



Complex dynamics may limit prediction in marine fisheries

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Abstract

Complex nonlinear dynamics in marine fisheries create challenges for prediction and management, yet the extent to which they occur in fisheries is not well known. Using nonlinear forecasting models, we analysed over 200 time series of survey abundance and landings from two distinct ecosystems for patterns of dynamic complexity (dimensionality and nonlinear dynamics) and predictability. Differences in system dimensionality and nonlinear dynamics were associated with time series that reflected human intervention via fishing effort, implying the coupling between human and natural systems generated dynamics distinct from those detected in the natural resource subsystem alone. Estimated dimensionality was highest for landings and higher in abundance indices of unfished species than fished species. Fished species were more likely to display nonlinear dynamics than unfished species, and landings were significantly less predictable than abundance indices. Results were robust to variation in life history characteristics. Dynamics were predictable over a 1-year time horizon in seventy percent of time series, but predictability declined exponentially over a 5-year horizon. The ability to make predictions in fisheries systems is therefore extremely limited. To our knowledge, this is the first cross-system comparative study, and the first at the scale of individual species, to analyse empirically the dynamic complexity observed in fisheries data and to quantify predictability broadly. We outline one application of short-term forecasts to a precautionary approach to fisheries management that could improve how uncertainty and forecast error are incorporated into assessment through catch limit buffers.

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Introduction

Fisheries are framed by the intersection of a diverse set of physical, biological, economic, cultural and governance considerations (Allen and McGlade 1987; Liu *et al.* 2007). The complex features that emerge from these social-ecological systems (Berkes and Folke 1998; Ostrom 2009) present challenges for the implementation of ecosystem-based management strategies (Waltner-Toews *et al.* 2008; Horan *et al.* 2011). For example, chaotic dynamics increase the likelihood of fishery collapses (Mullon *et al.* 2005) and limit the accuracy of long-term prediction because, in chaotic systems, small differences in initial conditions diverge significantly over time (Lorenz 1963). However, while such nonlinear dynamics may limit the time horizon over which predictions are accurate, over short time horizons prediction may be possible with the proper tools (Ellner and Turchin 1995).

The term 'dynamic complexity' applies to a suite of characteristics describing dynamical systems (May and Oster 1976). Here, we examined two metrics relevant to fisheries: system dimensionality and the presence of nonlinear dynamics in time series. Dimensionality reflects the number of interacting processes generating the deterministic component of a time-evolving system (Lorenz 1963; Packard *et al.* 1980). Low-dimensional systems contain fewer driving variables and, mechanistically, suggest simple models may describe a system adequately. High-dimensional systems result from the action of many variables and can produce dynamics indistinguishable from random noise (Coulson *et al.* 2004), making prediction difficult or impossible. In the approach used here, the

detection of nonlinear dynamics suggests the observed behaviour is state dependent and cannot be modelled as a linear (additive) combination of individual state variables (Abarbanel *et al.* 1993; see Box 1). Together, these two metrics can inform the structure of fishery models and place practical limits on predictability (Fussman and Heber 2002).

We examined evidence for nonlinear dynamics in fishery-independent and fishery-dependent time series. Theories underpinning fishery dynamics ultimately rest on nonlinear functional relationships between fishing intensity and yield or between spawning stock biomass and recruitment. Some of these nonlinear models also can exhibit nonlinear dynamics in which small changes to an input variable (e.g. yield or recruitment) at certain parameter values. Ricker (1954) first demonstrated the possibility of dynamic complexity in simple ecological models. The distinction between nonlinear models characterized by globally stable equilibria and those exhibiting complex dynamical behaviour is critical for our purposes (May 1974). Classical concepts such as maximum sustainable yield are based on the former, while the latter encompasses a much broader spectrum of possible dynamical behaviours, including rapid shifts in state. Understanding the potential for nonlinear dynamics in fishery systems emerges as a critical need in assessing the possibility of unexpected changes in marine populations.

In this study, we used nonlinear forecasting models to examine the dynamic complexity evident in a wide variety of fisheries data and to quantify the predictability achievable in those systems. We compared the dynamics governing fisheries at two scales of observation: the natural resource subsystem (represented by survey-derived indices of abun-

dance of unfished and fished species) and the encompassing fishery social-ecological system (represented by landings). Nonlinear dynamics have been identified in individual marine species (Dun-
 gness crab, Berryman 1991; Pacific halibut, Conklin and Kolberg 1994; *Pomacentrus amboinensis*, Dixon *et al.* 1999; bluefin tuna, Royer and Fromentin 2006; Atlantic herring, Casini *et al.* 2010; albacore tuna, Glaser *et al.* 2011) and in aggregated multi-species assemblages (Hsieh *et al.* 2005a). However, the extent (or lack thereof) of nonlinear dynamics and the dimensionality of species-level observations of fish communities has not been quantified. We expect differences in dynamic complexity based on the exploitation status of the species and the data type examined. Abundance indices of fished species and landings should be higher dimensional and more likely to contain nonlinear dynamics because layers of processes associated with the additional human component of the fishery should add dimensions and strengthen nonlinear behaviour (Mullon *et al.* 2005; Chapin *et al.* 2006; Anderson *et al.* 2008; Rouyer *et al.* 2008).

Methods

Data

Scientific surveys are preferred for estimating fish abundance because the confounding effects of fisher behaviour are removed. Landings, on the other hand, reflect the dominant human intervention in the fishery and are an important input to stock assessment models (Froese *et al.* 2012). Although no single metric can capture fully the richness of the coupled human-resource system, landings integrate changes in resource abundance, market demand, harvesting practices, institutions and management. Thus, survey abundance indices and landings provide two distinct (but not independent) observations of fish population dynamics and fishery systems. The California Current System (CCS) and the Northeast U.S. Continental Shelf System (NES) are well studied, data-rich Large Marine Ecosystems (LME) on the West and East Coasts of the United States, respectively. These systems differ in their exploitation histories, species composition, and fundamental oceanographic and ecological characteristics. Fishery-independent surveys of abundance have occurred since 1951 (CCS) and 1963 (NES).

We analysed 206 time series of abundance and landings belonging to 145 unique taxa (Table 1).

Table 1 Time series of 206 fish and invertebrate populations.

Data type	Location	No. time series	No. unique taxa
Abundance	CCS	67	67
Abundance	NES	45	35
Landings	CCS	53	53
Landings	NES	41	31

CCS, California current system; NES, Northeast shelf system.

Sixty taxa were unfished, and 85 were fished. In some cases, taxonomic groups were aggregates at the generic or family level of identification (see Table S1). For the CCS, landings data were collected primarily from the California Department of Fish and Game landings database (PFEL 2009) and supplemented with landings data from stock assessment reports (PFMC 2010). Data were summed across all California ports and through a given year, from 1928 to 2009, to measure total annual landings in metric tons. Abundance indices were from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys in the Southern California Bight during 1951–2007 (CalCOFI 2012). Average annual abundance indices (larvae m⁻²) for the 67 most commonly occurring taxa were selected according to the criteria of Hsieh *et al.* (2005b). We assume larval abundance represents adult spawning abundance, an assumption demonstrated for some but not all species surveyed by CalCOFI (e.g. Moser and Watson 1990). For the NES, annual landings data were collected from stock assessment reports and date ranges varied (NEFSC 2008). Abundance indices (mean weight tow⁻¹) came from the Northeast Fisheries Science Center fall bottom trawl for the period 1963–2008 for 45 taxa. If separate indices were developed for geographically distinct stocks of one species, stock structure was retained in forecasting models. In final statistical analyses, stock replicates of the same species were excluded. Series were trimmed to cover the same time spans within a LME. We examined a paired data subset ($n = 51$ pairs) of same-species abundance and landings series to control for inter-species life history differences (Table S2). Size data (maximum length in cm) were collected for as many taxa as possible from Fish Base (Froese and Pauly 2012), stock assessment reports and primary literature.

State space reconstruction

In a dynamical system, a state space defines the geometry of a deterministic model governing that system, and the axes in the space represent independent variables (Packard *et al.* 1980). For example, in a system governing fish abundance, if population dynamics are a function of prey and temperature, the state space will contain three dimensions and thus three axes (the third representing the fish population). A point in state space is defined by the ordered triple (fish, prey, temperature). By plotting many three-dimensional points, the emergent attractor defines the trajectory of the deterministic system. In practice, important variables might not have been identified or monitored (Bjornstad and Grenfell 2001), and the shape of the attractor could be unknown.

Takens (1981) offered a solution to this dilemma: a D -dimensional system can be reconstructed from the lags of a one-dimensional time series. In our example, the influences of prey and temperature on fish at time t (x_t) can be approximated by x_{t-1} and x_{t-2} . The dynamic effects of prey and temperature are contained in the historical observations of the fish population. Then, coordinates (x_t, x_{t-1}, x_{t-2}) reconstruct a shadow attractor or embedding (Fig. 1). The shadow attractor may appear squeezed or stretched compared with the

'real' attractor, but it is topologically invariant and retains mathematical properties of the full state space (Takens 1981; Abarbanel *et al.* 1993; Deyle and Sugihara 2011). According to the Whitney embedding theorem (Whitney 1936), a system of dimensionality D can be embedded in E dimensions where $D \leq E < 2D + 1$. The embedding dimension therefore provides an index of complexity of the system. State space reconstruction has a long history in diverse fields (Casdagli 1991; Abarbanel *et al.* 1993; Sugihara 1994; Kaplan and Glass 1995; Kantz and Schreiber 2003). However, its application to ecology is complicated by short time series and high observation noise which may result in poorly defined attractors.

Nonlinear forecasting models

We employed two nonparametric, nonlinear forecasting models predicated on state space reconstruction through lagged-coordinate embedding that were developed specifically for short, noisy time series (Hsieh *et al.* 2005b, 2008; Glaser *et al.* 2011). Simplex projection (Sugihara and May 1990) calculated the best E for a time series. Sequentially weighted global linear maps (S-map, Sugihara 1994) classified system dynamics as linear or nonlinear (see Box 1). Both models produced short-term forecasts that characterized system predictability.

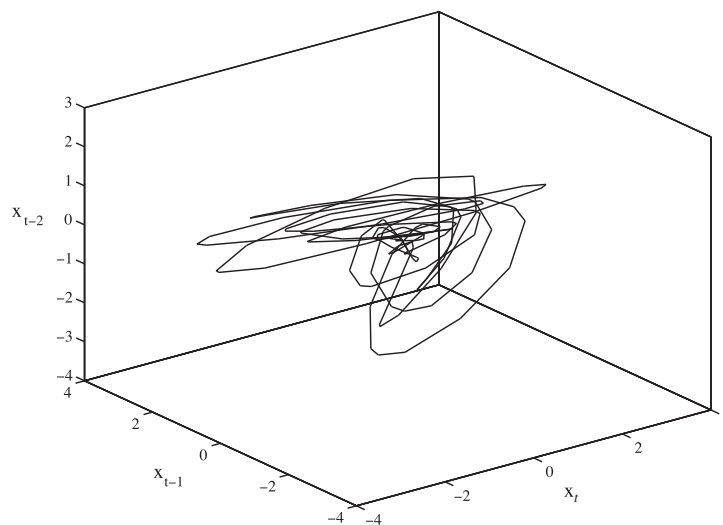
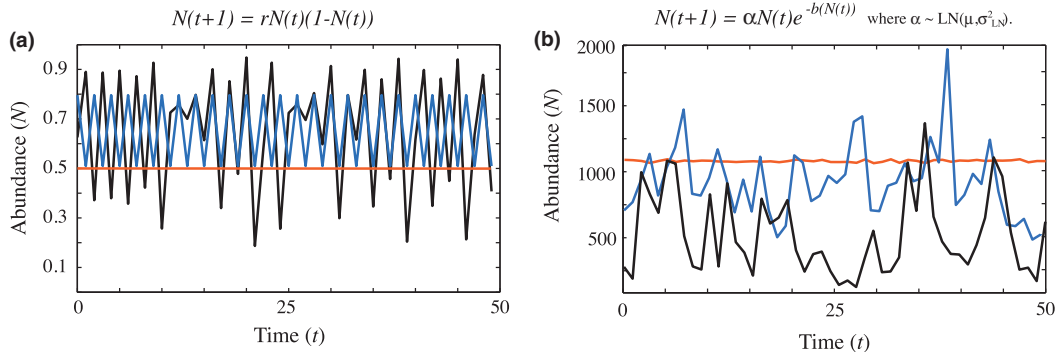


Figure 1 State space reconstruction of a three-dimensional attractor in a time series of fawn cusk eel (*Lepophidium profundorum*, Ophidiidae) abundance indices from the Northeast Fisheries Science Center fall bottom trawl survey. Each point is a time-lagged coordinate vector, $\mathbf{x}_t = \langle x_t, x_{t-1}, x_{t-2} \rangle$. Discrete points are connected by a spline function to show a smooth attractor.

Box 1. Model examples of linear and nonlinear dynamics and methodological glossary



Linear or nonlinear dynamics may result from two common models of fish population dynamics. Both models have a nonlinear functional form but can produce either linear or nonlinear dynamics given differences in growth rate (a) or degree of process noise (b). Panel (a) shows 50 years of output from a discrete logistic growth model with varying intrinsic growth rates (r). For $r = 2.0$ (orange), dynamics are at equilibrium. For $r = 3.0$ (blue), dynamics are a stable limit cycle. For $r = 3.8$ (black), dynamics are chaotic. Panel (b) shows 50 years of output from a Ricker model of a semelparous species. Process noise has been added to the reproductive rate (α) by drawing it from a log-normal distribution (where $\mu = 2.0$) with increasing variance [$\sigma^2 = \text{low}$ (orange), $\sigma^2 = \text{medium}$ (blue), $\sigma^2 = \text{high}$ (black)]. For either model, the attractor describing the deterministic (no noise) behavior of the system is a point for equilibrium dynamics or an ellipse for limit cycles. In a system with nonlinear dynamics, the attractor geometry is non-repeating (see Fig. 1) and demonstrates state dependence whereby neighboring trajectories may diverge significantly over time. The S-map model identifies the presence of such nonlinear dynamics and is especially skilful when the deterministic signal is convolved with non-additive noise.

Below are statistics associated with S-map modeling of 1000 years of output (500 predicting 500) from the six model runs. Note the perfect forecast skill for the logistic model, even when dynamics were chaotic.

Logistic model (deterministic)			Ricker model (with noise)		
$r = 2.0$	$r = 3.0$	$r = 3.8$	$\sigma^2 = \text{low}$	$\sigma^2 = \text{medium}$	$\sigma^2 = \text{high}$
$E = 2$	$E = 2$	$E = 2$	$E = 2$	$E = 2$	$E = 2$
$\rho = 1.0$	$\rho = 1.0$	$\rho = 1.0$	$\rho = 0.10$	$\rho = 0.17$	$\rho = 0.32$
$\Delta\text{MAE} = 0$	$\Delta\text{MAE} = 0$	$\Delta\text{MAE} = 0.17$	$\Delta\text{MAE} = 0$	$\Delta\text{MAE} = 0.01$	$\Delta\text{MAE} = 0.06$
$\theta = 0$	$\theta = 0$	$\theta = 10$	$\theta = 0$	$\theta = 0$	$\theta = 2$
Linear	Linear	Nonlinear	Linear	Linear	Nonlinear

Embedding dimension (E) – Technically, the number of consecutive time lags used to reconstruct the system state space using lagged coordinates. Heuristically, a relative index of the complexity of the system, or how many interacting processes created the observed dynamics.

Linear dynamics – Dynamics best modeled by global information, such as a mean value or as an autoregressive process, either because the deterministic system is stable or because dynamics cannot be distinguished from a purely stochastic process.

Nonlinear dynamics – Dynamics best modeled by local information (where ‘local’ is defined by the location of trajectories on an E-dimensional state space reconstruction) because the system is state dependent. Dynamics are not labeled ‘chaotic’ because a Lyapunov exponent is not estimated.

θ – A nonlinear tuning parameter in the S-map model (see Methods). When $\theta = 0$, the model calculates forecasts using all available data (global information). When $\theta > 0$, the model calculates forecasts

preferentially using a smaller neighborhood of data (local information). The magnitude of θ determines the weighting given to nearest neighbors producing the forecast.

Forecast skill (ρ) – The metric by which the best model of system dynamics is chosen. Calculated as the Pearson correlation coefficient between observed values and out-of-sample model forecasts of that value. The value of ρ , ranging from -1.0 to 1.0 , quantifies the amount of deterministic signal in the data. Therefore, $1-\rho$ quantifies the amount of noise in the data and ρ provides a measure of prediction that can be compared between datasets.

ΔMAE – The improvement in model mean absolute error as S-maps tunes θ above 0 .

Time series were selected on the basis of sufficient length [minimum 30 years of annual data (Hsieh et al. 2008)], the first difference was calculated ($\Delta x = x_t - x_{t-1}$) and then data were transformed to standard normal deviates (mean = 0, SD = 1). Processing reduced short-term autocorrelation, preserved stationarity and allowed direct comparison of model error between data sets of different magnitudes (Diggle 1990; Bjornstad and Grenfell 2001). A time series was divided into a set of fitting or library vectors $\{\mathbf{x}_{\text{lib}}\}$, from which the model was built, and prediction vectors $\{\mathbf{x}_{\text{pred}}\}$, which were held out-of-sample and on which model *forecast skill* (defined below) was tested. For these short time series, $\{\mathbf{x}_{\text{lib}}\}$ was comprised of all E -length vectors in a time series except one prediction vector $\mathbf{x}_{\text{pred}} = \langle x_t, x_{t-1}, \dots, x_{t-E+1} \rangle$, and \mathbf{x}_{pred} advanced through the series; that is, one vector at a time was left out in a cross-validation approach (Sugihara et al. 1996).

Simplex projection iteratively models times series at different values of E (here, 1 through 10), and the model producing the highest *forecast skill* and lowest error identifies the best E for the system. For consistency with original nomenclature, let us rename $\{\mathbf{x}_{\text{lib}}\} \equiv \{\mathbf{x}_i\}$ and $\mathbf{x}_{\text{pred}} \equiv \mathbf{x}_t$. First, a time series of length T was decomposed into a set of non-overlapping vectors of length E ; the coordinates of these vectors defined the lagged-coordinate embedding (e.g. Fig. 1). Second, for a time step t , the prediction vector \mathbf{x}_t was defined as $\langle x_t, x_{t-1}, \dots, x_{t-E+1} \rangle$ and the remaining vectors comprised the library $\{\mathbf{x}_i\}$. The Euclidean distances between \mathbf{x}_t and $\{\mathbf{x}_i\}$ were calculated, and the $E + 1$ vectors in $\{\mathbf{x}_i\}$ nearest to \mathbf{x}_t were selected to define the simplex around \mathbf{x}_t . $E + 1$ mathematically defines the minimum number of points needed uniquely to locate \mathbf{x}_t in E dimensions. Third, the simplex was projected ahead in coordinate space t_p time steps (usually $t_p = 1$). The forward trajectories of the nearest neighbour vectors in $\{\mathbf{x}_i\}$ were defined by the observed points $\{y_i\}$, and the forecast (\hat{y}_t) for \mathbf{x}_t was calculated as a

weighted average of $\{y_i\}$. Thus, the single forecast for time t was defined by the trajectories of its nearest neighbours in reconstructed state space. The process was repeated for all t , ultimately producing $T - E - t_p + 1$ forecasts for each series.

Two model selection metrics were calculated from the observed and forecast values: model *forecast skill* (ρ) defined by the Pearson correlation coefficient and mean absolute error (MAE). The best E for the system was chosen from maximum ρ and minimum MAE. When ρ_{max} and MAE_{min} did not agree, E was selected according to highest ρ_{max} unless $\rho_{\text{max}} < 0$, in which case minimum MAE was used. The best E was input to S-map to define the dimensionality of the state space.

S-map compares a global linear forecasting model (an autoregressive model of order E which serves as our null model) to a nonlinear forecasting model, similarly using library and prediction vectors. First, the embedding was defined by the set of time-lagged coordinates of length E , and for each time step t , one prediction vector was defined as $\mathbf{x}_t = \langle x_t, x_{t-1}, \dots, x_{t-E+1} \rangle$. Second, the library vectors $\{\mathbf{x}_i\}$ were projected forward t_p time steps. S-map uses all $\{\mathbf{x}_i\}$ (not only $E + 1$ nearest neighbours) to make forecasts. The forecast \hat{y}_t for \mathbf{x}_t was calculated from all $\{\mathbf{x}_i\}$ forecasts $\{y_i\}$ using a function (defined below) that exponentially weights library vectors by distance to the prediction vector in the embedded state space. The weighting function includes a nonlinear tuning parameter, θ . When $\theta = 0$, S-map weights all library vectors equally and represents a global linear model with identical coefficients defining the projections for all \mathbf{x}_t in one time series. When θ is tuned above 0 , the neighbourhood around \mathbf{x}_t becomes more important (weighted) and forecast coefficients are recalculated for each \mathbf{x}_t in the time series. If the global linear model outperforms the local nonlinear model based on MAE, forecasts are best approximated by all available information (similar to using an average value, as one might do in a system at equilibrium). If the

local nonlinear model outperforms, the system is state dependent and library vectors nearby \mathbf{x}_t in state space at time t are expected to diverge over time, losing their predictive value. Thus, S-map measures the tendency for nearby trajectories in an attractor to diverge and is not simply characterizing a nonlinear functional form.

Specifically, again defining the projections for library vectors $\{\mathbf{x}_i\}$ as $\{y_i\}$ and setting $x_t(0) \equiv 1$, the forecast \hat{y}_t for the prediction vector \mathbf{x}_t is calculated as

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

\mathbf{c} is solved by singular value decomposition as $\mathbf{b} = \mathbf{Ac}$, and

$$b(j) = w(\|\mathbf{x}_i - \mathbf{x}_t\|) y_i$$

$$A(i, j) = w(\|\mathbf{x}_i - \mathbf{x}_t\|) \mathbf{x}_i(j)$$

The weighting function

$$w(d) = e^{\frac{-\theta d}{\bar{d}}}$$

defines the model as global linear or local nonlinear where d is the Euclidean distance between one library vector \mathbf{x}_i and the prediction vector \mathbf{x}_t , and \bar{d} is the average distance between all $\{\mathbf{x}_i\}$ and \mathbf{x}_t . We began with $\theta = 0$ and iterated the model for increasing values of θ $\{0, 0.001, 0.005, 0.01, 0.025, 0.05, 0.075, 0.1, 0.2, 0.3, 0.4, 0.5, 0.75, 1, 2, 5, 7, 10\}$.

As in simplex projection, model selection was based on ρ_{\max} and MAE_{\min} , but here, we also calculated the improvement in MAE as θ was tuned above 0. The best θ for modeling the system was chosen from ρ_{\max} because a P -value can be assigned by Pearson's product moment. Models that were not significant at $P \leq 0.05$ were excluded from further analysis because forecasts (and therefore estimates of E and nonlinearity) were not reliable. Time series that met the significance criterion were then classified as nonlinear if the change in error when moving from a linear to nonlinear model ($\Delta\text{MAE} = \text{MAE}_{\theta=0} - \text{MAE}_{\min}$) was positive and significant at $P \leq 0.10$. Significance was assigned by a randomization test (Hsieh and Ohman 2006). The test statistic ΔMAE was computed from the data. Then, the time series order was shuffled randomly, S-map was repeated, and a null ΔMAE was calculated. We randomized the data 500 times, creating a null distribution against which our test ΔMAE was compared.

To quantify the predictive potential inherent in these fisheries data, we analysed the forecasts produced from S-map as a function of how many time steps into the future (t_p) forecast skill persisted. For this analysis, t_p ranged from 1 to 5 years. We focused on forecasts made from S-map rather than simplex projection because it produces better forecasts when data contain a strong noise component (Sugihara 1994).

Statistical analysis

We analysed the relation of data type, exploitation status and life history (size) to system dimensionality (E), the detection of nonlinear dynamics and model forecast skill (ρ). We analysed the maximum ρ achieved by S-map (at $t_p = 1$) for each of 206 time series to understand the factors related to whether a time series was predictable or not.

Generalized linear models (GLMs) were used to analyse E , the detection of nonlinear dynamics and ρ (Table 2). For ρ , we analysed the full data set of 206 series. For E and nonlinear dynamics, only time series for which ρ from S-map was significant at $P \leq 0.05$ were included ($n = 145$). Furthermore, for species replicated by multiple time series within a data type due to separate stock structure, one stock was randomly included while remaining stocks were excluded. Once assigned, the stock included did not change in subsequent analyses. This removed the possibility of pseudo-replication and reduced the full data set from 206 to 186 time series, and the number of time series producing statistically significant ρ from 145 to 135. E , an ordered categorical variable, was analysed using a cumulative link model (Gaussian distribution). The binary classification of nonlinear dynamics was analysed using a logit link function (binomial distribution). ρ was analysed using an identity link function (Gaussian distribution).

Step-wise model selection using AIC was performed. The models were the following:

- (1) $E \sim \text{Data Type} + \text{Exploitation} + \text{Size} + \text{Location} + \text{CV} + N + \text{CV} * \text{Data Type} + \text{CV} * \text{Exploitation}$
- (2) $\text{Nonlinear} \sim \text{Data Type} + \text{Exploitation} + \text{Size} + \text{Location} + \rho + \text{CV} + N + \text{CV} * \text{Data Type} + \text{CV} * \text{Exploitation}$
- (3) $\rho \sim \text{Data Type} + \text{Exploitation} + \text{Size} + \text{Location} + \text{CV} + N + \text{CV} * \text{Data Type} + \text{CV} * \text{Exploitation}$

Data Type was 'abundance' or 'landings'. *Exploitation* status was 'unfished' or 'fished'. *Size* was the

Table 2 Generalized linear model analysis of dynamic complexity in fisheries data.

DV	Const.	DT = landings	Expl = fished	Loc = NES	Size (cm)	CV	N	ρ	CV \times DT	CV \times Expl	n
NL	-7.55 (1.55)****	0.91 (0.55)*	1.28 (0.55)**	-	-	2.36 (0.84)***	-	6.92 (2.01)****	-	-	135
E	-	0.96 (0.40)**	-3.46 (1.57)**	-	-	-3.46 (1.50)**	0.06 (0.03)**	N/A	-	3.04 (1.59)	135
ρ	3.45 (1.99)****	-0.18 (0.03)	-	-	-	-	-	N/A	-	-	184

Coefficient estimates and (standard errors). * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$.DV, Dependent variable; DT, Data Type (landings/abundance); Expl, Exploitation (fished/unfished); Loc, Location (NES/CCS); CV, Coefficient of variation; N, Annual points in series; ρ , Forecast skill; -, Variable dropped in step-wise regression; E, Embedding dimension.

maximum length (cm) for a species or average maximum length for a taxon. *Location* was 'CCS' or 'NES'; this variable tested for intercoastal differences and controlled for differences in fishing and survey techniques. CV, the coefficient of variation calculated from first-differenced data, was included as a control to eliminate the possibility that non-linearity was detected as an artefact of higher variability (Fogarty 1995). *N* was the number of annual values in a time series and was included as a control because nonlinear dynamics may be obscured if series are too short (Hsieh *et al.* 2008; Glaser *et al.* 2011). Although series were trimmed to cover the same periods within a LME, some series had missing data and the periods were slightly different between the CCS and NES. ρ at $t_p = 1$ was included as a control variable for classification of nonlinear dynamics. A high ρ indicates the deterministic signal in the data is stronger than the noise. There was no *a priori* reason to assume that, as a class, either linear or nonlinear models would have higher ρ . Finally, the interactions of *Data Type* and *Exploitation* with CV controlled for statistical artefacts (e.g. fished species tend to be more variable). Analysis was performed in R with functions *glm*, *glm* and *step*. For *step*, NaNs are not allowed in independent variable columns, and we lacked size estimates for a handful of species. Therefore, the initial model was run as a whole, and if *Size* was not significant, it was removed from the model and stepwise regression was run.

Paired comparisons of abundance and landings for the same stock or species were made to control for the effects of life history and the environment. By definition, species with both abundance and landings data were fished, preventing a comparison of the effect of exploitation (unfished vs. fished in the same species) on this subsample. Again, only those series with S-map ρ significant at $P \leq 0.05$ were included. Based on results of the GLM analysis, we tested the hypotheses that $E_{abundance} < E_{landings}$, abundance data were more likely to contain linear dynamics than landings data, and $\rho_{landings} < \rho_{abundance}$. We used a Wilcoxon signed rank test for *E*, Cochran's Q test for nonlinear classification and a one-tailed paired *t*-test for ρ .

Results

Of 206 time series analysed, 145 were modelled by S-map with significant ($P \leq 0.05$) forecast skill.

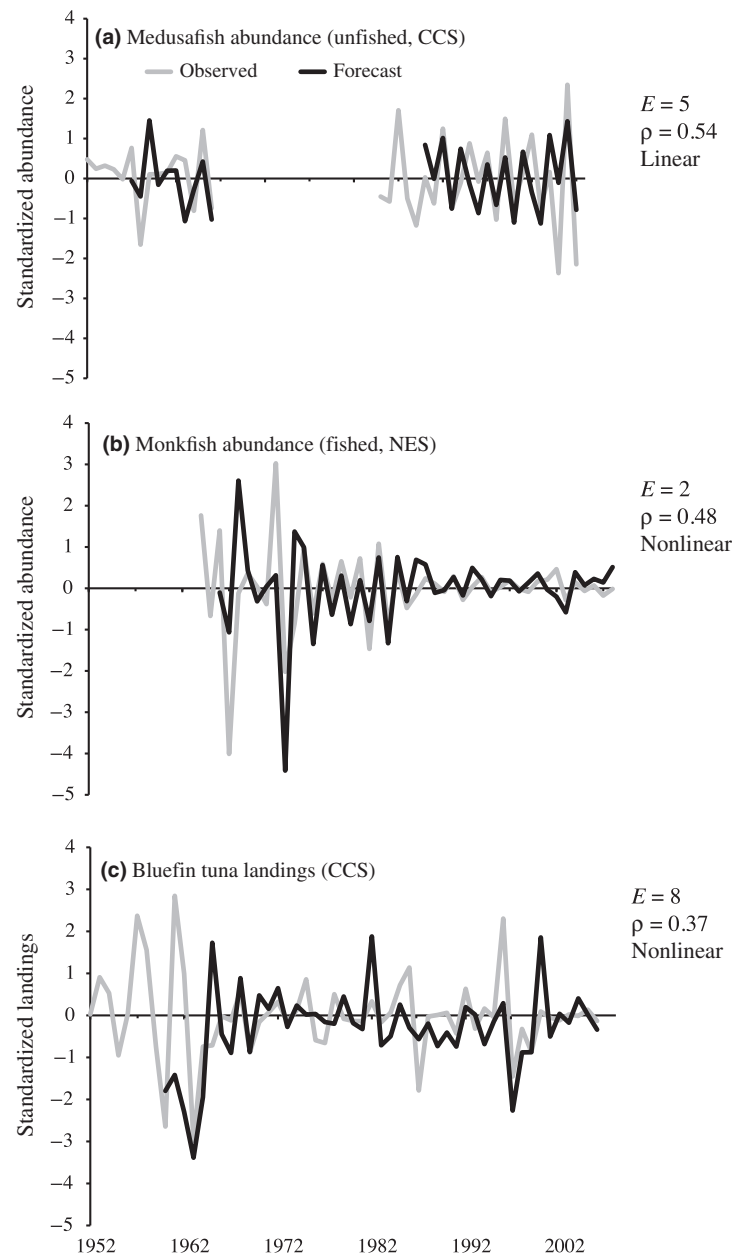


Figure 2 Example time series of observations and S-map forecasts for three categories of fisheries data and their associated dynamic complexity metrics: (a) abundance of an unfished species, medusafish (*Ichthyos lockingtoni*, Centrolophidae); (b) abundance of a fished species, monkfish (*Lophius americanus*, Lophiidae); (c) landings of bluefin tuna (*Thunnus thynnus*, Scombridae). E is embedding dimension, ρ is maximum forecast skill achieved with S-map models, and dynamics were classified as linear or nonlinear.

Figure 2 shows representative time series forecasts for three categories of fisheries data; examples were selected from within a category with median values of ρ . Estimated dimensionality was highest for landings, but higher in unfished abundance than in fished abundance (Fig. 3). Nonlinear dynamics were significantly more likely to be

found in observations of landings and fished abundance than in unfished abundance (Fig. 4). Finally, landings data had significantly lower ρ than abundance data (Fig. 5) but there was no difference in ρ between fished and unfished taxa. We found no evidence of a life history (size) explanation for observed patterns. Results were

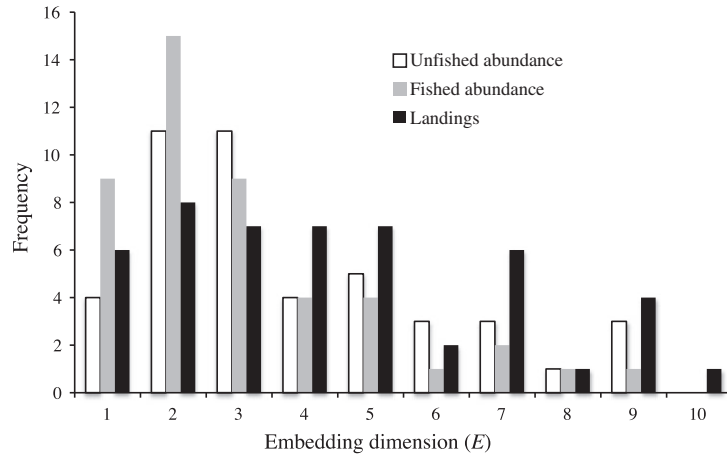


Figure 3 Embedding dimensions for fisheries data ($n = 135$ series). Abundance estimates of fished taxa had lowest E while landings had highest.

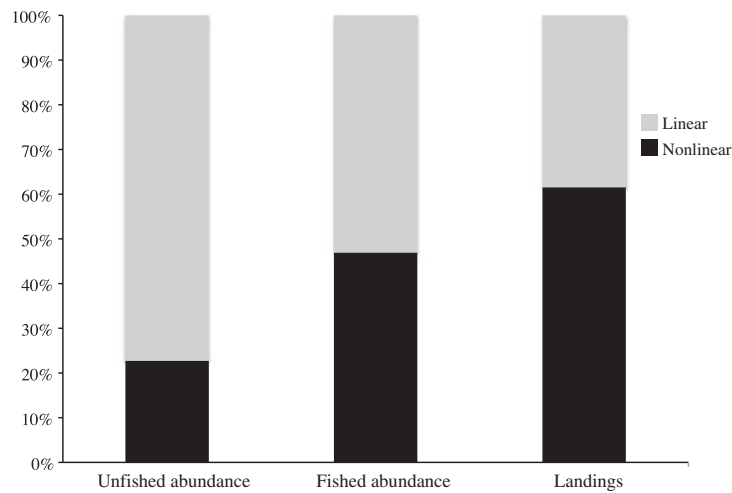


Figure 4 Classification of dynamics in fisheries time series ($n = 135$). Observations of abundance for fished taxa were 3.6 times more likely than for unfished taxa to contain nonlinear dynamics. Landings series were 2.5 times more likely than abundance series to contain nonlinear dynamics.

replicated on the same-species paired subsample of abundance and landings.

Estimated dimensionality was significantly higher in landings than abundance data ($P = 0.015$), but within abundance data types, unfished taxa had significantly higher E than fished taxa ($P = 0.028$) (Table 2). GLM results were validated with a test of distributions (Kruskal-Wallis test, $P = 0.037$; Fig. 3). Median E was four for landings, three for unfished abundance and two for fished abundance. Thirty-seven percent of abundance and 62% of landings time series contained evidence of nonlinear behaviour (Fig. 4). Landings series were 2.5 times more likely

(odds ratio, $P = 0.09$) than abundance series to exhibit nonlinear behaviour, and fished taxa were 3.6 times more likely to have nonlinear dynamics than unfished taxa ($P = 0.02$; Table 2).

Altogether, 70% of time series (145 of 206) were classified as predictable according to the maximum *forecast skill* achieved by S-map using a 1-year forecast horizon. Landings data were least likely to be predictable ($P < 0.001$; Table 2): only 56% of landings time series were predictable, whereas 83% of abundance series were predictable. The percentage of time series that produced significant ρ , and were thus labelled predictable, declined significantly over a 5-year forecast horizon (Table 3). Likewise, maxi-

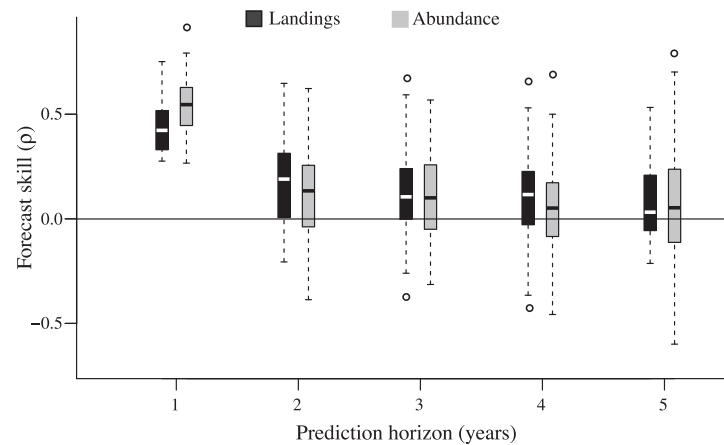


Figure 5 Trends in forecast skill (ρ) as the time horizon (prediction time, t_p) over which forecasts are made increases.

Table 3 Percentage of time series (of 206 total) producing statistically significant ($P \leq 0.05$) forecasts over increasing time horizons.

	Year 1	Year 2	Year 3	Year 4	Year 5
Landings	56.4	21.3	13.8	18.1	13.8
Abundance – fished	86.0	17.5	15.8	12.3	17.5
Abundance – unfished	80.0	21.8	20.0	16.4	16.4
Combined	70.9	20.4	16.0	16.0	15.5

mum ρ for a given taxa declined rapidly in both landings and abundance series over 5 years (Fig. 5). Finally, series for which nonlinear dynamics were detected had higher ρ for 1-year-ahead forecasts in both abundance and landings time series (Fig. 6).

Of 51 paired abundance-landings series, 25 produced significant forecasts ($P \leq 0.05$) for both

members of the pair. Accordingly, the power of paired statistical tests was considerably reduced relative to the full data set. Nevertheless, results were consistent with the full data set (Table S2). Abundance series had significantly lower E values than landings series (Wilcoxin rank test, $P = 0.049$). Nine abundance series had nonlinear dynamics (36%), while 14 landings series had nonlinear dynamics (56%). These percentages are similar to those in the full dataset, but we could not detect a statistical difference between the groups (Cochran's Q test, $P = 0.13$). However, of the 14 nonlinear landings series, only six counterpart abundance series had nonlinear dynamics and eight counterparts had linear dynamics. In contrast, of the 11 linear landings series, eight abundance counterparts had linear dynamics and only three had nonlinear dynamics. That is, we were unlikely to find a linear landing series paired with a nonlinear abundance counterpart. Finally, forecast skill in landings data was significantly lower than for abundance data (t -test, $P = 0.022$).

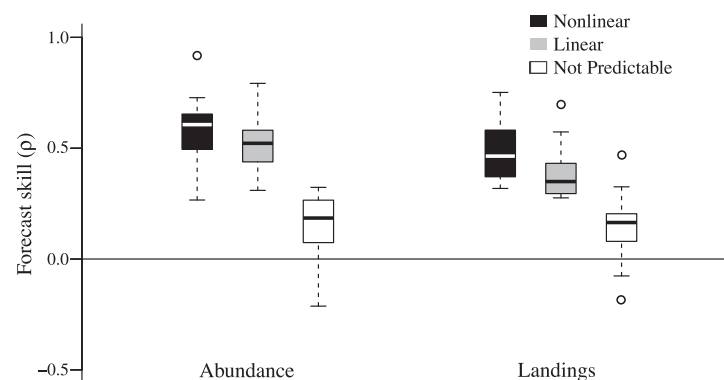


Figure 6 Forecast skill achievable when predicting over a 1-year horizon. Dynamics were classified as linear or nonlinear.

Discussion

Dynamic complexity reflects human intervention in coupled human and natural systems

The recognition that fish populations can exhibit complex dynamical behaviour can be traced to the seminal studies of W.E. Ricker (1954). In the present study, we demonstrate the dynamics of fisheries systems as represented by landings are significantly different from the dynamics of the underlying fish populations, perhaps reflecting the influence of human intervention. To our knowledge, this is the first cross-system comparative study, and the first at the scale of individual species, to analyse empirically the dynamic complexity observed in fisheries data and to use a uniform modelling approach to quantify predictability. We compared over 200 time series, including invertebrates, mesopelagic fishes, ground fishes, small pelagic fishes and highly migratory top predators, from two ecologically distinct coastal ecosystems to demonstrate robust patterns in complexity related to the method of observation (landings vs. abundance) and exploitation status. Differences in system dimensionality and nonlinear dynamics were associated with time series that reflected human intervention via fishing effort, implying the coupling between human and natural systems generated dynamics distinct from those detected in the natural subsystem alone. While such patterns have been hypothesized and shown theoretically (Horan *et al.* 2011), empirical evidence is more rare (Benton *et al.* 2006; Liu *et al.* 2007).

The differences in embedding dimension, related to data type and exploitation status, add nuance to our understanding of the effects of fishing on populations. While there is not a direct one-to-one relationship between the real dimensionality of the system and that estimated by E (see Whitney embedding theorem), results indicate relatively more interacting processes created the observed landings dynamics and therefore models of landings require more information (Bjornstad and Grenfell 2001). Those dimensions could be the effects of regulation, input costs or market prices on fishing effort (Liu *et al.* 2007) in addition to the variables that control fish abundance. Contrary to expectations, however, estimates of abundance for fished species had lower dimensionality than unfished species. If the dimensions of the systems were merely additive, we would expect abundance of fished spe-

cies to have E intermediate between unfished abundance and landings. Consequently, the patterns we observed may emerge uniquely at these different scales of observation. We speculate that fishing acts to simplify (reduce) the processes controlling exploited species relative to unexploited species. If so, this could represent a loss of resiliency or redundancy in the system as a result of reduced population sizes (Walker *et al.* 2004; Hsieh *et al.* 2006).

Exploitation was associated with a higher likelihood of detecting nonlinear dynamics when observing the natural resource subsystem through abundance metrics, but when exploitation was observed as landings that integrate the influence of social processes, nonlinear dynamics were even more likely. Complex dynamics in fishery-level metrics such as landings could arise because the underlying resource exhibits nonlinear behaviour that is then reflected in the fishery metric (Royer and Fromentin 2006; Anderson *et al.* 2008; Glaser *et al.* 2011). Yet, we found nonlinear dynamics were less common in the resource. This suggests a unique contribution of the human-governed subsystem to fishery dynamics. Various feedback mechanisms could explain these patterns. For example, a positive feedback loop between resource abundance and fishing effort induced chaotic behaviour in *Dungeness crab* (Berryman 1991). Anderson *et al.* (2008) showed that a higher intrinsic rate of population growth, resulting from age-selective harvesting, explained greater nonlinearity in exploited fishes. Steele and Henderson (1984) demonstrated the addition of noise to otherwise stable equilibrium fisheries models created alternate stable states, and Shelton and Mangel (2011) linked fishing mortality to higher observed CV in fished populations. We speculate that processes producing linear dynamics in the fishery are stabilizing feedbacks, while those that result in nonlinear dynamics are destabilizing. For example, natural sources of mortality such as predation and disease are endogenous to the evolution of fish populations, while fishing mortality reflects exogenous forces that have only recently (on evolutionary time scales) interacted with fish populations. Perhaps the natural mortality imposed within the resource subsystem produces, on balance, systems that appear to be linear (Fussman and Heber 2002), but fishing mortality imposed from outside the system interacts in a fundamentally different way to produce nonlinear dynamics (Chapin *et al.* 2006).

We failed to detect nonlinear dynamics in 63% of abundance series. However, the importance of nonlinear dynamics in 37% of abundance time series (and, in particular, in 47% of abundance time series of fished species) should not be discounted (Sugihara *et al.* 2011). Nearly half of all fished species contained nonlinear dynamics, predisposing them to rapid and unpredictable population fluctuations that can severely impact food security and economic well being (Mullon *et al.* 2005) and highlighting the short time horizon over which these populations may be predictable. Evidence of nonlinear dynamics in terrestrial organisms is more rare: Turchin and Taylor (1992) found only one example of chaotic dynamics in 36 species. The methodologies employed in this study are not the same as those used by Turchin and Taylor. However, the different degrees of nonlinear dynamics may highlight the direct effects of commercial hunting on wild fish populations compared with indirect effects of humans on wild terrestrial species. That is, the harvesting of reproductively active individuals by fishing may be more likely to induce nonlinear behaviour in a population compared with indirect effects on mortality resulting from pollution or habitat destruction.

While transitions between multiple basins of attraction are not inevitable in complex adaptive systems, the potential for rapid and unanticipated shifts in state are particularly problematic for resource managers (Mullon *et al.* 2005; Vert-pre *et al.* 2013). Nonlinear dynamics make rapid transitions between ecosystem states more likely (Scheffer *et al.* 2001). While this analysis is not a test of the occurrence of regime shifts, it does test for the presence of dynamics that are necessary (but not sufficient) for a regime shift to occur (Hsieh *et al.* 2005b). Methods to detect incipient transitions in time series observations have been explored (e.g. Mantua 2004; Biggs *et al.* 2009; Scheffer *et al.* 2009) and should be used routinely in resource assessment as potential early warning systems. Evidence of increased variance and autocorrelation in indicator series has been linked to the onset of regime shifts in some systems (Carpenter and Brock 2006). However, regime shifts are notoriously difficult to predict (Collie *et al.* 2004), particularly in short, noisy time series, and therefore an important commitment to both precautionary and adaptive management strategies is essential.

Prediction and implications for fisheries assessment models

While there is widespread agreement that long-term (>10 years) prediction in fisheries is limited, here we demonstrate that medium-term (2–5 years) prediction also is limited. The implications of our findings are three-fold. First, asking assessment scientists to predict changes in abundance beyond a few years' time may be unrealistic if nonlinear dynamics are manifest in the system. Second, while long-term prediction generally is not possible in nonlinear systems, short-term predictions (1–2 years) are attainable when the correct models are applied. Third, the dynamic differences between landings and abundance time series should be considered when implementing assessment models.

The establishment of overfishing limits, mandated by the Magnuson-Stevens Act re-authorization, requires the estimation of current fish biomass and the projection of biomass into the future. S-map produced statistically significant predictions 1 year ahead for 83% of abundance time series (and only 56% of landings series), but *forecast skill* declined significantly over 5 years. Although there have been evaluations of the quality of predictions in fisheries (Frank 1991; Brander 2003; Ralston *et al.* 2011; Vert-pre *et al.* 2013), these focus exclusively on within-sample or between-model performance. Most studies examine uncertainty surrounding prediction of unknown biomass given different parameter values, model specifications or data. To our knowledge, there has been no systematic attempt to compare, for a large range of species, the predictions made by assessment models to subsequent observations. Our results demonstrate increasing forecast error for both indices of abundance and landings as prediction horizons lengthen; this would translate into even greater forecast error for estimates of total biomass in traditional assessment models. However, both the overall level of exploitation and demographic selectivity patterns can determine the degree to which fishing will contribute to the emergence of nonlinear dynamical behaviour (Ricker 1954; Basson and Fogarty 1997) and can, in theory, be used to manage some aspects of this interactive process.

Over 1-year horizons, nonlinear models produced better forecasts for species with nonlinear dynamics than linear models did for species with

linear-stochastic dynamics. In a system with nonlinear dynamics, a linear model should fail rapidly, while a nonlinear model will make good predictions over short time horizons (Sugihara 1994). We found series with strong nonlinear dynamics demonstrated a drop-off in ρ , consistent with theory (Abarbanel *et al.* 1990). For series with linear dynamics, the same observed drop-off could be due either to poorly resolved attractors (high levels of noise). The value of ρ achieved with our models quantifies the variability in the system explained by deterministic dynamics. Thus, $1 - \rho$ gives a relative level of noise or undefined dynamics in a system (Bjornstad and Grenfell 2001). While 70% of time series were deemed 'predictable', the low values of ρ (overall average = 0.39) suggest a strong noise component to the data.

Traditional approaches to stock assessment may fail for some species. For one, the inclusion of many parameters may overfit data and fail to improve out-of-sample forecasting for low-dimensional systems. Nonlinear forecasting models allow researchers to be agnostic to the structure or functional form of population models, which is advantageous when systems are underdetermined. Our phenomenological approach uses structurally identical models with only two unknown parameters (E and θ) estimated directly from the data rather than life history parameters that are estimated, measured or tuned. There is also no assumption of equilibrium in our models. In dynamic systems, sensitivity to initial conditions means the evolution of the system changes its properties so that estimates made in the past may no longer be appropriate (Hastings *et al.* 1993; Ellner and Turchin 1995). In nonlinear forecasting models, this is overcome by weighting local information over global information and re-estimating coefficients for each prediction vector.

We provide evidence of higher nonlinearity and dimensionality in landings time series relative to abundance estimates for the same species/stocks. We posit this reflects the layered complexity of the fishery system as a whole, through which nonlinearities can occur at one or more steps in the chain of events leading to landed fishes. Mullan *et al.* (2005) demonstrated a greater risk of fisheries collapses in systems with chaotic signatures in landings data; however, their observed patterns may overestimate the likelihood of collapse in abundance. Both landings and fishery-independent abundance estimates often are used in traditional stock assessment methods. In some cases, particu-

larly in data-limited situations, landings are used directly to make inferences about underlying abundance levels. It is clear, however, that landings can reflect more complex interactions within the coupled social-ecological system comprising the fishery. Ralston *et al.* (2011) pointed out that, paradoxically, assessments for data-rich species may produce higher levels of uncertainty than for data-poor species because the former include uncertainty associated with a greater number of parameters (such as life history or environmental variables). Our results demonstrate, to the contrary, that data-rich assessments using survey-derived indices of abundance should have greater *forecast skill* and therefore lower uncertainty (a point also made by Ralston *et al.* (2011)).

Operationalizing the precautionary principle

Nonlinear forecasting models overcome many challenges stemming from structural uncertainty in mechanistic models. Uncertainty in fisheries models can arise in estimates of biomass, model structure and parameter estimates, fishing effort and the role of climate (Hilborn and Peterman 1996; Ralston *et al.* 2011). Caddy and Seijo (2005) point out that stock-recruitment relationships estimated during periods of high spawning stock biomass may no longer be valid for some stocks, leading to an overestimation of abundance. As mechanistic models become more complex by incorporating species interactions and climate effects, the number of estimated parameters also increases, propagating uncertainty.

The precautionary principle, when applied to fisheries management, suggests a conservative approach to setting overfishing limits given uncertainty in abundance (Hilborn and Peterman 1996; Barkely Rosser 2001). In practice, this often translates into catch targets some fraction below the optimal yield estimated from stock assessment models (e.g. a buffer of 75%). Caddy and Seijo (2005) coined the phrase 'operationalizing the precautionary approach' as a means of expanding the ways in which the principle could be applied to fisheries. The application of nonlinear forecasting models to fisheries data is a novel way in which the precautionary approach could be further incorporated into management. The models quantify how far into the future reliable forecasts can be made and thus provide a measure of forecast error, an important and relatively unexamined

component of assessments [Ralston *et al.* (2011); but see Shertzer *et al.* (2008) for an example of forecast error given parameter uncertainties]. For the vast majority of species examined here, the precautionary approach would suggest we make predictions about landings or abundance only 1–2 years into the future.

Examination of forecasts can identify further whether models are overestimating or underestimating changes in abundance and landings. Because our models produce cross-validated forecasts of each time step in a series, out-of-sample forecasts can be compared to observations of the data at each time step. Rather than having simply an estimate of how well the model does on average (such as indicated by ρ), we also can quantify how well the model performs for each of N observations. For example, a measure of mis-estimation can be calculated as

$$\text{Mis-estimation}(x_t) = \frac{(\text{forecast}(x_t) - \text{observed}(x_t))}{\text{observed}(x_t)}.$$

This calculation is similar to mean absolute percentage error traditionally used to assess accuracy of time series models, but it is calculated at each value rather than summing over all values and demonstrates in which direction (positive or negative) the mis-estimation occurs.

The tendency for the model to mis-estimate the observed dynamics can be directly translated into an application of the precautionary approach. Figure 7 shows measures of model mis-estimation for survey abundance indices of three fished species. Recall that analysis was completed on first differences and we are therefore forecasting positive or negative changes in landings or abundance. Of most concern are overestimates of positive changes, in which case catch limits might be set too high (Fig. 7, blue circles), or underestimates of negative changes, in which case crashes are unanticipated (Fig. 7, red circles). Of less concern, from a precautionary point of view, are underestimates of ups or overestimates of downs (Fig. 7, black circles) because these mis-estimates will not result in changes to catch targets that will lead to overexploitation. (The corollary, of course, is that economic efficiency may be sacrificed in this rubric, but such a risk is inherent in the precautionary approach). Model tendencies like those seen in the Pacific sardine (*Sardinops sagax*, Clupeidae) suggest there is wide mis-estimation of ups and downs, so

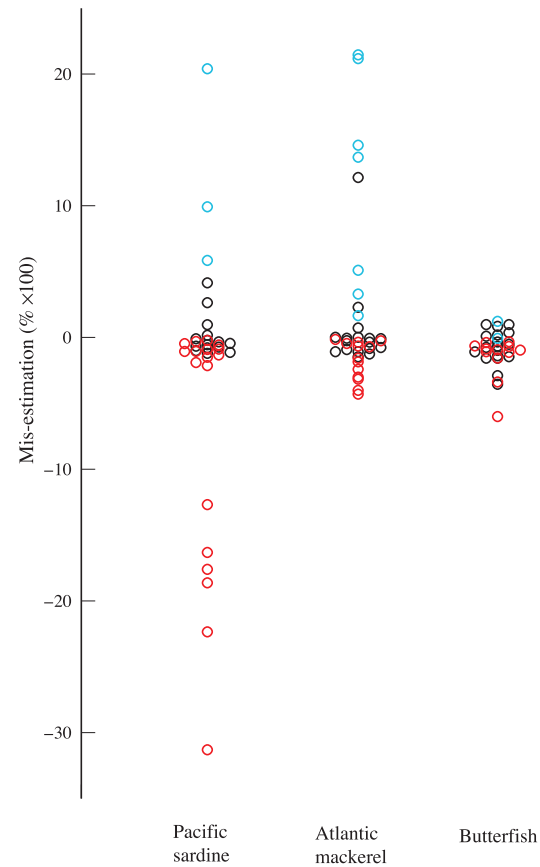


Figure 7 Forecast mis-estimation can inform uncertainty. In an application of the precautionary principle, we should minimize overestimating future positive changes in abundance (blue circles) and minimize underestimating future negative changes in abundance (red circles). Mis-estimation could be symmetrical, as in the model for Pacific sardine (*Sardinops sagax*, Clupeidae). Or, forecasts could significantly overestimate ups but more accurately estimate downs, as in the model for Atlantic mackerel (*Scomber scombrus*, Scombridae). Finally, forecasts could be well-estimated, as in the model for butterfish (*Peprilus triacanthus*, Stromateidae).

catch targets should be conservative and the buffer large (Fig. 7a). Tendencies like those seen in the Atlantic mackerel (*Scomber scombrus*, Scombridae) suggest the model is correctly estimating downs but significantly overestimating ups (Fig. 7b). Finally, tendencies like those seen in butterfish (*Peprilus triacanthus*, Stromateidae) suggest the model is consistently and reliably estimating both the ups and downs (Fig. 7c), and the buffer might be smaller. Depending on the species under assessment and the acceptable risk of overfishing, these estimates of

forecast mis-estimation can be used to place bounds on certainty and quantify catch limit buffers.

As fisheries adopt new approaches to ecosystem-based management, indicators of human-ecological interactions are important for developing practical frameworks (Leslie and McLeod 2007; Ralston *et al.* 2011). Of great importance is the recognition and acceptance that our ability to model complex systems with incomplete datasets, and therefore to make predictions for adaptive management, may be more limited than we would prefer. For example, the Magnuson-Stevens Act requires 10-year rebuilding plans for species deemed over-exploited. While setting such goals is critical, 10-year-ahead predictions based on current data should be treated as moving targets. The price of living in a complex world is sustained vigilance through effective monitoring, rapid responses to shifting resource conditions, and preservation of ecological resilience in the face of profound transformations in both the state of a resource and the nature of its supporting ecosystem.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Each species or stock analysed in this study and results of simplex projection and S-map modeling, as well as the values of explanatory variables used in generalized linear model analysis.

Table S2. Results of paired analyses to compare nonlinearity, dimensionality, and forecast skill for abundance and landings in the same species.