



Technical note

Re-evaluation of the environmental dependence of Pacific sardine recruitment

Juan P. Zwolinski^{a,*}, David A. Demer^b^a Institute of Marine Sciences, University of California Santa Cruz, Earth and Marine Sciences Building, Rm A317, Santa Cruz, CA 95064, United States^b Fisheries Resource Division, Southwest Fisheries Science Center, NMFS-NOAA, 8901 La Jolla Shores Dr., La Jolla, CA 92037, United States

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ABSTRACT

The environment influences the recruitment of small pelagic fishes, so environmental indices are used to match fishing mortalities to the stocks' productivities. For example, the exploitation fraction for the northern stock of Pacific sardine in the Northeastern Pacific is a function of sea-surface temperature (SST). The functional relationship changes, however, because our perception of the environmental effects on sardine recruitment is based on assessment models that are periodically updated with new input data and assumptions. In this paper, we use data from recent stock assessments to re-examine previously identified correlations of sardine recruitment success (the logarithmic ratio of recruitment and spawning stock biomass) with indices of SST off Southern California and the Pacific Decadal Oscillation (PDO). We show that the earlier correlation with SST is likely invalid, and the persistent correlation with the PDO is weaker. Because many environmental stock-recruitment relationships fail upon re-examination, environmental proxies for fish productivity might not always prescribe the correct amount of fishing mortality and should be avoided. Alternatively, for species assessed periodically, dynamic fishing mortalities could be based on measurements of recent stock productivity inferred directly from surveys, or from the results of analytical assessments based on those observations.

1. Introduction

Forage fishes (e.g. sardine, anchovy and mackerels) in eastern boundary upwelling ecosystems experience large swings in abundance, often affecting upper trophic levels and fishing industries (Alheit and Bakun, 2010; Schwartzlose et al., 1999). Many of these species alternate between regimes of high productivity that allow for large exploitations, and regimes of low productivity in which virtually no fishery is sustainable (Jacobson and MacCall, 1995). Exploitation strategies that ignore fluctuations in stocks' productivities can be slow to reduce fishing pressure during periods of deficient production, which can amplify the environmental effects and result in more frequent, more severe, and longer stock collapses (Essington et al., 2015). Conversely, exploitation strategies that match removals to the natural cycles of productivity may result in larger average catches, higher profits, and lower risk of stock collapses (King et al., 2015). However, successful application of dynamic fishing rules relies on early detection of changes in stock productivity. Because such changes are difficult to identify in stocks with moderate to high exploitation (Essington et al., 2015), environmental proxies for productivity are used in some management schemes to implement productivity-based harvest control rules (HCRs).

One of the first such rules has been applied to the northern stock of Pacific sardine (*Sardinops sagax*) in the Northeast Pacific (PFMC, 1998).

During at least the last 100 years, the sardine biomass co-varied with basin-scale environmental conditions (Alheit and Bakun, 2010; MacCall, 1996; Zwolinski and Demer, 2012). More specifically, Jacobson and MacCall (1995) concluded that sardine surplus production varies with ocean temperature, and a HCR was adopted to modulate fishing pressure as a function of SST measured at the pier of the Scripps Institution of Oceanography (SIO) in La Jolla, California (PFMC, 1998). Fifteen years later, a re-analysis by McClatchie et al. (2010) indicated that there was no longer a correlation between SST_{SIO} and sardine recruitment, so the environment-informed HCR was eliminated (Hill et al., 2011). Three years later, the Pacific Fisheries Management Council (PFMC, 2014) adopted another environment-informed HCR, based on a correlation that Lindegren and Checkley (2013) found between sardine recruitment success and a SST index (SST_{annual}) measured off Southern California during California Cooperative Oceanic Fisheries Investigations (CalCOFI). They analyzed the sardine spawning stock biomass (B_{SS}) and recruitment (R) output from the 2010 sardine assessment (Hill et al., 2010), which we also found to co-vary significantly with a Pacific Decadal Oscillation (PDO) based index

* Corresponding author.

E-mail address: jzwolins@ucsc.edu (J.P. Zwolinski).

Table 1

Time-series of B_{SS} and Recruitment from Hill et al. (2016) and Hill et al. (2017). CalCOFI SST was obtained from Hill et al. (2017) and the monthly PDO values (Mantua et al., 1997) were obtained here <http://research.jisao.washington.edu/pdo/PDO.latest.txt> and arranged as per Zwolinski and Demer (2014). Details for the sources of data used to create the original indices can be found in the respective references.

Year	SST_{annual} (°C)	$PDO_{combined}$ (°C)	Model 2016		Model 2017	
			B_{SS} (*10 ⁵ t)	Recruitment (1000s)	B_{SS} (*10 ⁵ t)	Recruitment (1000s)
1994	16.4762	2.79	3.89395	6,352,900		
1995	15.9241	0.614	5.3345	2,122,680		
1996	16.3252	2.268	6.3004	3,402,270		
1997	16.695	2.056	6.30932	10,871,200		
1998	16.7719	3.208	5.96042	7,671,780		
1999	15.2843	-1.168	6.81023	1,270,570		
2000	15.7907	-1.438	7.66577	1,395,120		
2001	15.5535	-1.354	6.81193	2,901,170		
2002	14.9414	-1.466	5.34937	360,040		
2003	16.0328	1.202	3.95682	14,281,900		
2004	15.8849	1.18	2.80332	6,909,280		
2005	15.4585	1.61	4.06208	11,917,900	3.24261	25,300,000
2006	15.9157	0.524	5.83424	3,658,480	10.7	7,800,000
2007	15.1543	0.064	7.57295	5,718,360	12.2	6,940,000
2008	15.2724	-1.41	7.63427	1,956,750	10.4	3,440,000
2009	15.3583	-2.596	6.99527	5,563,750	7.76752	6,670,000
2010	15.552	0.122	5.8647	1,559,350	5.4047	7,630,000
2011	15.5618	-1.848	5.07364	2,27,700	3.9939	601,265
2012	15.2939	-2.478	4.15388	68,950	3.36083	140,769
2013	14.9097	-2.012	2.49089	104,030	2.01812	185,878
2014	14.1932	0.2	1.31188	382,260	1.04351	971,184
2015	17.4765	2.556			0.60262	663,664

(Zwolinski and Demer, 2014). We cautioned however, that the environmental recruitment models in both Lindegren and Checkley (2013) and Zwolinski and Demer (2014) could be affected by erroneous estimates of the spawning B_{SS} and R . This is because the 2010 assessment model for the northern stock also included fishery data (fishing mortality and demographics) from a separate southern stock (Demer and Zwolinski, 2014; Félix-Uraga et al., 2004), sometimes referred to as the central stock.

Here, we re-examine the relationships in Zwolinski and Demer (2014) between assessment-modeled sardine recruitment and both SST_{annual} and $PDO_{combined}$, using B_{SS} and R pairs from the 2016 and 2017 assessments formulations for the northern stock that exclude data from the central stock (Hill et al., 2016, 2017). Although this analysis is specific to the northern stock of sardine in the Northeast Pacific, we discuss how the implications are generically relevant for the science and management of small pelagic fishes.

2. Methods

Since 2007, statistical catch-at-age assessment models of the northern stock of Pacific sardine have been fit with Stock Synthesis (SS; Methot, 2010) using a variety of fisheries independent and dependent data (Hill et al., 2017). Until 2013, these assessments included landings data collected from Ensenada, Mexico, to the northern end of Vancouver Island, Canada, potentially from both the northern and central stocks (Demer and Zwolinski, 2014; Félix-Uraga et al., 2005; Hill et al., 2014). Since 2014, however, the assessments for the northern stock have excluded data from the central stock based on their association with an indicative range of satellite-sensed SST (Hill et al., 2014). This new modeling approach invalidated the results of earlier models in describing the dynamics of the northern stock.

Currently, the two valid model configurations for the northern stock are from 2014 (Hill et al., 2014) – this model was updated in 2016 and spans from 1994 through 2014 (Hill et al., 2016) –, and 2017, spanning from 2005 through 2017 (Hill et al., 2017). For the overlapping years, the two models share the same catch and composition data. Salient differences between these models are summarized below, and additional details can be found in Hill et al. (2017) and references therein.

The 2016 model is length-based, it uses a time-invariant growth model, and is fit with fisheries-independent estimates of total egg production (TEP) or spawning stock biomass (B_{SS}) derived from egg surveys (Lo et al., 2009), and biomass estimates for one year and older sardine (age 1+) from acoustic-trawl method (ATM) surveys (Zwolinski et al., 2014). The natural mortality coefficient of the population was set to 0.4, and the catchability coefficients for the egg-based indices were estimated, whereas the catchability coefficient for the ATM biomass indices (spring and summer) were fixed at 1 (Hill et al., 2016). The 2017 model is age-based, it uses an empirical length-at-age model, and includes fisheries-independent data only from the ATM surveys (Zwolinski et al., 2014). The natural mortality coefficient was set to 0.6 (Zwolinski and Demer, 2013) and the catchability coefficient was estimated within the model as 1.1 (Hill et al., 2017).

Because these models are semi-independent characterizations of the northern subpopulation of Pacific sardine, we posit that significant environmental influences on recruitment success should be evident in either realization. If the environmental dependence is only evident in one of the most recent stock assessments, it indicates that it might be a statistical artifact of a particular model run, or if it is indeed real, it means that at least one of the assessment models is not capturing the real dynamics of the stock. To elucidate the environmental dependence of northern stock sardine recruitment (R), we fit the B_{SS} - R data pairs from the 2016 and 2017 assessments within a single environmentally-dependent stock-recruitment model. The statistical dependence of the information from the two assessments in the overlapping years, i.e., from 2005 through 2014, is considered explicitly by fitting a mixed version of the linearized Ricker model with the following structure:

$$E(\log(R/B_{SS})) = \beta_0 + \beta_1 \times B_{SS} + \beta_2 \times I_{2017} + \beta_3 \times environment + \gamma_{year} + \epsilon \tag{1}$$

$$\gamma_{year} \sim N(0, \sigma_{year}^2); \epsilon \sim N(0, \sigma^2),$$

where β_0 , β_1 , β_2 , and β_3 are estimated coefficients; R is expressed as abundance of age-0 fish in July; B_{SS} is the spawning stock biomass estimated in January of the same year; I_{2017} equals 0 or 1 for data from the 2016 or 2017 models, respectively; $environment$ is an environmental index, here either SST_{annual} or $PDO_{combined}$ because they provided by far

the best results in Zwolinski and Demer (2014) – see Table 1 for the data and their sources; γ_{year} is a vector of annual random effects; and ε is a vector of random errors with constant variance. The mixed version of a static (or conventional) Ricker model, i.e., a model without environmental influence, is similar to that of Eq. (1) without the $\beta_3 \times \text{environment}$ term. We used the Ricker model because it can fit a range of stock-recruitment relationships, e.g., linear, asymptotic, and compensation. The models were fit using the *lme* function from the *nlme* package for R (R Core Team, 2016).

To overcome the uncertainty in parameter inference that is inherent to mixed models with small sample sizes (Gurka, 2006), and to minimize the possibility of finding a spurious model (Brooks and Deroba, 2015), we test the quality of competing models using a semi-parametric approach based on the models’ out-of-sample prediction errors. The out-of-sample or “leave one out cross-validation” error is the deviation between an observed value and its predicted counterpart when the observation is not used to fit the model. This approach evaluates the models on their predictive ability rather than on the asymptotic significance of their parameters. To compare the various models, we calculate the mean-square prediction error (MSPE), which is the arithmetic mean of the squared out-of-sample errors. Among competing models, the model with smallest MSPE is the best predictive model. Additionally, we compute the pseudo out-of-sample r^2 (pseudo- r^2) as the square of the Pearson correlation coefficient between the predicted and observed values of $\log(R/B_{SS})$, and we test the independence of the residuals by plotting their auto-correlation. Finally, we test for significant reductions in the variance of the out-of-sample errors of pairs of competing models using a variance ratio F test (Selvin, 2005). In combination with graphic diagnostics (McCullagh and Nelder, 1989), we use the MSPE and the variance test to select the best performing model.

3. Results

The Static Ricker model, i.e., a Ricker recruitment model without environmental predictors, has little to no explanatory power (Fig. 1; Table 2) and therefore performs about the same as the arithmetic

average of recruitment success (not shown). The model with SST_{annual} as the environmental predictor in Eq. (1) has a lower MSPE than the Static Ricker (Fig. 1; Table 2), but the out-of-sample error variance is not significantly smaller than that of the Static Ricker. The Pearson correlations between SST_{annual} and $\log(R/B_{SS})$ for the 2016 and 2017 data sets are 0.53 ($p = 0.01$) and 0.20 ($p = 0.56$), respectively. The model with PDO_{combined} as the environmental predictor in Eq. (1) has the smallest MSPE, the out-of-sample error variance is significantly smaller than that of the Static Ricker (Table 2; Fig. 1), and the pairs of observed and predicted values are closest to the 1:1 line (Fig. 1). The correlations between PDO_{combined} and $\log(R/B_{SS})$ for the 2016 and 2017 data sets are 0.75 ($p < 0.01$) and 0.73 ($p = 0.01$), respectively. These results indicate that sardine recruitment success, as estimated by the 2016 and 2017 northern stock-differentiated assessments, is not significantly informed by SST_{annual} , but is significantly informed by PDO_{combined} . The pseudo- r^2 for the model using SST_{annual} is 0.10. In contrast, pseudo- r^2 for the model using PDO_{combined} is 0.44, which indicates that about half of the variance of the data is explained by the model (Fig. 2). These results are confirmed when using only the 2016 assessment model results within a non-mixed linearized Ricker model (Fig. S1). The 2017 B_{SS} - R time series is probably too short to provide sensible results on its own. For completeness, the model diagnostics provided here in $\log(R/B_{SS})$, are presented in $\log(R)$ in Fig. S2.

4. Discussion

The variability in recruitment of forage species depends on a series of events that begins before the spawning season. For capital breeders like sardine, the feeding season prior to spawning controls energy storage and seemingly the start and duration of spawning (Ganias et al., 2007). This determines the conditions in which the eggs and larvae are reared, and modulates recruitment through processes that include, amongst others, advection (Parada et al., 2008), turbulence (Lasker, 1981), appropriate food supply (Lasker, 1978), and predation (Bjornstad et al., 1999). The complex interactions of these factors are insufficiently understood, at least partly because data are unavailable on critical temporal and spatial scales. Therefore, stock assessment

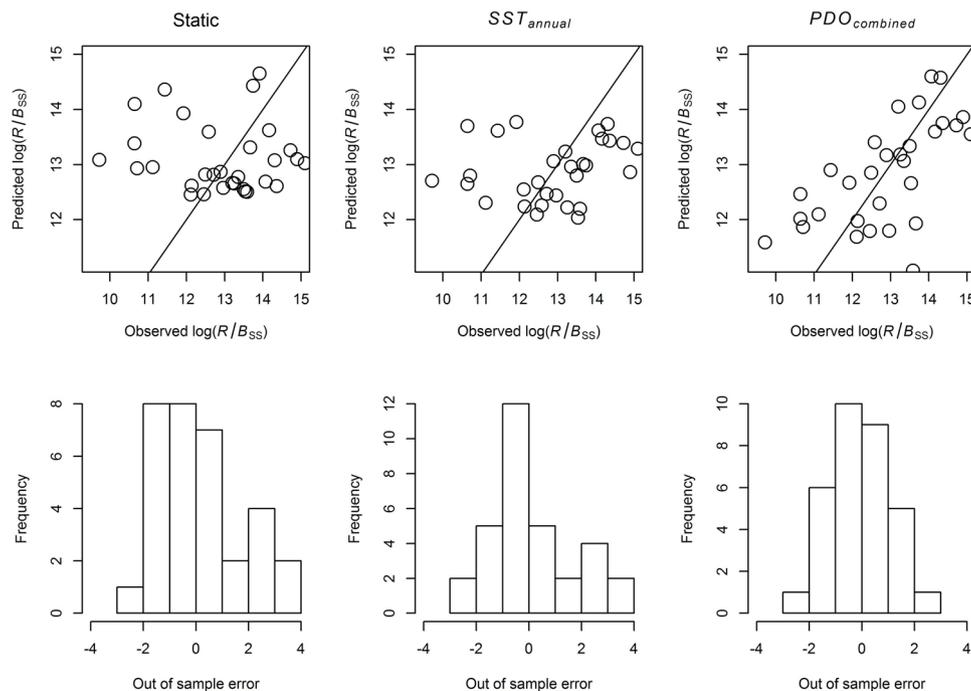


Fig. 1. Diagnostics for the three linearized Ricker mixed-models tested including observed $\log(R/SSB)$ versus out-of-sample predicted $\log(R/SSB)$ (top row), and histograms of out-of-sample errors (bottom row).

Table 2

Coefficients of the fixed component of the linearized Ricker mixed-models estimated using all observations (a full model summary is available in Table S2). Mean squared prediction error refers to the out-of-sample errors. The variance test was calculated against the out-of-sample error variance of the the static Ricker model. Pseudo- r^2 was calculated using all observations.

Ricker Model	Coefficients $\beta_0, \beta_1, \beta_2, \beta_3$	Mean squared prediction error	Variance test	Pseudo- r^2
Static	13.855; -0.184; 0.841; NA	2.45	NA	0.00
SST_{annual}	0.0216; -0.176; 0.833; 0.878	2.21	F = 1.10, p = 0.40	0.10
$PDO_{combined}$	13.500; -0.126; 0.781; 0.548	1.24	F = 1.97, p = 0.03	0.44

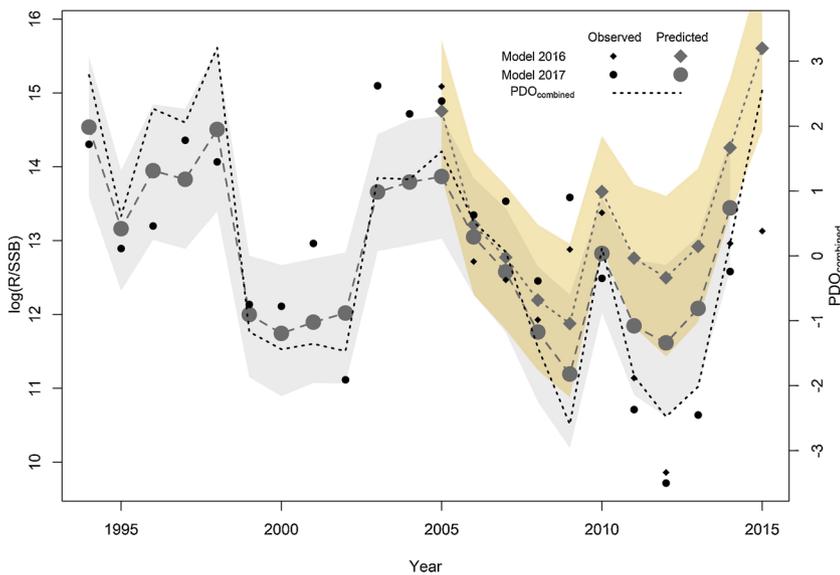


Fig. 2. Time series of recruitment success (small black dots) overlaid on $PDO_{combined}$ Ricker model predictions (gray lines and large gray dots). The gray and yellow bands represent, respectively, approximate 95% confidence intervals of the expected reproductive success for the 2016 (dashed) and 2017 models (dotted). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

models and management strategy evaluations use statistical low-complexity stock-recruitment relationships (Munch et al., 2005). Although simpler, these models ignore the mechanistic complexity of the recruitment process and therefore exhibit large variances (Szuwalski et al., 2015). The inclusion of appropriate environmental variables (Subbey et al., 2014), has been shown to reduce the unexplained variability of stock-recruitment models (Myers, 1998). The covariates are proxies for the combination of processes involved in recruitment (Zwolinski and Demer, 2014), and enable models with good hind-casting properties (Myers, 1998). However, the majority of environmental-recruitment models fail upon re-analysis with new data (Myers, 1998). Case in point, (McClatchie et al., 2010) used data from the 2010 stock assessment (Hill et al., 2010) to re-analyze the model proposed by Jacobson and MacCall (1995) and concluded that sardine recruitment does not vary significantly with SST_{SIO} . Jacobson and McClatchie (2013), however, acknowledged “statistical short-comings” in the analysis by McClatchie et al. (2010) and concluded that SST_{SIO} may still predict sardine recruitment. Lindegren and Checkley (2013) restricted their analysis to data from 1983 to 2010 and found that sardine recruitment did vary significantly with SST_{annual} . Jacobson and McClatchie (2013) endorsed the use of SST_{annual} because, in part, SST_{annual} is derived from SST data collected in the sardine spawning area. However, using data from the latest, stock-differentiated assessments, we show that sardine recruitment does not vary significantly with SST_{annual} .

We offer two related explanations for the spurious relationship between sardine recruitment success and SST_{annual} . First, SST_{annual} does not represent the average SST within the recent spawning area because the range of SST associated to the northern stock (Demer and Zwolinski, 2014) has shifted north in recent years (Fig. 3). Second, as the northern stock shifted north, the landings data from Ensenada, Mexico, and San

Pedro, California, included fewer sardine from the northern stock and more from the central stock that is associated to a higher range of SST (Demer and Zwolinski, 2014; Félix-Uraga et al., 2004). Consequently, the 2010 sardine assessment, as well as all assessments prior to separation of the stocks, may have confounded immigration with local production as suggested by Jacobson and MacCall (1995). This potential error is mitigated in the 2016 and 2017 assessments by excluding data from landings that occurred outside the SST range associated to the northern stock (Demer and Zwolinski, 2014).

Although the 2016 and 2017 assessments exclude data from the central stock, which in theory would result in a better model for the northern stock, the recruitment model presented here has a lower pseudo- r^2 than that derived from the 2010 assessment (Zwolinski and Demer, 2014). This counter-intuitive result coincides with progressively weaker stock-recruitment relationships observed in assessment models after 2010. For example, in the 2014 and 2015 model runs (Hill et al., 2014, 2015; respectively), there was virtually no evidence that R depended on B_{SS} within the observed ranges of B_{SS} . Despite this trend, it is notable that sardine recruitment success modeled by two substantially different assessment formulations, i.e., 2016 and 2017, continues to vary significantly with $PDO_{combined}$. We theorize that $PDO_{combined}$ may be a more robust indicator of sardine recruitment than SST_{SIO} and SST_{annual} because it was constructed considering the feeding and spawning timings of the of the northern stock of Pacific sardine (Zwolinski and Demer, 2014), and the PDO has been shown to correlate with multiple atmospheric, oceanographic, and biological time-series representative of large areas of the Northeast Pacific (Beamish, 1993; Clark et al., 1999; Hare and Mantua, 2000).

Although the significant correlation between $PDO_{combined}$ and sardine recruitment does not reveal a causal mechanism, it does add to the list of statistical relationships found between the PDO and other fish

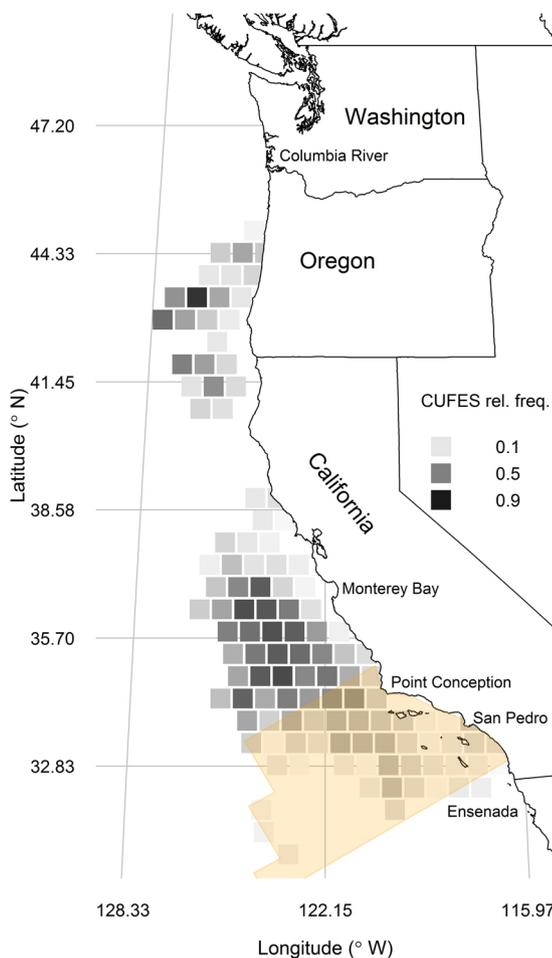


Fig. 3. Relative frequency of occurrence of continuous underway fish egg samples (CUFES) with at least one sardine egg during spring surveys from 2010 to the present.¹ The shaded region corresponds to the CalCOFI survey area within which SST_{annual} is derived.

stocks in the California Current Ecosystem (Beamish, 1993; Clark et al., 1999). Nonetheless, this correlation between recruitment and the environmental indices may also eventually fail. In addition, although the stock productivity may vary significantly with a particular environmental index, the unexplained annual variability could be sufficiently large to prevent an accurate prediction of the real productivity. With a marginally significant correlation, the environmental recruitment model can over- or underestimate recruitment success for short periods of time (e.g., 2003–2005 and 2011–2013 in Fig. 2), and inaccurately predict surpluses or deficits. Therefore, for stocks that are surveyed and assessed annually, the measured productivity, averaged over the species reproductive longevity, could be used to modulate the fishing fraction instead of an environmental proxy. This approach would allow the exploitation rate to match the stock productivity, irrespective of our understanding of the current environment.

On the other hand, even a marginally statistically significant environment-dependent recruitment model may be useful. For example, if required by the HCR, it could be used to predict recruitment in the management year and forecast the stock biomass into the following year more precisely than a model without environmental influence. Finally, the model could still be of use to simulate recruitment within a management strategy evaluation, to estimate optimal fishing mortalities and biological reference points.

¹Data available here: <http://coastwatch.pfeg.noaa.gov/erddap/tabledap/erdCalCOFIcufes.html>.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2019.03.022>.

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