et al., 2008), as subtle changes in fishing behaviors by fleets have dramatic influences on the fisheries (Branch et al., 2005). Glaser et al. (2014) found that abundance indices of fished species were 3.6 times as likely to contain nonlinear dynamics as those of unfished species. Of the indices we considered, two demonstrated significant nonlinearity and these were both in the eastern Gulf. Given the exploitation status of red snapper, we suggest that the relatively low system dimension and the presence of nonlinearity in the dynamics of the eastern subpopulation is likely the result of heavy overexploitation throughout the study period (Cowan et al., 2010).

With regard to population structures of the species, our results further suggest that eastern and western subpopulations are not dynamically similar. Genetic studies have shown little evidence to dispute the assumption of a single stock (Camper et al., 1993; Gold et al., 1997; Heist and Gold, 2000; Pruett et al., 2005). However, ecological research on tag recapture (Patterson et al., 2001), size and age at maturity distribution (Woods et al., 2003), growth rates and morphometrics (Fischer et al., 2004), otolith and microchemistry (Patterson et al., 2008), and index trends (Cowan, 2011) suggest that there is limited intermixing between the eastern and western populations red snapper in the Gulf. Our results are consistent with these ecological studies and with the two-stock structure assumed by the recent benchmark assessment (SEDAR 31, 2013).

Spatial variations in dynamics and structures of fish stocks could be driven by differences in resources, physiological tolerances, predation, mortality, and oceanographic processes. Population processes, ecological interactions, environmental forcing, and human impacts are major causes of fluctuations and complexity in biological systems. Most red snapper reside in the western Gulf, where the majority of the shrimp trawling effort and red snapper bycatch occur (Porch, 2007; Cowan, 2011). Demographic variations in population growth and morphometrics of red snapper differ significantly off Alabama and Louisiana from those off Texas (Fischer et al., 2004), that is, red snapper residing in the waters off Texas reach smaller maximum sizes at faster rates and have a consistently lower total weight at age than those off Alabama and Louisiana. All of these biological features, ecological processes, and human interventions are potentially driving the regional dynamics of the species and could be responsible for the different dynamics observed between the eastern and western subpopulations.

We examined dynamics of red snapper regarding a set of Gulf-wide ecosystem indicators and additionally showed that dynamics of red snapper between the two regions displayed different patterns when considered in light of environmental forcing. The results showed that dynamics of red snapper between the two regions displayed different patterns responding to the environmental variables, which provides additional evidence to support the distinct dynamical features between the eastern and western subpopulations disclosed by the univariate NLTS approach. Ecosystem components sharing similar dynamics to abundance indices are considered together as functional units (Liu et al., 2012). The effort of ecosystem considerations combined with the NLTS approach can be further explored for screening ecologically meaningful environmental indicators of fish to model and to forecast their stock abundance, since fish species living in a geographic area potentially interact with each other and experience similar natural and anthropogenic perturbations.

Examining dynamic complexity in fish is a prerequisite for modeling and forecasting status of fish stocks. Our findings indicate that the dynamics of red snapper are generally of low dimensionality, which is consistent with studies of various marine fish (Anderson et al., 2008; Dixon et al., 1999; Glaser et al., 2011, 2014; Liu et al., 2012; Royer and Fromentin, 2006). Dimensions can be thought of as variables representing the key drivers of the deterministic structure of the system. The finding of low dimensions implies that the system can be further modeled with few potential driving variables to achieve relatively high forecast skills. Key environmental and oceanographic processes underlying the system dynamics could be further explored using multivariate NLTS methods (Dixon et al., 1999). Overall, the NLTS prediction skill was 0.37 for fisheries-dependent indices and 0.45 for fisheries-independent indices and comparable with a general pattern of a cross-system synthesis

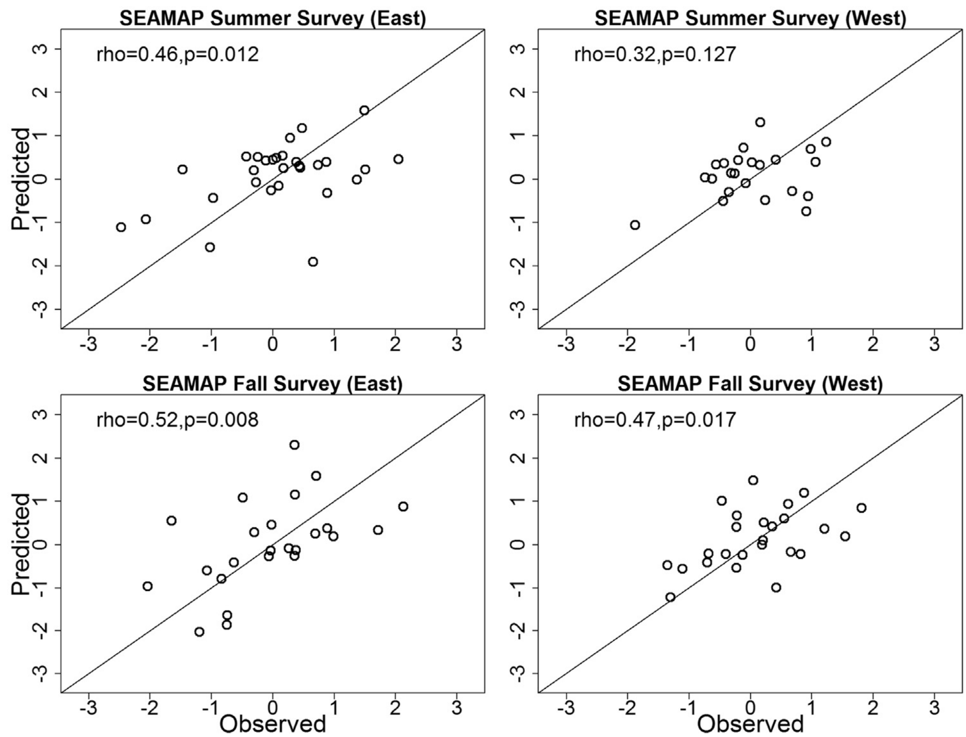

Fig. 3. S-map forecasts of fisheries-independent indices of red snapper (*Lutjanus campechanus*) separated for the eastern and western U.S. Gulf of Mexico.

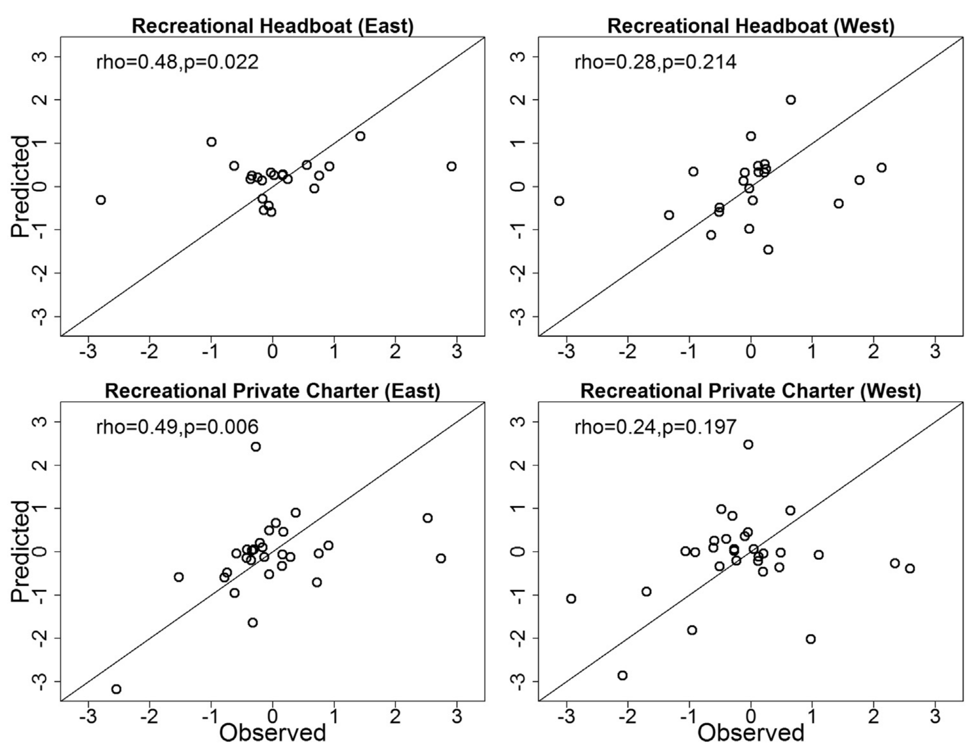

Fig. 4. S-map forecasts of fisheries-dependent indices of red snapper (*Lutjanus campechanus*) separated for the eastern and western U.S. Gulf of Mexico.

(Glaser et al., 2014). Compared to the quality of time series in the California Current system and on Georges Bank (Glaser et al., 2014; Liu et al., 2012), the performance of NLTS models on the relatively short time series of red snapper appeared even more appealing and is worth further evaluation.

Prediction scales in time and space are essential in terms of the NLTS forecast skill (Sugihara and May, 1990; Sugihara, 1994). An effective increase in data points of time series can significantly improve the NLTS forecasts and the detection of nonlinearity, such as, extending length of data series either over time through con-

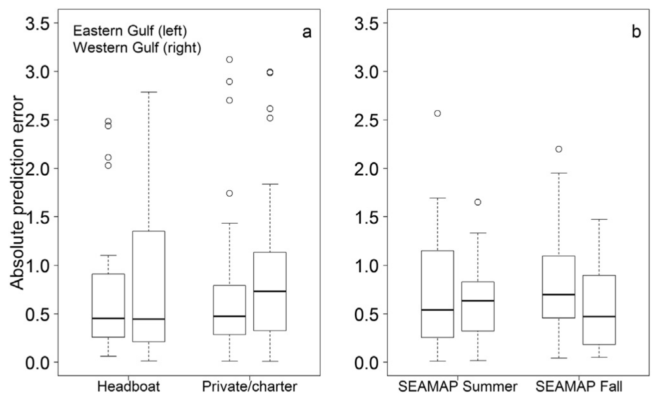

Fig. 5. Comparisons of prediction errors (absolute error between observations and predictions) on abundance indices of red snapper (*Lutjanus campechanus*) by data types and regions.

catenation of multiple time series (Hsieh et al., 2008) or across space by stitching spatial structured data at finer spatial scales (Glaser et al., 2011). One objective in this study was to explore the utility of NLTS models for generating short term forecasts of stock indices, which could then potentially inform traditional stock assessments. Normally, assessments and management of fish stocks are performed at an annual scale over a large geographic region defined according to the stock structures of fish. In this study, the relatively short annual time series and a broad spatial range accommodating the stock structures of red snapper might lessen the possibility of detecting nonlinear behaviors and reduce model forecast skills, as spatial averaging tends to diminish signals of local nonlinear dynamics (Sugihara, 1994). In any event, the spatial and temporal scales employed in our analyses are deliberately suited for a real practice of the NLTS approach to be useful for assessments and management of fish stocks. A recent analysis of retrospective bias for stocks in the Northeast U.S. region reported that the main source of bias in stock projections is the assessment model estimates of numbers at age in the first year following the terminal model year of data (Brooks and Legault, 2015). Forecasting the short-term abundance indices to be input into the assessment, which inform these numbers at age in the unobserved years, is one potential way that the NLTS method can be used to improve assessments and management of fish stocks. If the models exhibit predictability on abundance indices, then in theory the inclusion of an NLTS estimate should reduce the bias in retrospective projections of fish stocks.

The motivations of the present work were both to understand whether red snapper subpopulations displayed dynamics similarity and to explore the utility of NLTS to be useful for stock assessments. An incomplete understanding of population dynamics and stock structures limits the ability to forecast the population status and develop successful ecosystem based management plans (Megrey et al., 2009). The NLTS approach provides a new perspective in thinking about the stock structures of fish, which has implications for assessments and management of the species. Our results indicate that the utility of NLTS models for generating short term forecast is appealing; dynamics of the species represented by the abundance indices tend to differ between the eastern and western Gulf. Further, the dynamic associations between fish and the environment derived in the NLTS models hint at the underlying mechanisms controlling the dynamics of fish, and are worthy of further exploration in forecasting the dynamics of red snapper for better assessments and management of the species in the U.S. Gulf of Mexico.

Acknowledgements

We thank all those who participated in the SEDAR (Southeast Data, Assessment and Review) process over many years. We thank Mike Fogarty, George Sugihara, John Walter and Chris Legault for valuable discussion on this study. This study was funded by the National Oceanic and Atmospheric Administration, National

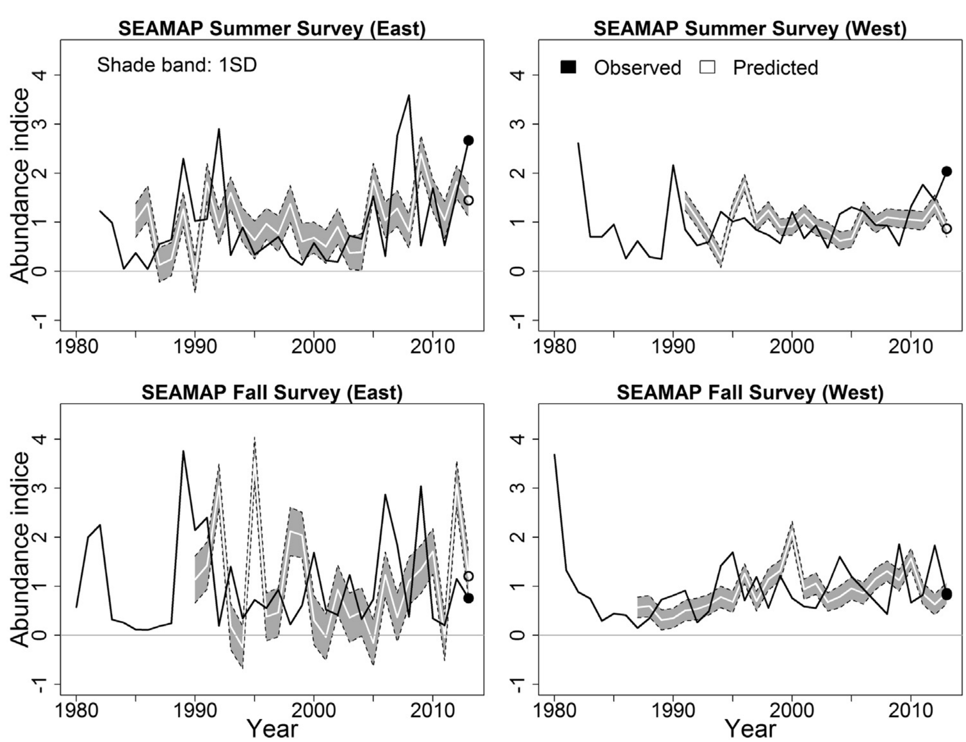

Fig. 6. Near-term nonlinear time series prediction (one year ahead) with the estimated uncertainty on fisheries-independent indices of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico.

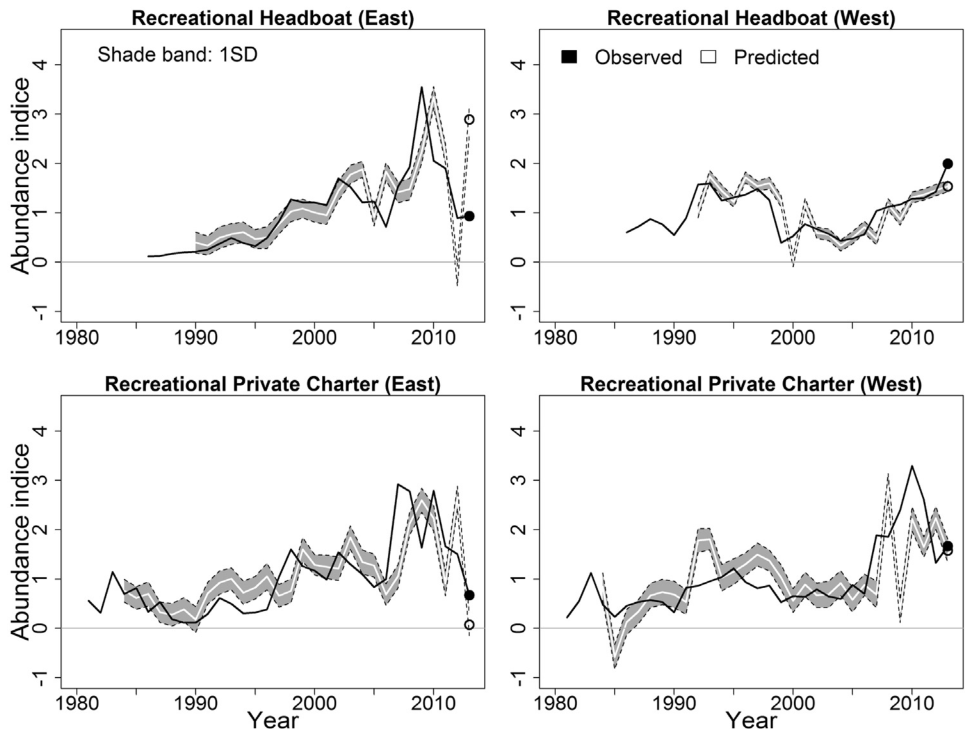

Fig. 7. Near-term nonlinear time series prediction (one year ahead) with the estimated uncertainty on fisheries-dependent indices of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico.

Marine Fisheries Service, Fisheries and The Environment (FATE) program.

References

Anderson, C.N.K., Hsieh, C.H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. Nature 452, 835–839.

Bradley, E., Bryan, C.E., 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970–1974. Proc. Gulf Caribb. Fish. Inst. 27, 77–106.

Branch, T.A., Hiborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. Can. J. Fish. Aquat. Sci. 62, 631–642.

Brooks, E.N., Legault, C.M., 2015. Retrospective forecasting – evaluating performance of stock projections for New England groundfish stocks. Can. J. Fish. Aquat. Sci. 73, 1–16.

Calay, S.L., Porch, C.E., Goethel, D.R., Smith, M.W., Matter, V., McCarthy, K.J., 2015. Stock Assessment of Red Snapper in the Gulf of Mexico 1872–2013 – with Provisional 2014 Landings. SEDAR Red Snapper 2014 Update Assessment Report: September 7, 2015, http://sedarweb.org/2014-update-sedar-31-gulf-mexico-red-snapper.

Camber, C.I., 1955. A Survey of the Red Snapper Fishery of the Gulf of Mexico, with Special Reference to the Campeche Banks. State of Florida Board of Conservation Technical Series 12. Marine Laboratory, St. Petersburg.

Camper, J.D., Barber, R.C., Richardson, L.R., Gold, J.R., 1993. Mitochondrial DNA variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. Mol. Mar. Biol. Biotechnol. 2, 154–161.

Collins, J.W., 1885. The red snapper grounds in the Gulf of Mexico. Fish. Bull. 5, 145–146.

Collins, J.W., 1887. Notes on the red snapper fishery. Fish. Bull. 6, 299–300.

Cowan Jr., J.H., Grimes, C.B., Patterson III, W.F., Walter, C.J., Jones, A.C., Lindberg, W.J., Sheehy, D.J., Pine III, W.E., Powers, J.E., Campbell, M.D., Lindeman, K.C., Diamond, S.L., Hilborn, R., Gibson, H.T., Rose, K.A., 2010. Red snapper management in the Gulf of Mexico: science- or faith-based? Rev. Fish Biol. Fish. 21, 187–204.

Cowan Jr., J.H., 2011. Red snapper in the Gulf of Mexico and U.S. south Atlantic: data, choices and conclusion. Fisheries 36 (7), 319–331.

Deyle, E.R., Fogarty, M., Hsieh, C.H., Kaufman, L., MacCall, A.D., Munch, S.B., Perretti, C.T., Ye, H., Sugihara, G., 2013. Predicting climate effects on Pacific sardine. Proc. Natl. Acad. Sci. U. S. A. 110, 6430–6435.

Dixon, P.A., Milicich, M.J., Sugihara, G., 1999. Episodic fluctuations in larval supply. Science 283, 1528–1530.

Efron, B., Tibshirani, R.J., 1994. An Introduction to the Bootstrap. Chapman & Hall, CRC Press, New York.

Ellis, R.W., Rosen, A., Moffett, A.W., 1958. A Survey of the Number of Anglers and Their Fishing Effort and Expenditures in the Coastal Recreational Fishery of Florida. Florida State Board of Conservation Marine Laboratory, Technical Series 24.

Fischer, A.J., Baker Jr., M.S., Wilson, C.A., 2004. Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics. Fish. Bull. 102, 593–603.

Glaser, S.M., Ye, H., Maunder, M., MacCall, A., Fogarty, M.J., Sugihara, G., 2011. Detecting and forecasting complex nonlinear dynamics in spatially-structured catch-per-unit-effort time series for North Pacific albacore (*Thunnus alalunga*). Can. J. Fish Aquat. Sci. 68, 400–412.

Glaser, S.M., Fogarty, M.J., Liu, H., Altman, I., Hsieh, C.H., Kaufman, L., MacCal, A., Rosenberg, A.A., Ye, H., Sugihara, G., 2014. Complex dynamics may limit prediction in marine fisheries. Fish Fish. 15, 616–633.

Gold, J.R., Saillant, E., 2007. Population structure of red snapper in the northern Gulf of Mexico. In: Patterson III, W.F., Cowan Jr., J.H., Fitzhugh, G.R., Nieland, D.L. (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. Am. Fish. Soc. Symp. 60, Bethesda, Maryland, pp. 181–195.

Gold, J.R., Sun, F., Richardson, L.R., 1997. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. Trans. Am. Fish. Soc. 126, 386–396.

Heist, E.J., Gold, J.R., 2000. DNA microsatellite loci, and genetic structure of red snapper in the Gulf of Mexico. Trans. Am. Fish. Soc. 129, 469–475.

Hsieh, C.H., Anderson, C.N.K., Sugihara, G., 2008. Extending nonlinear analysis to short ecological time series. Am. Nat. 171, 71–80.

Karnauskas, M., Schirripa, M.J., Craig, J.K., Cook, G.S., Kelble, C.R., Agar, J.J., Black, B.A., Enfield, D.B., Lindo-Atichati, D., Muhling, B.A., Purcell, K.M., Richards, P.M., Wang, C., 2015. Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico. Global Change Biol. 21 (7), 2554–2568.

Kwiatkowski, D., Phillips, P.C.B., Schmidt, P., Shin, Y., 1992. Testing the null hypothesis of stationarity against the alternative of a unit root. J. Econom. 54, 159–178.

Liu, H., Fogarty, M.J., Glaser, S.M., Altman, I., Hsieh, C.H., Kaufman, L., Rosenberg, A.A., Sugihara, G., 2012. Nonlinear dynamic features and co-predictability of the Georges Bank fish community. Mar. Ecol. Prog. Ser. 464, 195–207.

Liu, H., Fogarty, M.J., Hare, J.A., Hsieh, C.H., Glaser, S.M., Ye, H., Deyle, E., Sugihara, G., 2014. Modeling dynamic interactions and coherence between marine zooplankton and fishes linked to environmental variability. J. Mar. Syst. 131, 120–129.

Lorenz, E.N., 1963. Deterministic nonperiodic flow. J. Atmos. Sci. 20, 130–141.

Lyles, C., 1965. Fishery statistics of the United States. 1963. Bureau of Commercial Fisheries Statistical Digest 57.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27 (2), 209–220.

Matter, V., 2012. Recreational Survey Data for Red Snapper in the Gulf of Mexico. SEDAR31-DW04. SEDAR, North Charleston, SC, 22 pp.

Megrey, B.A., Link, J.S., Hunt Jr, G.L., Moksness, E., 2009. Comparative marine ecosystem analysis: applications, opportunities, and lessons learned. Prog. Oceanogr. 81, 2–9.
Moe, M.A., 1963. A Survey of Offshore Fishing in Florida. Florida State Board of Conservation, Marine Laboratory, pp. 5–117, Professional Papers Series 4.
Ortiz, M., Cass-Calay, S.L., 2004. Assessments of red snapper stocks in the eastern and western Gulf of Mexico using an age-structured-assessment-procedure. SEDAR7-AW-64.
Patterson, W.F., Watterson, J.C., Shipp, R.L., Cowan Jr., J.H., 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 130, 533–545.
Patterson, W.F., Cowan Jr., J.H., Wilson, C.A., Chen, Z., 2008. Temporal and spatial variability in juvenile red snapper otolith elemental signature in the Northern Gulf of Mexico. Trans. Am. Fish. Soc. 137, 521–532.
Patterson, W.F., 2007. A review of movement in Gulf of Mexico red snapper: implications for population structure. In: Patterson III, W.F., Cowan Jr., J.H., Fitzhugh, G.R., Nieland, D.L. (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. Am. Fish. Soc. Symp. 60, Bethesda, Maryland, pp. 245–261.
Pollack, A.G., Ingram, G.W., Foster, D.G., 2012. Red Snapper Abundance Indices from SEAMAP Groundfish Surveys in the Northern Gulf of Mexico. SEDAR31-DW20. SEDAR, North Charleston, SC, 236 pp.
Porch, C.E., 2007. An assessment of the red snapper fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured model. In: Patterson III, W.F., Cowan Jr., J.H., Fitzhugh, G.R., Nieland, D.L. (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. Am. Fish. Soc. Symp. 60, Bethesda, Maryland, pp. 325–351.
Pruett, C.L., Saillant, E., Gold, J.R., 2005. Historical population demography of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico based on analysis of sequences of mitochondrial DNA. Mar. Biol. 147, 593–602.
Royer, F., Fromentin, J.M., 2006. Recurrent and density-dependent patterns in long-term fluctuations of Atlantic bluefin tuna trap catches. Mar. Ecol. Prog. Ser. 319, 237–249.
SEDAR31 (Southeast Data, Assessment, and Review), 2013. Gulf of Mexico Red Snapper Stock Assessment Report. SEDAR, North Charleston, SC, 1103 pp.
Stearns, S., 1883. Fluctuations in the fisheries of the Gulf of Mexico, and the proposed investigation of them. Fish. Bull. 3, 467–468.
Sugihara, G., May, R.M., 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. Nature 344, 734–741.
Sugihara, G., 1994. Nonlinear forecasting for the classification of natural time-series. Philos. Trans. R. Soc. A 348, 477–495.
Takens, F., 1981. Detecting strange attractors in turbulence. Lect. Notes Math. 898, 366–381.
Woods, M.K., Fischer, A.J., Cowan Jr., J.H., Nieland, D.L., 2003. Size and age at maturity of female red snapper *Lutjanus campechanus*in the northern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 54, 526–537.
Ye, H., Beamish, R.J., Glaser, S.M., Grant, S.C.H., Hsieh, C.H., Richards, L.J., Schnute, J.T., Sugihara, G., 2015. Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. Proc. Natl. Acad. Sci. 112, E1569–E1576, http://dx.doi.org/10.1073/pnas.1417063112.