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Nonparametric modeling reveals environmental effects on bluefin tuna recruitment in Atlantic, Pacific, and Southern Oceans

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ABSTRACT

Environment-recruitment relationships can be difficult to delineate with parametric statistical models and can be prone to misidentification. We use nonparametric time series modeling which makes no assumptions about functional relationships between variables, to reveal environmental influences on early life stages of bluefin tuna and demonstrate improvement in prediction of subsequent recruitment. The influence of sea surface temperature, which has been previously associated with larval growth and survival, was consistently detected in recruitment time series of bluefin tuna stocks that spawn in the Mediterranean Sea, the North Pacific, and the Southern Ocean. Short time series for the Gulf of Mexico stock may have precluded a clear determination of environmental influences on recruitment fluctuations. Because the nonparametric approach does not require specification of equations to represent system dynamics, predictive models can likely be developed that appropriately reflect the complexity of the ecological system under investigation. This flexibility can potentially overcome methodological challenges of specifying structural relationships between environmental conditions and fish recruitment. Consequently, there is potential for nonparametric time series modeling to supplement traditional stock recruitment models for fisheries management.

KEYWORDS

Sea surface temperature, tuna fisheries, nonlinear modeling, *Thunnus thynnus, Thunnus orientalis, Thunnus maccoyii*

Introduction

Since the Thompson-Burkenroad debates, the relative importance of environment versus fishing on the variability of fisheries has remained both unresolved and highly contentious (Burkenroad, 1946; Thompson and Bell, 1934; Vert-pre et al., 2013). Variability in year class strength of fishes can depend on exploitation patterns and biological and environmental conditions, including those experienced during early life stages (Cushing, 1969; Hjort, 1926; May, 2011). Among biological contributions to year class variability, egg production and early life stage starvation, predation, and cannibalism have formed the basis of stock-recruitment theory (Beverton and Holt, 1957; Ricker, 1954; Shepherd and Cushing, 1980). With regards to environmental contributions, there is renewed interest in environmental effects on recruitment variability, as lengths of environmental and fisheries time series continually increase. Recent reconsideration of time series such as the RAM legacy database has rekindled the environment-fisheries debate and has suggested that the environment does, in many cases, have a substantial impact on fisheries productivity (Ricard et al., 2012; Szuwalski et al., 2015). The multitude of environmental time series available for evaluation almost always leads to multiple hypothesis testing, which requires correcting for the level of significance (Dunn, 1961). Accordingly, even when significant correlations are found, they do not necessarily imply causation.

A variety of parametric statistical methods have been considered in evaluating whether environmental conditions influence recruitment (Alheit and Hagen, 1997; Govoni, 2005; Myers et al., 1993; Quinn and Deriso, 1999). Problematically, evidence of environment-recruitment relationships can appear to be ephemeral, existing as positive correlations at some times and as negative correlations at other times (Beamish et al., 2004; Carscadden et al., 2000; Myers, 1998; Ravier and Fromentin, 2004). The ephemeral nature of environment-recruitment relationships can reflect the presence of nonlinear dynamics and weak coupling among variables, both of which are typically not amenable to modeling through linear (additive) statistical methods (Clark et al., 2015; Glaser et al., 2014a; Hsieh et al., 2008; Sugihara et al., 2012). As an alternative to parametric empirical analysis, nonparametric approaches are demonstratively useful in detecting ecological interactions (Glaser et al., 2014b; Liu et al., 2014; Perretti et al., 2013).

Advances in nonparametric time series modeling have improved our ability to distinguish causative relationships from spurious correlations (Sugihara et al., 2012). In addition, where parametric modeling may be insufficient to capture complex dynamical interactions in natural systems, a more robust approach is offered via nonparametric empirical dynamic modeling (EDM; Deyle and Sugihara, 2011; Deyle et al., 2013). Complex dynamics are pervasive in marine environments and arise because of high system dimensionality (i.e. the number of interacting processes in natural systems, including fishery exploitation) and the interdependence of variables that produce nonlinear population dynamics (Anderson et al., 2008; Glaser et al., 2014a; Hsieh et al., 2005; Liu et al., 2012; Steele and Henderson, 1984; Walters and Collie, 1988). As a nonparametric method, EDM offers considerable modeling flexibility because no *a priori* sets of equations are needed to represent system dynamics (e.g. structural modeling equations). Instead, EDM relies on the structure of the data to identify interacting variables by utilizing dynamical similarities between sequences of observations, which can accordingly accommodate a variety of dynamical system behaviors (Glaser et al., 2011; Perretti et al., 2013).

In traditional fisheries stock assessments, recruitment of fish to the population is modeled as a parametric function of the spawning stock size through a stock-recruitment relationship, for which the strength, functional form or even existence of a relationship remains a fundamental source of uncertainty (Gilbert, 1997; Maunder and Deriso, 2003; Myers and Barrowman, 1996). Further, as the stock recruitment relationship defines the benchmarks by which stock status is evaluated and forms the basis for projected future recruitment levels that determine allowable catches, it remains highly controversial (Rose et al., 2001). Few species epitomize the controversial nature of assumptions surrounding the stock-recruitment relationship as the global bluefin tuna stocks which include the eastern and western Atlantic (*Thunnus thynnus*, Scombridae), Pacific (*Thunnus orientalis*) and Southern Oceans (*Thunnus maccoyii*). Assessments of Western Atlantic bluefin tuna have struggled for many years with the divergent high versus low recruitment hypotheses with little resolution (Fromentin, 2002; Rosenberg et al., 2013) and likely little potential for resolution through classical parametric stock-recruitment model fitting approaches (Porch and Lauretta, 2016). For this reason, and as many of the early life history processes that define appropriate larval survival appear to be environmentally driven, bluefin tuna represent an excellent focal species for demonstrating how nonparametric EDM approaches can be used to identify environmental variables that improve recruitment predictions.

Bluefin tuna spawn in narrowly defined geographic areas (Block et al., 2005; Farley and Davis, 1998; Garcia et al., 2005; Satoh et al., 2008). We leveraged these four well-defined spawning distributions to reveal a consistent pattern in relationships between sea surface temperature (SST) occurring in spatiotemporal proximity to larval abundance and subsequent recruitment to the fishery. SST has been an important environmental factor in descriptions of bluefin tuna spawning and larval habitat (Alemany et al., 2010; Davis et al., 1990; Garcia et al., 2005; Muhling et al., 2012; Satoh, 2010; Tanaka et al., 2007; Teo et al., 2007). Prevailing environmental conditions are proposed to influence growth and survival in a density-dependent manner (Bakun, 2013; Bakun and Broad, 2003; Masuda et al., 2002; Matsuura et al., 1997; Reglero et al., 2011; Tanaka et al., 2006; Young and Davis, 1990). Consequently, our study is less about addressing an ecology gap in defining larval tuna habitat, and more about demonstrating the utility of nonparametric predictive models that reflect the complexity of the ecological system under investigation. Given the potential complexity of larval bluefin tuna ecology, it may be unreasonable to expect relationships between environmental conditions and recruitment to align with simple mechanistic models (Bakun, 2010; Fromentin and Restrepo, 2001). Accordingly, we demonstrate the utility of nonparametric time series modeling and compare models that include environmental variables to those that do not. Nonparametric predictive performance is also compared with a parametric stock-recruitment model. Finally, EDM is used to demonstrate how model predictions and related uncertainty measures can be useful in conveying scientific advice.

Methods

Time series of recruitment estimates and fishery-dependent recruitment indices

Age-1 recruitment for the eastern Atlantic stock that spawns in the Mediterranean Sea and for the western Atlantic stock that spawns in the Gulf of Mexico were both estimated using virtual population analysis that did not impose a stock-recruitment function (Table 1). We excluded years 2004-2013 from analysis of the eastern Atlantic stock to avoid estimates that were potentially prone to retrospective bias, a condition where the estimated values change depending on the terminal year of the assessment (Anonymous, 2014a; Mohn, 1993). Age-0 recruitment for the Pacific stock was estimated using a fully-integrated stock assessment model, from which 1952 and 2009-2012 were excluded to avoid retrospective bias (Anonymous, 2014b). Terminal and, sometimes, initial years of recruitment are often poorly informed by data, hence a common practice is to consider estimates for these years as unreliable (Anonymous, 2014a). Stock assessment of Pacific bluefin tuna incorporated a Beverton-Holt stock-recruitment function (Methot and Taylor, 2011); however, alternative versions of this assessment that did not functionally constrain recruitment estimates produce nearly identical results (M. Maunder, personal communication). Thus, Pacific recruitment estimates were thought to reflect environment and spawning conditions rather than being affected by an assumed stock-recruitment relationship. Age-0 recruitment for Southern Ocean bluefin tuna was also available from a stock assessment (Anonymous, 2014c).

By necessity, recruitment estimates used in this analysis were model-derived products rather than empirical measures of recruitment, though they are little constrained by a stock-recruitment relationship. Recruitment estimates integrated multiple sources of information such as age or length composition and relative abundance indices to obtain consistent estimates of recruitment. Ideally we would want to consider only empirical indices of recruitment, however, despite the global importance of bluefin tuna there exist very few long-term scientific surveys and few that would permit, either by length of time series or by perceived reliability as indicators of recruitment, exploration using EDM. EDM tends to perform better on time series that are longer than 40 observations (Glaser et al., 2011, 2014a; Sugihara et al., 1996). Most of the other indices that exist generally are fishery-dependent and reflect multiple age classes. Even the single scientific survey for western Atlantic bluefin tuna- a larval index – is considered a better indicator of the spawning stock than of recruitment. This leaves only two indices – an age-0 trolling index in the Pacific Ocean and the Spanish baitboat index for ages 2 and 3 in the eastern Atlantic Ocean – that permit exploration by EDM.

These two fishery-dependent recruitment indices were thus used to further evaluate environmental effects on bluefin tuna recruitment. For the years of 1964 to 2006, an age-aggregated index of 2 and 3 year old fish harvested by the Spanish baitboat fishery was analyzed (Table 1). Although this index begins in 1952 and extends beyond 2006, 1952-1963 and 2007 and beyond were excluded because fleet selectivity changed during these time periods (Anonymous, 2014a). For the north Pacific stock, standardized catch-per-unit-effort for the period of 1980-2012 from the Japanese coastal troll fisheries of Kochi, Wakayama, and Nagasaki Prefectures has been used as an age-0 index in stock assessment and was included in our analysis (Anonymous, 2014b).

Time series of SST

In delineating spatial and temporal extents of SST measurements to be used in the analysis, we utilized spatial information about spawning and larval distributions, as well as temporal information about spawning events, and timing of flexion and gastric development (Kaji et al., 1996; Kitagawa et al., 2010; Sawada et al., 2005). We summarized SST patterns by first taking the broadest possible spatial view, followed by more localized pattern characterization. We constrained the temporal extent of our analysis to months of the year closely preceding, during, and following reported spawning peaks. Non-interpolated monthly mean SST was obtained from the International Comprehensive Ocean-Atmosphere Data Set at 2-degree spatial resolution (ICOADS; National Climatic Data Center). SST at 2-degree grid cell resolution was aggregated into larger bounding boxes using grid cell sample size to compute weighted means and variances. We also obtained seasonal and annual indices of Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation (PDO); these broad-scale climate indices are particularly useful to consider because they are readily available for testing, and can represent the combined effects of a range of regional-scale processes thought to affect recruitment success.

Atlantic bluefin tuna spawn in the Mediterranean Sea in June and July in proximity to the Balearic Archipelago and eastward towards Sicily (Garcia et al., 2005). We delineated a bounding box surrounding the Balearic Archipelago (35^o to 43^o North and -5^o to 8^o East) and three sequentially smaller boxes covering the south-west Mediterranean Sea, the extent of surveys conducted by the *Instituto Español de Oceanografía*, and an area south of the archipelago where high larval densities have been reported (Fig. 1A; Alemany et al., 2010; Garcia et al., 2005). In the Gulf of Mexico, larval bluefin tuna tend to occur in the Loop Current (LC) front and in the boundaries of anticyclonic mesoscale features outside of the LC region of influence (Lindo-Atichati et al., 2012). Spawning occurs during the months of April, May, and June (Block et al., 2005). Four bounding boxes were specified, the largest of which encompassed the northern Gulf of Mexico (25^o to 29^o North and 265^o to 276^o East), followed by the region of immediate influence (ROI) of the spring LC, the area west of the LC where spawning and larvae have been observed, and an area north of the LC (Fig. 1B; Lindo-Atichati et al., 2012; Muhling et al., 2013; Teo et al., 2007).

North Pacific bluefin tuna spawn in proximity to Chinese Taipei, the Ryukyu Islands, and in the Sea of Japan (Satoh, 2010). Spawning occurs in the Sea of Japan in August and in proximity to the Ryukyu Islands and Chinese Taipei from April to June (Satoh et al., 2008). Larval bluefin tuna have been collected south and east of Chinese Taipei (Itoh, 2006; Kitagawa et al., 2010). We specified four bounding boxes, the largest of which encompassed the East China Sea (22^o to 38^o North and 123^o to 142^o East), followed by an area surrounding the Ryukyu Islands, the area east of Chinese Taipei, and the area in the eastern Sea of Japan (Fig. 2A). Southern Ocean bluefin tuna spawn in a narrow area between northern Australia and the Indonesian Island chain west of Java during a protracted season that occurs from September to March (Farley and Davis, 1998; Farley et al., 2014). Larvae have been collected between 7^{o} to 20^{o} South and 102^{o} to 124^{o} East (Farley and Davis, 1998) and a spatial bounding box was defined for this area (Fig. 2B).

Detecting environmental effects on recruitment

The underlying premise of nonparametric time series modeling is that dynamical sequences of observed events arise from latent ecological and environmental processes. If a response process, like fish abundance, is influenced by a forcing process, then fish abundance should contain information about the forcing process in addition to information about its own internal dynamics (Sugihara et al., 2012; Takens, 1981). Taken's (1981) theorem shows that time-delayed coordinate embedding captures properties of the original dynamic system. Time-delayed embedding involves transforming a time series into a set of time-delayed coordinate vectors, $\mathbf{X}_t = \left[x_t, x_{t-\tau}, x_{t-2\tau}, \dots, x_{t-(E-1)\tau} \right]$, where x is a time series variable of interest, t is time, τ is the time lag, and E is the embedding dimension. The embedding dimension is the number of time-delayed coordinates used in reconstruction (Glaser et al., 2014a; Sugihara and May, 1990).

Simplex projection utilizes the idea that coordinate vectors that are similar at time t are also expected to have similar trajectories at $t+1$. In generating predictions, different values of the embedding dimension E (integers between 1 and 10) were evaluated to determine the dimensionality that provides best prediction skill. To calculate prediction skill, coordinate vectors were divided into sets of library vectors (to build the model) and prediction vectors (to test the predictive skill of the model). Prediction skill was calculated as the Pearson correlation coefficient (ρ) between observed and predicted values. Euclidean distance was calculated between the prediction vector $\mathbf{X}_t$ and all library vectors, and the $E+1$ nearest library vectors to the prediction vector were identified. The forward trajectories of the nearest neighbors, $x_{j,t+1}$, where j denotes the index of the $E+1$ neighbors, were then used to generate weighted predictions, $\hat{x}_{t+1}$, for $\mathbf{X}_t$:

$$\hat{x}_{t+1} = \left(\sum_{j=1}^{E+1} w_{j,t} x_{j,t+1} \right) \Big/ \sum_{j=1}^{E+1} w_{j,t} . \quad (1)$$

Weights are $w_j = \exp\left(-d\left(\mathbf{X}_t, \mathbf{X}_j\right)/\bar{d}\right)$, which is the Euclidean distance, $d\left(\mathbf{X}_t, \mathbf{X}_j\right)$, to neighbor vector j relative to the nearest neighbor vector $\bar{d}$. Because our recruitment time series tended to be short, predictions were made using leave-one-out cross-validation, rather than splitting the datasets into library and prediction vectors. All analyses were conducting in the R statistical computing environment using the rEDM library (R Development Core Team, 2012; Ye et al., 2015a). Data were first-differenced ($\Delta x = x_{t+1} - x_t$) and normalized (mean = 0, standard deviation = 1). It is a typical practice in EDM to first-difference and scale data inputs, as scaling allows time series comparison in relative terms and differencing addresses nonstationarity.

To determine whether environmental signals could be detected in recruitment dynamics, we used Convergent Cross Mapping (CCM; Sugihara et al., 2012). CCM is simplex-based EDM technique that was used to address whether a response time series can be used to reconstruct a forcing time series. This approach may appear counter-intuitive, but corresponds to Takens's theorem that a response process should contain an information signature about a related forcing process (Sugihara et al., 2012). In addition, time delays (lags) in cross-mapping are informative in understanding the timing of effects between variables (Ye et al., 2015b). Time series of sequentially increasing length, L, were used to reconstruct the forcing variable and to evaluate the presence of convergent behavior, i.e. that prediction skill improves as L increases. This criteria is used to distinguish causality from simple correlation, because prediction skill should increase as more information is included in the analysis (Sugihara et al., 2012). All possible library vectors of length L were compared to the prediction data, which results in n estimates of prediction skill. Convergence was considered to occur if mean prediction skill at the longest L was greater than 0 (i.e. centered 80% of n observations did not include 0) and greater than prediction skill at the shortest L (Clark et al., 2015).

Short-term forecasting using environmental indices

While CCM is useful for detecting relationships between variables, it is not designed to generate short-term predictions *per se*. Deyle et al. (2013) describes the related technique of EDM that relies on both the response and forcing data to generate time series predictions. EDM advances Takens's approach to situations where multiple system components are analyzed together (Deyle and Sugihara, 2011). In our analysis, multivariate embedding was constructed that included a forcing variable, y (e.g., $\left[x_t, x_{t-\tau}, x_{t-2\tau}, \ldots, x_{t-(E-1)\tau}, y_t\right]$). While Taken's theorem suggests that information about a forcing variable should already be contained in a response time series, it is not redundant to include stochastic forcing variables in multivariate embedding because stochastic variables lack deterministic signals. Thus, including stochastic variables in multivariate embedding should improve prediction (Deyle et al., 2013).

We included SST variables that were previously selected using CCM analysis in simplex-based EDM and evaluated whether relative improvement in predictive skill was obtained. We first used a null model to calculate probabilities that predictive skill could be improved by an unrelated environmental time series. Permutation testing involved shuffling the actual SST variable, *y*, to remove any relationship with recruitment *x*, and then we included the shuffled variable in predictions of *x*. Then, a null distribution of prediction skill consisting of 1,000 permutations was calculated. The null distribution was used to calculate the probability that null model prediction skill exceeded prediction skill from the actual recruitment and SST time series. EDM predictions were also compared to maximum likelihood fits of a parametric stock-recruitment relationship that included the same SST variables selected using CCM (Bolker, 2015; R Development Core Team, 2012). We used a Ricker functional form for its flexibility to fit different shapes of the stock-recruitment relationships. As the focus of the project was not to explore different functional forms, we did not evaluate the fits of alternative models.

Two additional analyses were carried out to address directionality of recruitment responses to environmental variables and to quantify prediction uncertainty. Firstly, given that EDM enables prediction in a state-dependent manner, directionality of recruitment responses to SST must be determined through *post hoc* analysis, which is termed scenario exploration (Deyle et al., 2013). Scenario exploration proceeds by modifying the actual SST observation at the time lag associated with its effect on a single recruitment data point. A recruitment prediction is made under a small positive SST increase (0.5°C). If a hypothetical increase in SST would have led to a hypothetical increase in predicted recruitment, the relationship at that data point is positive. The process is also repeated using a small SST reduction. This two-step process is repeated at each data point to identify trends in recruitment response directionality, had temperatures hypothetically been cooler or warmer. Secondly, to quantify prediction uncertainty, confidence envelopes were calculated by summing variance terms attributed to (1) recruitment estimation uncertainty, reflecting imprecision of recruitment estimates used as data inputs ($\mathrm{var}(R_{t+1})$) and (2) EDM prediction uncertainty ($\mathrm{var}(\hat{x}_{t+1})$), given an assumed independence between these variance terms. EDM prediction variance was calculated using mean annual recruitment estimates as (Ye et al., 2015a):

$$\mathrm{var}(\hat{x}_{t+1}) = \frac{\sum_{j=1}^{E+1} w_j \left(x_{j,t+1} - \hat{x}_{t+1} \right)^2}{\sum_{j=1}^{E+1} w_j}. \qquad (2)$$

Variance attributed to recruitment estimation uncertainty was quantified using 500 bootstrapped recruitment time series. Bootstrapped estimates reflected the range of likely outcomes of recruitment estimates while incorporating temporal autocorrelation between annual recruitment estimates. Recruitment estimation uncertainty was the variance between point estimates made from each bootstrap iteration.

Observation error effects on prediction skill

Given that employing model-derived recruitment estimates is not ideal, and yet the high level of observation error seen in many fishery-dependent or fishery-independent indices may preclude the detection of any true signal, it was informative to simulate observation error effects on prediction skill. The process of estimating recruitment in stock assessment models is likely to impart some level of autocorrelated error and potentially some bias as the estimates are products of an underlying model structure. Simple time series were simulated using a random walk model of the form $x_t = x_{t-1} + env_{t-1}$, where *env* is a normally distributed white noise process (mean = 0, standard deviation = 0.2) representing an environmental influence on *x*. Observation error was introduced as lognormally-distributed error about the true values $I_t = x_t \exp\left(\varepsilon_t - {}^{\delta^2}\!/\!_2\right)$. Observation deviates, ε_t, were calculated as $\varepsilon_t = \phi\varepsilon_{t-1} + \eta\sqrt{1+\phi^2}$, where η is a normally distributed random deviate with mean 0 and standard deviation δ and ϕ is the autocorrelation coefficient. Simulations consisted of using EDM to reconstruct time series when provided with the observed time series, *I*, and the observed environmental variable, *env*. In these simulations, prediction skill was measured as Pearson correlation coefficient (ρ) between EDM predictions and the true values of variable *x*. Simulations were carried out 1,000 times for combinations of varying levels of δ and ϕ.

Results

Detecting environmental effects on recruitment

Using CCM, a similar pattern emerged for three of four bluefin tuna stocks regarding environmental effects on recruitment. Our analysis of the Mediterranean stock revealed that regional SST series could be reconstructed from recruitment estimates (Table 2). Repeatedly, at each of the four bounding box spatial scales, convergent behavior of CCM was evident in the reconstruction of July SST; a month associated with peak spawning (Fig. 3). Reconstruction of July SST reflected a 1-year time lag in its association with recruitment of 1-year-old fish. This effect of SST on recruitment was unidirectional, meaning that CCM confirmed the intuitive possibility that SST could affect recruitment dynamics, and correctly dismissed the implausible reverse relationship. Our analysis of recruitment in the Gulf of Mexico suggested no dynamic similarity between recruitment and SST for this stock. In the north Pacific, convergent behavior in reconstruction of May SST was evident for the area east of Chinese Taipei (Table 2). At a broader spatial scale, July and August SST could be reconstructed for the bounding box that encompassed the East China Sea. In the north Pacific region, SST reconstructions corresponding to May and July reflect the spawning mid-point and the month immediately following spawning, respectively. In addition, reconstruction of SST in the Sea of Japan most strongly demonstrated convergent behavior during August, which is when spawning has been reported for this region. Analysis of recruitment in the Southern Ocean was more challenging, given the protracted nature of spawning in this region, but nevertheless CCM revealed a signal in recruitment dynamics that was associated with January SST.

In analysis of both Atlantic stocks and the north Pacific stock, convergent behavior was also evident in the reconstruction of ocean basin-wide climatic variability, namely AMO and PDO (Fig. 4). Given the basin-wide effects of these climate variables, the spatial distributions of larval, post-larval, or juvenile stages were of little help for inferring the timing of any effect between climate and recruitment. Instead, we relied strictly on time delays or lags between forcing and response variables. We examined cross mapping skill across a sequence of time delays (-3 to +3 years) between forcing variables and recruitment response. In the Atlantic Ocean, the strongest effect of AMO on Gulf of Mexico and Mediterranean Sea recruitment occurred in winter, with no lag between the forcing variable and the age-1 recruitment response. Fall PDO could be reconstructed from age-0 north Pacific recruitment with no time lag (Fig. 4).

Short-term forecasting using environmental indices

In constructing EDM-based recruitment predictions for each bluefin tuna stock, we took a synoptic view of the spatial extent of SST effects on recruitment, meaning that we assumed that large scale SST should generally affect all larvae in a broad area in a similar way. This approach enabled recruitment predictions to be based upon SST that was coarsely estimated across large ocean expanses. In each oceanic region where spawning takes place, coarse regional temperature signals tended to reflect either the timing of peak spawning or the month immediately following spawning (Fig. 5). In the Mediterranean Sea, recruitment prediction was improved by including July SST in EDM, and null model permutation testing produced a probability of 0.11 that predictive improvement occurred by chance. Likewise, parametric stock-recruitment predictions were improved when July SST was included as a multiplicative environmental effect. Compared to EDM-based predictions, parametric predictions were slightly better (Figs. 5A & 5B). For the north Pacific stock, EDM-based predictions were improved by including SST signals from either the East China Sea in July (bounding box *xii*; null model permutation prob. 0.07) or from the Sea of Japan in August (bounding box *xi*; null model permutation prob. 0.04). Neither SST time series improved parametric stock-recruitment predictions; consequently, EDM-based predictions were better overall (Figs. 5E & 5F). Predictions of Southern Ocean recruitment fared equally between EDM and parametric methods (EDM permutation prob. 0.26).

Using the two fishery-dependent indices, we found convergent behavior (via CCM) for the Mediterranean stock in terms of reconstructing SST signals in months associated with spawning. CCM also revealed signals of AMO (summer, fall, and annual indices) in the Spanish baitboat index, and these effects were detected at time lags of 2 and -3 years, which is not surprising as the index pertains to 2 and 3 year old fish. Evidence of PDO signatures in the north pacific age-0 trolling index were also found using CCM, and the strongest cross-mapping skill occurred for fall PDO, which was consistent with the fall PDO effect identified in the analysis of recruitment estimates. Moving from CCM to construction of predictive models using EDM, predictive skill was only improved slightly when SST was included in EDM-based predictions of the Spanish baitboat index and no improvement was observed for the north Pacific age-0 trolling index. (Table 3).

We used EDM to generate one-year ahead predictions for Gulf of Mexico and Mediterranean Sea recruitment (Fig. 6). Recruitment predictions for the Gulf of Mexico were made without inclusion of SST, as no SST variables improved prediction skill (Fig. 6B). We also used scenario exploration to reveal the underlying directionality of responses between SST changes and recruitment fluctuations (Fig. 7). For the Mediterranean stock, small adjustments to observed SST revealed a negative relationship with recruitment in 63% of predictions and a positive relationship in 37% of predictions. This result suggests that SST may influence recruitment in a state dependent manner. Negative effects of SST on recruitment were more consistently observed for north Pacific stock, with 75% of predictions demonstrating negative relationships with July SST in the east China Sea, and 92% of predictions demonstrating negative relationships with August SST in the Sea of Japan.

Observation error effects on prediction skill

Our simple simulations evaluated the effects of observation error on prediction skill. The first source of observation error was temporal autocorrelation and the second source of observation error was random noise. Temporal autocorrelation had little influence on prediction skill (Fig. 8). Conversely, random observation noise (δ) eroded prediction skill of EDM. When both sources of observation error were introduced using a factorial design, prediction skill was more rapidly eroded as observation noise was increased in comparison to increases in autocorrelation.

Discussion

Using CCM and EDM together, our analysis demonstrated that SST in temporal and spatial proximity to spawning events, improved global prediction of recruitment for three out of four bluefin tuna populations. Short time series for the Gulf of Mexico stock may have precluded a clear determination of environmental influences on recruitment fluctuations. We found comparative effects of SSTs at peak spawning or the month following peak spawning on bluefin tuna recruitment in the Mediterranean Sea, north Pacific, and Southern Ocean, but not for the Gulf of Mexico. Temperature can mediate growth rates, post-flexion survival, onset of piscivory, and cue spawning for bluefin tuna (Evans et al., 2012; Fromentin and Powers, 2005; Reglero et al., 2011; Sawada et al., 2005). As a potential spawning cue, we identified weak SST signals in recruitment time series in the months preceding spawning or associated with the onset of spawning in the Mediterranean Sea, north Pacific, and the Southern Ocean (Table 1). Southern bluefin tuna experience spawning peaks in October and February (Farley and Davis, 1998), suggesting that January SST could reflect either a spawning cue or an effect on recruitment success, or both. Likewise, SST signals in July and August in the East China Sea could be spawning cues, influence larval demography, or both. With respect to forcing by climate indices, our analyses of recruits demonstrated an approximately instantaneous response between climate and age-1 recruitment for both Atlantic stocks. In this instance, a lag of 1 year may be a useful heuristic about the influence of climate sometime during the first year of life, rather than an exacting measure of time lags between events (Ye et al., 2015b). However, the instantaneous response between climate and age-1 recruitment does not preclude the possibility that climate influences catchability, with this effect on data inputs to stock assessment being retained in the recruitment estimates that we analyzed. But notably, the ages-2 and 3 fish captured in the Spanish baitboat indices responded with lags that would reflect the climatic influence on recruitment 2-3 years prior. Similar results have also been obtained for other fishes (Alheit and Hagen, 1997; Hollowed et al., 2001).

Using scenario exploration with EDM we found that, on average, temperature had a negative relationship with Mediterranean Sea and north Pacific recruitment. The state-dependent nature of EDM also revealed reasonably frequent positive recruitment responses to SST. The flexibility of EDM to characterize these relationships illustrates the potential for nonparametric methods to overcome methodological challenges of specifying structural relationships between environmental conditions and bluefin tuna recruitment (Fromentin, 2002; Pepin, 2015). The relative stability of bluefin tuna recruitment (in comparison to other fish stocks) may largely result from density-dependent survival at larval life stages, including interactions among conspecifics that hatch intermittently during a spawning period (Bakun, 2013; Royer and Fromentin, 2006). Bluefin tuna tend to spawn in lower productivity waters where convergence zones in ocean eddies work to aggregate larvae and potentially enhance cannibalism, which has been proposed to regulate recruitment fluctuations (Bakun, 2013; Kaji et al., 1996; Reglero et al., 2011; Young and Davis, 1990). Dynamic feedback between successive hatching of larval cohorts during a spawning period, and the environmentally-driven manipulations of growth and consumptive interactions, together illustrate the complex interdependence among variables that influence recruitment (Catalán et al., 2007). Capturing these potentially nonlinear interactions was accomplished by non-mechanistic approaches such as those employed here.

While our analyses shed some light on the potential environmental processes affecting bluefin tuna recruitment, the purpose of our study was not to construct nonparametric models that reflected all facets the species' larval ecology. Rather, our study was intended to demonstrate a process for identifying whether unique information about environmental time series is contained within a co-occurring biological time series (Sugihara et al., 2012; Ye et al., 2015b). In this sense, variable selection for development of nonparametric models is probably a more important consideration than contrasting predictive skill with parametric approaches. Sugihara et al. (2012) and Ye et al. (2015a) identify several considerations related to variable selection in nonparametric modeling, including the possibility that causative variables may not be informative on their own, but require interaction with other variables (in multivariate EDM, for example) to produce skillful forecasts. Where other variables could be added to our analysis to improve prediction, EDM may be preferable to parametric models because additional variables may reveal nonlinear state-dependent behaviors (Glaser et al., 2014a; Sugihara et al., 2012). Simulation testing conducted elsewhere has similarly shown that parametric fitting can be problematic when applied to nonlinear systems, even when the correct model is known, because useful information can otherwise be classified as observation or process error (Perretti et al., 2013; Ye et al., 2015a). As a caveat, variables that improve prediction do not necessarily imply causality, but these variables may be proxies for more direct causative relationships (Clark et al., 2015; Sugihara et al., 2012). Inclusion of metrics related to eddy activity or to the presence of convergence zones may improve prediction; however, the recruitment patterns that we analyzed predate the satellite era, thus requiring the use of a coarse-scale environmental data set.

If analyses based on high quality satellite-derived products were possible, a clearer signal about environmental relationships could potentially be obtained. In the Mediterranean Sea, the eastward progression of Atlantic surface waters from the Strait of Gibraltar produces meanders that generate mesoscale anticyclonic eddies of diameters of ~100 km to ~150 km that last weeks to months (Garcia et al., 2005; Millot, 1999). Mesoscale eddies vary annually in intensity and in northward intrusion towards the Balearic Archipelago. These eddies create retention zones that may act to enhance biological interactions involving growing larvae (Bakun, 2013; Garcia et al., 2005). Similar zones of retention are created in the Gulf of Mexico, as the spring Loop Current intrudes northward from the Caribbean Sea with an anticyclonic flow that produces mesoscale eddies with diameters >300 km and which propagate westward for periods of days to ~1 year

(Elliott, 1982; Lee et al., 1995; Oey et al., 2003). Likewise, northeastward Kuroshio Currents intersect the Ryukyu Islands and produce mesoscale eddies of at least 500 km in diameter, as does Indonesian current flow between northern Australia and the Indonesian archipelago (Bray et al., 1997; Kimura et al., 2010; Lee et al., 2013; Satoh, 2010; Yang et al., 1999). The physical conditions that arise from the progression of surface waters are likely to influence larval growth (Pepin, 1991; Pepin and Myers, 1991; Reglero et al., 2011). Bluefin tuna larvae have relatively early onset of flexion and gastric development, on the order of 15 days post-hatch, and these developmental events coincide with the onset of piscivory (Kaji et al., 1996; Miyashita et al., 2001). Following these developmental events, larger and faster growing post-flexion individuals survive to subsequent developmental phases (Tanaka et al., 2006). Comparatively, these developmental events appear to align with the timing of SST effects that we identified.

Recruitment forecasting using nonparametric methods has also focused on salmon, for which direct estimates of recruitment back to natal rivers are often available (Ye et al., 2015a). For many species empirical estimates of recruitment are not available; indeed, for highly migratory species such as bluefin tuna, recruitment surveys are usually not feasible. Furthermore, when surveys are available they often have extremely high levels of observation error. While it is desirable to only use empirical data, often their absence and the high level of observation error associated with empirical observations necessitate use of model-based products in subsequent statistical analyses. When such use of stock assessment is unavoidable, it is advisable to: 1) consider uncertainty and bias in the stock assessment estimates themselves, 2) perform cross-validation to evaluate predictive capability, 3) confer directly with analysts involved in the stock assessments, and 4) consider multiple lines of supporting evidence in drawing conclusions (Brooks and Deroba, 2015). Each of these recommendations was followed in this study, and additionally we carried out a simulation analysis evaluating the tradeoff between induced autocorrelation, as might occur with model-based products, and observation error commonly seen in empirical estimates. We might expect model-based products to have reduced observation error but induced autocorrelation due to the modeling process itself. This is certainly the case for western and eastern stocks of Atlantic bluefin tuna where age-slicing of length composition data dampens recruitment signals (Anonymous, 2014a). Observation error may also explain why we observed a small predictive improvement in model-based recruitment and no improvement in the empirical age-0 index for the north Pacific stock. Our simulation indicates that increased observation error erodes predictability of EDM methods relatively quickly, while increased autocorrelation has a more moderate effect on prediction skill. With the appropriate cautions (see Brooks and Deroba, 2015), use of model-derived products may be a viable step toward improving recruitment predictions in cases where no direct recruitment estimates are available or where observation error in empirical estimates is high. We note, however, that our simulation was not exhaustive and did not consider situations where either the model output or the empirical data may exhibit bias; scenarios that would clearly confound the ability to recover the true signal.

Nonparametric approaches encompass a variety of related techniques that enable identification of causal links and can guide the construction of near-term prediction without requiring specification of structural equations (Deyle et al., 2013; Sugihara et al., 2012; Ye et al., 2015b). Such nonparametric approaches do not negate the importance of stock-recruitment functions for fisheries management. To the contrary, deterministic signals pertaining to parent stock strength should be contained in recruitment patterns, as per the theoretical foundation provided by Takens's (1981) theorem. Furthermore, future recruitment is fundamental to fisheries management, with nonparametric methods playing an increasingly relevant role in prediction (Munch et al., 2005). Near-term forecasts made using EDM could be particularly useful in instances where the newest cohorts have not yet become fully vulnerable to fishing, and thus may not be present in catch-at-age matrices. This is indeed the situation faced during stock assessments employing virtual population analysis, such as in assessments of Atlantic bluefin tuna (Anonymous, 2014a). This situation may also arise for assessments in which the newest cohorts are often the least reliably estimated yet have substantial influence on stock abundance and fisheries catches over temporal scales relevant to management (Brooks and Legault, 2015). Lastly, the detected influence of environmental drivers of recruitment in three out of four bluefin tuna stocks is promising for reconciling stock recruitment relationships that have remained so elusive for these species. Incorporating environmental factors such as SST, and likely several other environmental factors, into either a parametric recruitment relationship within a stock assessment model or a nonparametric approach, as done here, may reconcile deviations from a true stock recruitment relationship. Further, greater predictive skill of near-term recruitment may lead to determination of causes of historical changes in recruitment unrelated to spawning stock size, and consequently support improvements to bluefin tuna fisheries management.

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Figure captions:

Figure 1. Bounding boxes used to summarize sea surface temperatures in the Mediterranean Sea (A) and Gulf of Mexico (B). Latitude and longitude in decimal degrees.

Figure 2. Bounding boxes used to summarize sea surface temperatures in the north Pacific Ocean (A) and Southern Ocean north-west of Australia (B). Latitude and longitude in decimal degrees.

Figure 3. Convergent behavior demonstrating improvement of cross-mapping skill as time series library length increases. Convergence reveals forcing of recruitment dynamics by sea surface temperature (SST) through reconstruction of SST time series informed by the recruitment time series.

Figure 4. Cross-mapping skill (Pearson correlation coefficient) of climate variables as a function of cross-mapping lag in years. Closed circles indicating lags exhibiting convergent behavior. AMO is Atlantic Multidecadal Oscillation, PDO is Pacific Decadal Oscillation, Med. is Mediterranean Sea, GOM is Gulf of Mexico.

Figure 5. Comparison of empirical dynamic modeling-based prediction skill (dark red bars and closed circles) to that of a parametric stock-recruitment function (light red bars open circles).

Prediction skill is Pearson correlation coefficient calculated in original recruitment units. Mediterranean Sea recruitment prediction skill with the effect July SST (bounding box *iv*; A & B), Gulf of Mexico univariate prediction skill (C & D), north Pacific prediction skill with E. China Sea July SST (bounding box *xii*; E & F), and Southern Ocean prediction skill with January SST (bounding box *xiii*; G & H). Grey lines in B, D, F and H are observed recruitment.

Figure 6. Empirical dynamic modeling (EDM) predictions that incorporate July sea surface temperature effects on Mediterranean Sea recruits (A; bounding box *iv*) and predictions for Gulf of Mexico recruits based only on recruitment time series (B). Points are mean predictions with +/- 1 standard error. Grey lines are recruitment estimates from stock assessments.

Figure 7. Scenario exploration demonstrating the effects of July sea surface temperature (SST; bounding box *xii*) on Mediterranean Sea recruitment (in first-differenced and normalized units). Scenario exploration adjusts observed SST observations to examine how recruitment predictions would change if SST had been higher or lower (+/- 0.5^{o}C). Original predictions are shown by orange circles. Effects of increasing SST on recruitment are shown by red upward facing triangles and effects of decreasing SST are shown by blue downward facing triangles.

Figure 8. Prediction skill (Pearson correlation coefficient) when simulated random walk time series were subject to lognormally-distributed observation error in the form of correlated random deviates at varying levels of random noise (δ) and autocorrelation (ϕ).

Table 1. Time series of recruitment estimates and fishery-dependent indices.

Time series	**Ages**	**Years included**	**Assessment method**	**Source**
Recruitment estimates				
Gulf of Mexico stock	1	1971-2010	Virtual population analysis	(Anonymous, 2014a)
Mediterranean Sea stock	1	1951-2003	Virtual population analysis	(Anonymous, 2014a)
North Pacific stock	0	1954-2008	Stock synthesis	(Anonymous, 2014b)
Southern Ocean stock	0	1953-2009	Age-structured model	(Anonymous, 2014c)
Fishery-dependent indices				
Spanish baitboat index	2, 3	1964-2006		(Anonymous, 2014a)
Japanese troll fishery	0	1980-2012		(Anonymous, 2014b)

Table 2. Simplex predictions for recruitment estimates using variables selected from convergent cross mapping. n/a is not applicable, box refers to bounding boxes (Figs. 1 & 2), ρ is Pearson correlation coefficient and is calculated in original recruitment units, and univariate refers to the case where no environmental forcing variables are included in state-space reconstruction.

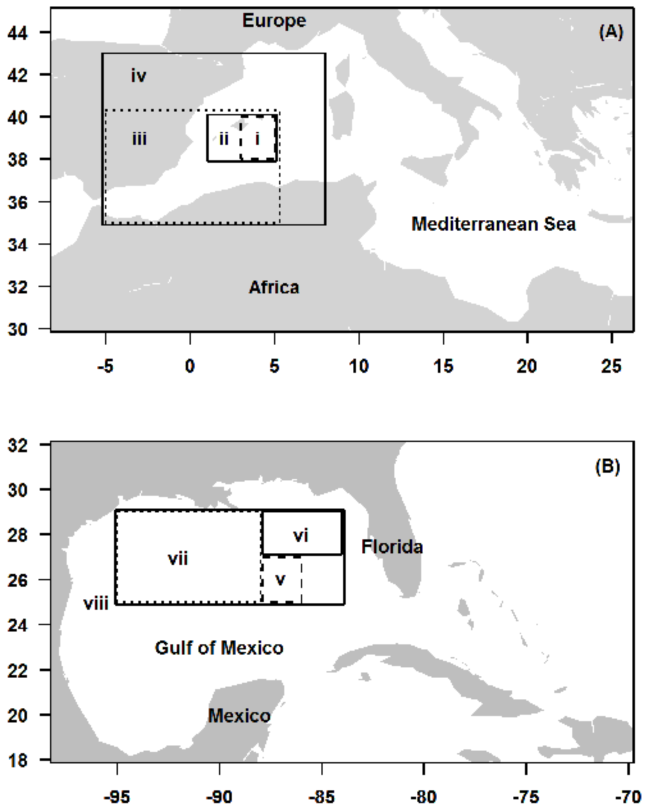
Stock	**Spawn timing**	**Prediction approach**	**Forcing variable**	**Bounding box**	**Forcing lag**	**E**	ρ
Mediterranean Age-1 recruits	Jun-Jul	EDM	Univariate	n/a	n/a	1	0.64
		EDM	July SST	i	-1	1	0.61
		EDM	July SST	ii	-1	1	0.59
		EDM	May SST	iii	-1	1	0.65
		EDM	July SST	iii	-1	1	0.69
		EDM	July SST	iv	-1	1	0.69

Gulf of Mexico Age-1 recruits	Apr-Jun	EDM	Univariate	n/a	n/a	3	0.51
North Pacific Age-0 recruits	Apr-Jun, Aug	EDM	Univariate	n/a	n/a	6	0.00
		EDM	May SST	ix	0	6	-0.03
		EDM	July SST	xi	0	6	-0.02
		EDM	Aug SST	xi	0	6	0.06
		EDM	July SST	xii	0	6	0.03
		EDM	Aug SST	xii	0	6	0.04
Southern Ocean Age-0 recruits	Sep-Mar	EDM	Univariate	n/a	n/a	3	0.73
		EDM	Jan SST	xiii	+1*	3	0.74

*Recruits occurring between September of year x and May of year x+1 are classified as year x, thus +1 lag affects age-0 recruitment.

Table 3. Simplex predictions for fishery-dependent indices using variables selected from convergent cross mapping. n/a is not applicable, box refers to bounding boxes (Figs. 1 & 2), ρ is Pearson correlation coefficient and is calculated in original index units, and univariate refers to the case where no environmental forcing variables are included in state-space reconstruction.

Stock	**Spawn timing**	**Prediction approach**	**Forcing variable**	**Bounding box**	**Forcing lag**	**E**	ρ
Mediterranean Spanish baitboat index	Jun-Jul	EDM	Univariate	n/a	n/a	9	0.07
		EDM	May SST	i	-3	9	0.10
		EDM	June SST	i	-3	9	0.09
		EDM	June SST	i	-2	9	0.08
		EDM	July SST	i	-2	9	0.10
		EDM	May SST	ii	-2	9	0.09
		EDM	June SST	iii	-3	9	0.12
		EDM	July SST	iii	-3	9	0.11
		EDM	July SST	iii	-2	9	0.10
		EDM	May SST	iv	-3	9	0.08
		EDM	June SST	iv	-3	9	0.10
North Pacific Japanese age-0 index	Apr-Jun, Aug	EDM	Univariate	n/a	n/a	1	0.28
		EDM	Mar SST	ix	0	1	-0.18
		EDM	July SST	ix	0	1	-0.14
		EDM	July SST	x	0	1	0.00
		EDM	Mar SST	xii	0	1	-0.29



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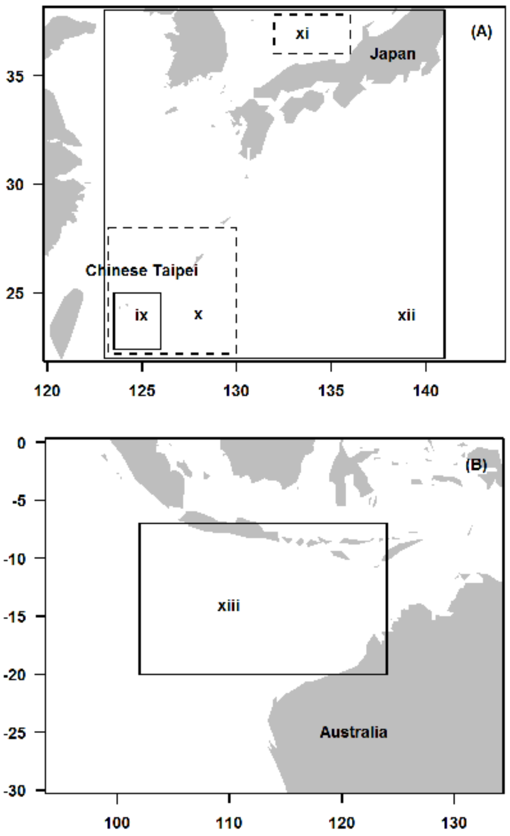

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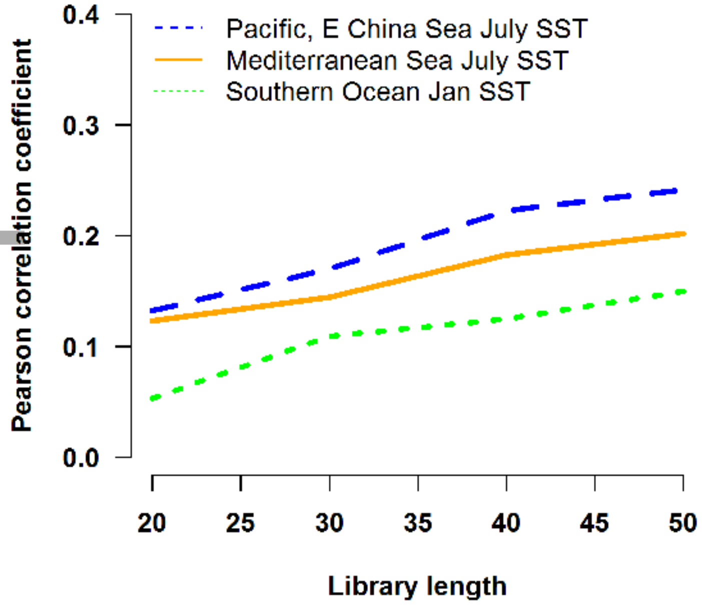

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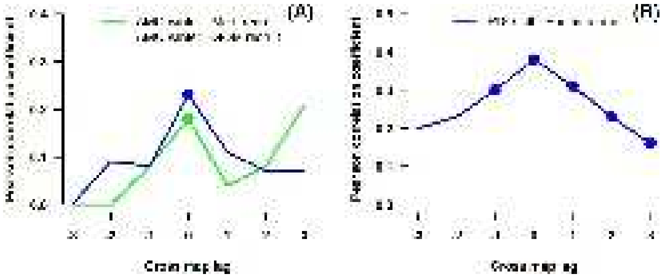

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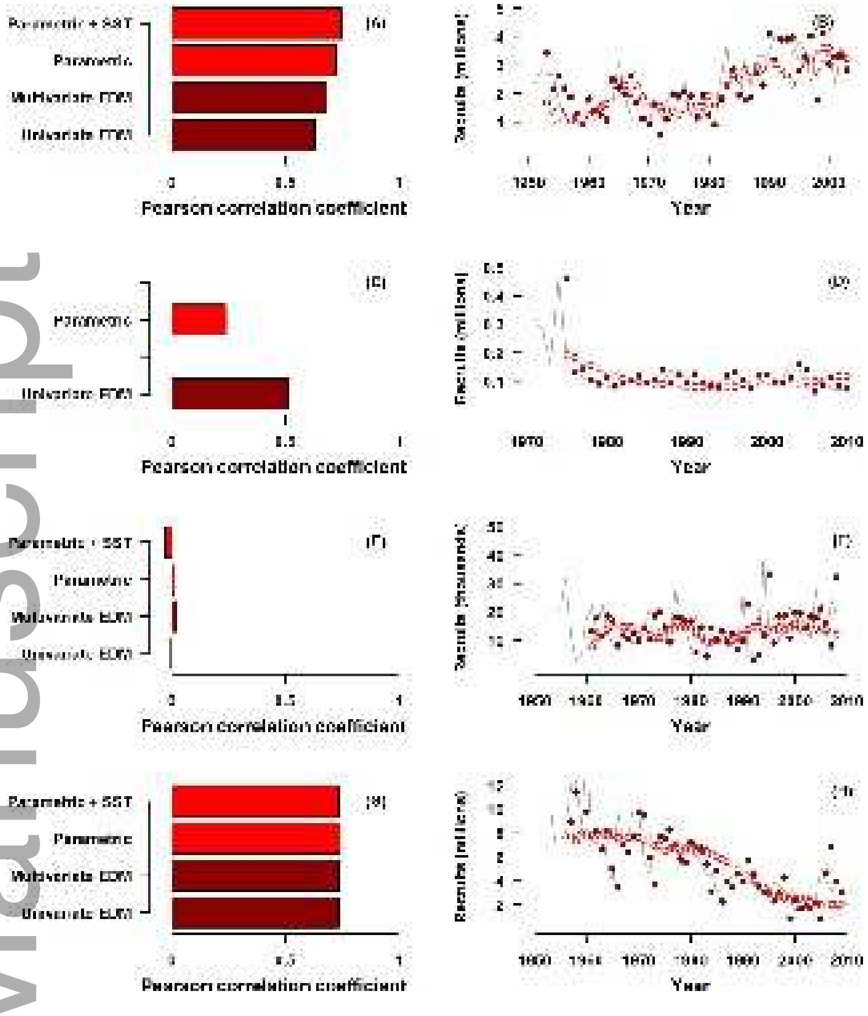

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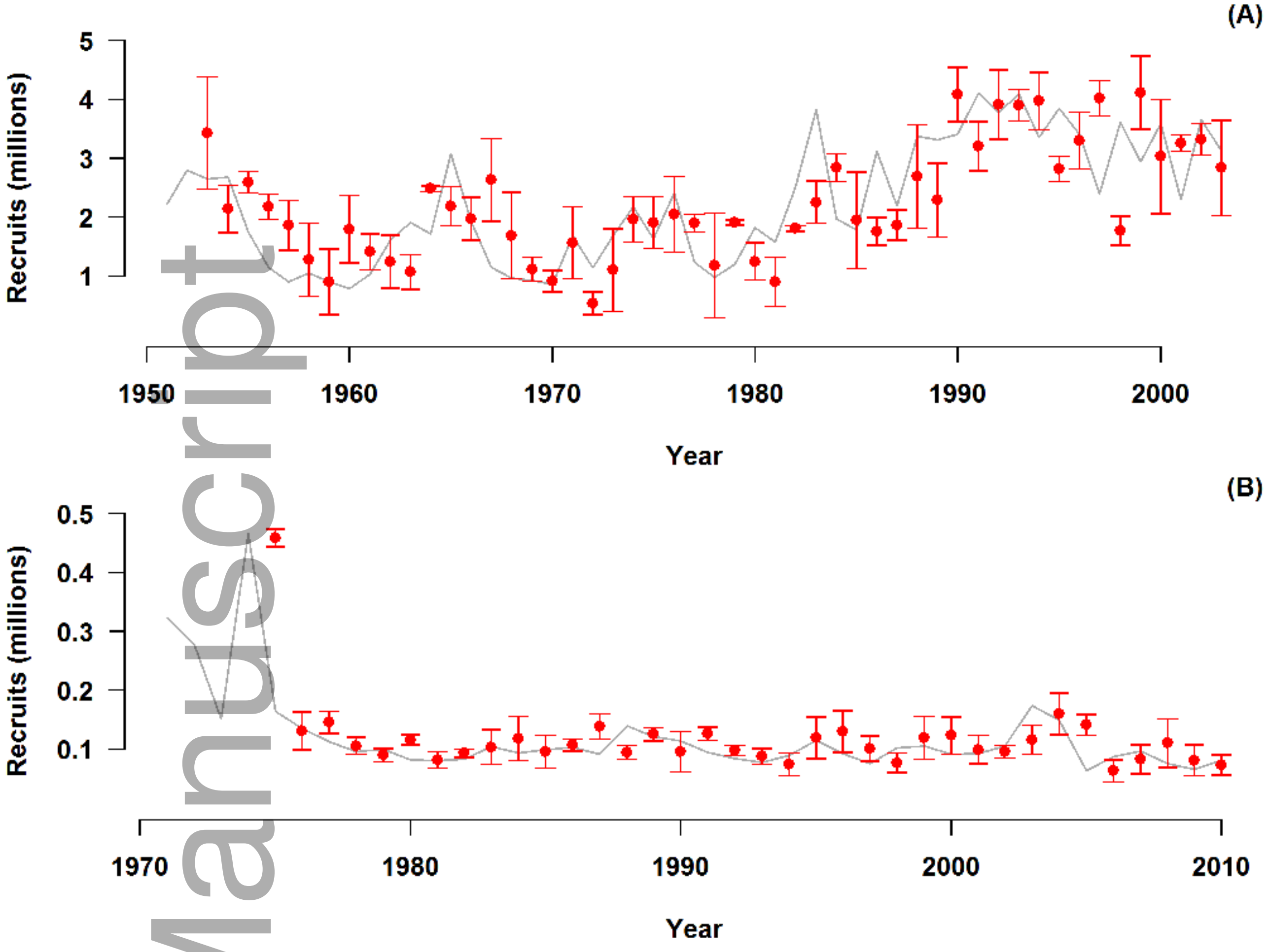

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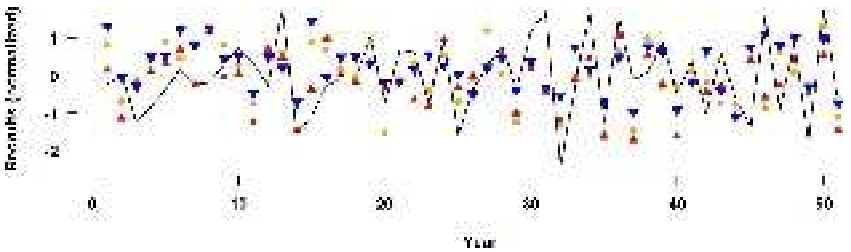

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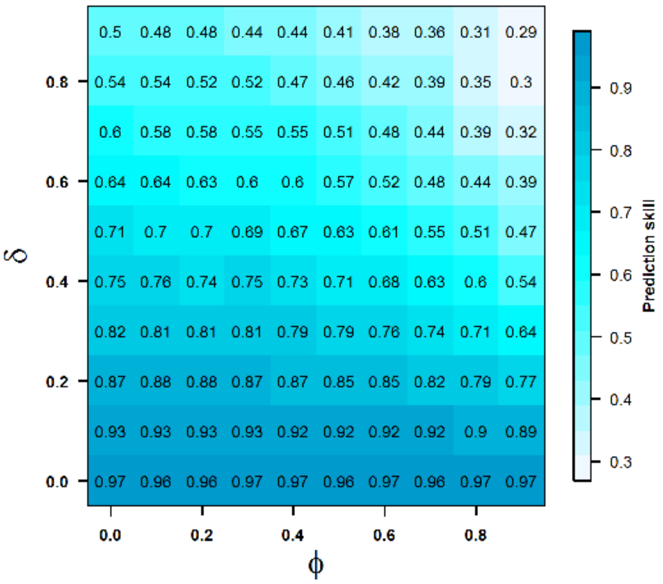

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