Re-assessment of the stock–recruit and temperature–recruit relationships for Pacific sardine (*Sardinops sagax*)

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Abstract: The harvest guideline for Pacific sardine (*Sardinops sagax*) incorporates an environmental parameter based on averaged surface temperatures at the Scripps Institution of Oceanography pier (SIO pier) in La Jolla, California, USA, which would be invoked after a series of cool years to reduce commercial catches using a precautionary decision rule. We revisit the stock–recruit and temperature–recruit relationships underpinning the currently used environmental parameter for sardine assessment and found that the temperature–recruit relationship no longer holds for the SIO pier when time series are updated with data from more recent years. The significance of the correlation between temperature and recruitment was also artificially increased by autocorrelation in the time series. In contrast, the stock–recruit relationship was still valid when recent data were added. SIO pier surface temperatures are warmer than 10 m-depth Southern California Bight (SCB) temperatures where the sardine spawn, and the difference has increased since the late 1970s. Sardine recruitment was also not related to offshore temperatures in the SCB. We demonstrate that the environmental proxy derived from SIO pier temperature, which has never affected the harvest guideline since its implementation, no longer predicts recruitment of Pacific sardine, and should be removed from sardine management.

Résumé : Les directives pour la récolte des sardines du Pacifique (*Sardinops sagax*) incorporent une variable environnementale basée sur la moyenne des températures en surface au quai de la Scripps Insitution of Oceanography (SIO) à La Jolla, Californie, É.-U., qui pourrait être invoquée après une série d'années fraîches afin de réduire les récoltes commerciales en utilisant une règle décisionnelle préventive. Nous réexaminons les relations stock-recrues et température-recrues qui sous-tendent la variable environnementale couramment utilisée pour l'évaluation des sardines et trouvons que la relation température-recrues n'est plus valable pour le quai de la SIO quand les séries chronologiques sont mises à jour avec les données des années récentes. La signification de la corrélation entre la température et le recrutement est aussi artificiellement haussée par l'autocorrélation dans la série chronologique. En revanche, la relation stock-recrues reste valide après l'addition des données récentes. Les températures de surface au quai de la SIO sont supérieures aux températures à la profondeur de 10 m dans le golfe du Sud de la Californie (SCB) où les sardines se reproduisent et la différence a augmenté depuis la fin des années 1970. Le recrutement des sardines n'est pas non plus relié aux températures du large dans la SCB. Nous démontrons que la variable environnementale de remplacement dérivée de la température au quai de la SIO ne permet plus de prédire le recrutement des sardines du Pacifique et devrait être exclue de la gestion des sardines.

[Traduit par la Rédaction]

Introduction

The paleoceanographic record shows that Pacific sardine (*Sardinops sagax*) populations fluctuated greatly in biomass long before the advent of commercial fishing (Baumgartner et al. 1992). Sardine stocks are prone to collapse, contraction in range, and re-expansion, as well as to shifts in dominance in the small pelagic fish community (Schwartzlose et al. 1999). To an unknown degree, the changes in sardine abundance are driven by changes in their environment. There are very few fisheries stock assessments or harvest policies that incorporate any measure of environmental variability (Schirripa and Colbert 2006; Schirripa et al. 2009). The Pacific sardine harvest policy is unusual because a proxy for environmental variability, 3 year average surface temperature at the Scripps Institution of Oceanography pier

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(SIO pier) in La Jolla, California, USA, is used as one parameter in the formula for a decision-rule-based harvest guideline (Pacific Fishery Management Council 1998; Hill et al. 2008). There is considerable uncertainty as to the relative contributions of density-independent factors such as temperature, the distribution of water masses, and climatic processes operating at different scales (e.g., El Niño-Southern Oscillation cycles and "regime shifts", Lluch-Belda et al. (1989)) and density-dependent factors such as competition, predation and food supply. It is also unclear which stage of life is most affected by environmental variability. Spawning habitat is strongly impacted by environmental variability, but recruitment success is thought to be determined by natural mortality at the late larval or juvenile stage (Watanabe et al. 1995; Takahashi and Checkley 2008). Despite uncertainties about the mechanisms by which environment exerts an effect on sardine biomass and recruitment, the possible range of effects makes it desirable to incorporate an index of environmental variability into the Pacific sardine stock assessment.

The maximum sustainable yield (MSY) control rule is a proxy for F_{msy} (i.e., the fishing mortality rate that achieves equilibrium MSY) and is presently constrained to range between 5% and 15% of total biomass. The SIO pier temperature index values observed from 1981 through 2008 have consistently been larger than the temperature threshold that would trigger the decision rule to reduce the exploitation fraction and consequently the F_{msy} exploitation fraction has been 15%. This remains the case under current oceanic conditions. Essentially this means that the environmental parameter has no effect on the harvest guideline under current conditions, nor has it ever been used to reduce catches since its implementation in 2000, but if SIO pier temperature index values drop this could lead to a management decision to reduce the exploitation fraction.

The calculation of the exploitation fraction in the MSY control rule is very sensitive to temperature. A drop in the SIO pier temperature index of less than 0.5 °C from the 2009 value would shift the exploitation fraction from 15% to 5%. This would reduce the harvest guideline for Pacific sardine by 2/3 if other variables were constant. Since the consequences of such a reduction in harvest are substantial for the fishing industry, it is timely to re-examine the relationship between the SIO pier temperature index and the temperatures in the offshore Southern California Bight (offshore SCB) where sardine spawn, now that a further 17 years of data are available.

In this paper, we pose two questions. First, is the SIO pier temperature index still an appropriate proxy for environmental variability in the Pacific sardine assessment? To answer this, we examine temporal trends in surface temperatures at the SIO pier and compare them with trends in the offshore SCB where sardine spawn. Second, are relationships between Pacific sardine recruitment and SIO pier temperature that were based on data from 1935–1963 and 1985–1990 still valid? To address this question we examine the relationships between Pacific sardine recruitment anomalies, SIO pier temperatures, and offshore SCB temperatures incorporating updated data from 1991–2008.

Materials and methods

Our strategy was to test the temperature–recruit relationship for Pacific sardine, adjusting for stock size, using recruitment anomalies, rather than simply recruits, to emphasize deviations from any trend. First we tested the temperature–recruit relationship with data from the early years used by Jacobson and MacCall (1995), and then we re-tested after updating with 17 more recent years of data. Next, we examined the difference in trends between temperatures in the offshore Pacific sardine spawning area and the SIO pier. Finally, we retested the temperature–recruit relationship with the offshore temperatures to determine whether the temperature–recruit relationship worked with the temperatures from the sardine spawning grounds.

Environmental control rule for Pacific sardine

The formula for the harvest guideline is

$$HG_{yr+1} = (BIOMASS_{yr} - CUTOFF) \times FRACTION \times DISTRIBUTION$$

where HG_{yr+1} (in metric tonnes (mt)) is the total USA (California, Oregon, and Washington) harvest guideline in the year following the assessment, $BIOMASS_{yr}$ (mt) is the estimated July 1 stock biomass (ages 1+) from the current assessment, CUTOFF (150 000 mt) is the lowest level of estimated biomass at which harvest is allowed, FRACTION is an environment-based percentage of biomass above the CUTOFF that can be harvested by the fisheries, and DISTRIBUTION is the percentage of $BIOMASS_{yr}$, assumed to be 87%, in US waters. Given F_{msy} and the productivity of the sardine stock have been shown to increase when relatively warm-ocean conditions persist (Jacobson and MacCall 1995), the following formula has been used to determine an appropriate (sustainable) FRACTION value: $F_{msy} = 0.248649805(T^2) - 8.190043975(T) + 67.4558326$ where T (°C) is the running average sea-surface temperature at the SIO pier during the three preceding seasons (July–June).

Comparison of SIO pier and offshore temperature trends

We assembled two temperature time series for analyses: one from the SIO pier and a second from the offshore SCB. The SIO pier temperature time series was obtained from the surface measurements of the Scripps Institution of Oceanography Shore Stations Program (shorestation.ucsd.edu). Daily temperature measurements were averaged by month for the time period 1916–2008 and a 3 year running average was calculated. The offshore SCB temperature data were obtained from the NOAA_ERSST_V3 data provided by the National Oceanic and Atmospheric Administration Office of Oceanic and Atmospheric Research Earth System Research Laboratory Physical Sciences Division, Boulder, Colorado, USA (Xue et al. 2003; Smith et al. 2008). These are monthly means of sea surface temperature for $2° \times 2°$ grids from 1854 to the present. Data were extracted for four grid squares (Fig. 1) and averaged for each time point. The grid squares were chosen to overlap areas where larger numbers of sardine eggs are detected by Continuous Underway Fish Egg Sampling (Checkley et al. 1997) during the March–April spawning season. Although the distribution of sardine

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Fig. 1. Locations of the $2° \times 2°$ grid squares in the Southern California region from which the offshore Southern California Bight temperature time series was extracted (denoted by heavy black lines). The grid squares are overlaid on counts of sardine eggs·s^{-1} collected in March–April–May 1997 to 2008 using the Continuous Underway Fish Egg Sampling system to show the location of the sardine spawning ground. Scale bar indicates counts of 0 to 2 sardine eggs·s^{-1}.
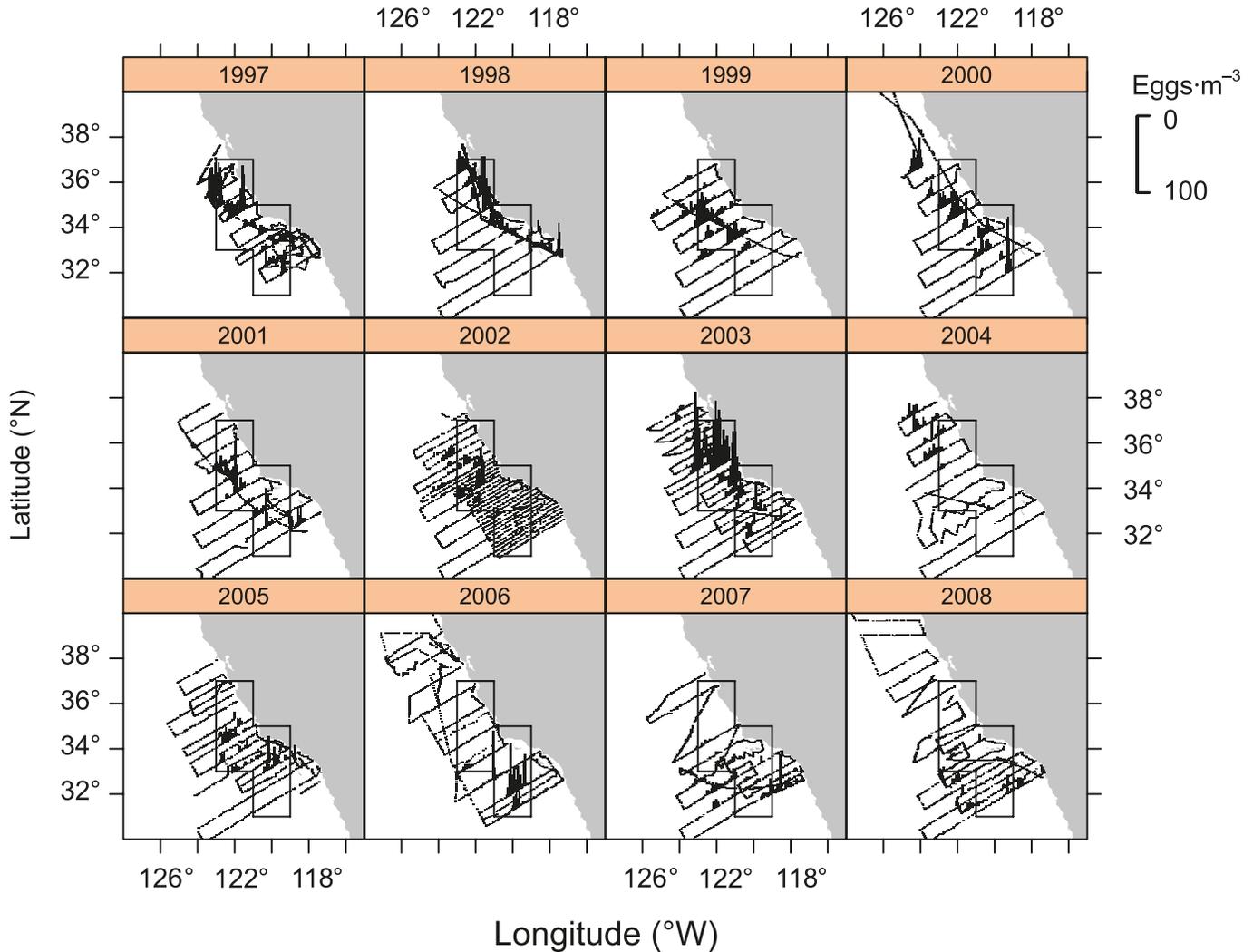
eggs shows large interannual variability, the spatial positions of higher egg counts (>2 eggs·min^{-1}) were well contained by the grid squares we used to determine temperatures in the offshore SCB sardine spawning area (Fig. 1). The exceptions to this generalization were in 2000 and 2004, when the eggs extended further north, and in 2007 and 2008 when there sardine eggs were found offshore as well as inshore of the grid square boundaries (Fig. 1).

SIO pier temperature and Pacific sardine recruitment

In the original work on the SIO pier temperature index (Jacobson and MacCall 1995), sardine recruitment (R) was related to spawning stock biomass (SSB) and SIO pier temperature (averaged over either 3 years or 5 years) using a generalized additive model (GAM) for the years 1935–1963 and 1985–1990. Their preferred management model used a LOWESS fit (Cleveland 1979) to the stock–recruit relationship (ln$R$ on SSB) and a linear fit to ln$R$ on the 3-year averaged surface temperature at the SIO pier (Jacobson and MacCall 1995). Jacobson and MacCall's (1995) stock–

recruit relationship for Pacific sardine was based on Virtual Population Analysis estimates and age-2 recruits (1935 to 1963) or age 1 recruits (1985 to 1990) corrected to age-2 using estimated mortality. Numbers of age-2 fish were used to estimate recruits to permit comparison with data from the early years. We also used age-2 fish as recruits to permit comparison with Jacobson and MacCall (1995), although the current assessment (Hill et al. 2008) treats age-0 fish as recruits. We updated Jacobson and MacCall (1995) results with more recent data from the Stock Synthesis 2 (SS2) integrated assessment model, lagging R by two years in relation to SSB. We re-evaluated both the stock–recruit relationship and the temperature–recruit relationship (adjusting for stock size) after including more recent data collected between 1991 and 2008. We fitted the stock–recruit relationship for Pacific sardine with a Ricker curve using both the early data (1935–1963 and 1985–1990), and the updated series (1935–1963, 1985–1990, and 1991–2008).

We tested the relationship between temperature and two measures of recruitment using anomalies because we consid-

Fig. 2. (*a*) Comparison of the 3-year average SIO pier surface temperature with the 3-year average 10 m depth reconstructed temperatures from the $2° \times 2°$ grid squares in Fig. 1. (*b*) Difference between the two time series calculated as SIO pier temperature – offshore SCB temperature.
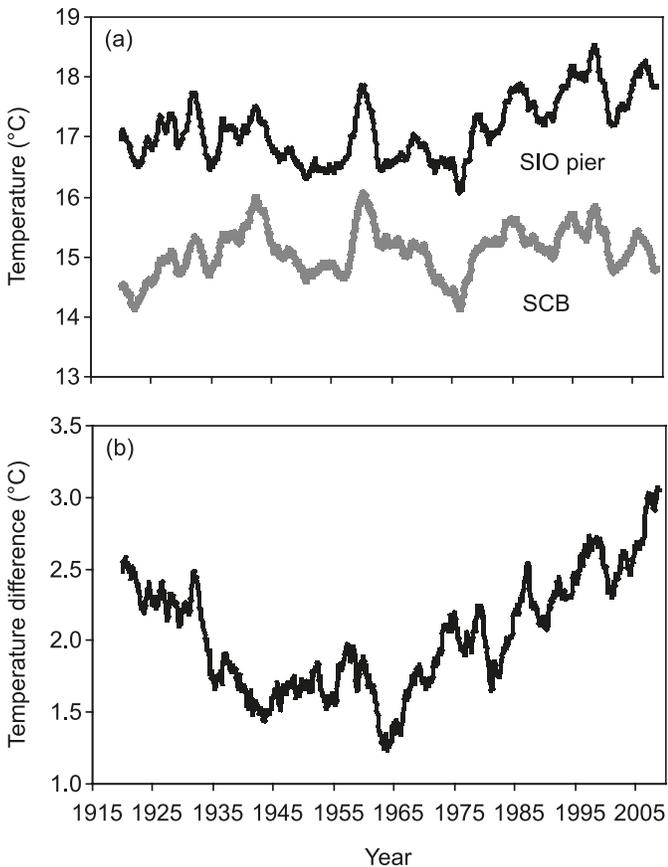
ered that deviations from the mean of the time series would best express the relationship with temperature. Anomalies were calculated by subtracting the mean and dividing by the standard deviation of the entire series. First we used the anomalies of the residuals from the stock recruitment model (SR anomalies) to remove effects SSB on the temperature–recruitment relationship. We then examined the relationship between temperature and reproductive success (R/S, number of age-2 fish/SSB) because it is considered to be more sensitive to environment than is the number of recruits (Wada and Jacobson 1998). Both the SR anomaly and the R/S anomaly remove the effect of stock size on the relationship between numbers of recruits and temperature. The R/S anomaly is more empirical in not assuming any underlying model for the stock–recruit relationship, whereas the SR anomalies are deviations from the fitted SR model. We regressed the recruitment anomalies against both the SIO pier 3-year mean temperatures and the offshore SCB 3-year mean temperatures.

Results

Comparison of SIO pier and offshore temperature trends

Visual inspection of the SIO pier and the offshore SCB temperature time series (Fig. 2*a*) indicates that the SIO pier

temperatures have been increasing over the last decades in contrast to the offshore SCB series that did not change noticeably. From 1940 to 1975 3-year means of monthly surface temperatures were 1.5–2 °C higher at the SIO pier compared with the offshore SCB fairly consistently (Fig. 2*b*). Since 1975, the SIO pier temperatures warmed more than the offshore SCB series, and in recent years the difference between the two temperature time series increased to about 3 °C (Fig. 2*b*). The SIO pier and the offshore SCB series are quite similar at high frequencies, and the major difference between them is in the low frequency trends, which have become increasingly different since 1975 (Fig. 2*b*).

### SIO pier temperature and Pacific sardine recruitment

The Ricker model for the early series (Fig. 3*a*) was $R = 7.303 \times 10^3 \text{SSBexp}^{5.128 \times 10^{-7} \text{SSB}}$ where R represents age-2 recruits and SSB represents spawning stock biomass of sardines. The Ricker model for the updated series (Fig. 3*b*) was $R = 5.834 \times 10^3 \text{SSBexp}^{4.298 \times 10^{-7} \text{SSB}}$. The model fit both data sets ($p = 0.0017$ for the regression slope and $p = 0.0013$ for the intercept of the early series; $p = 2.03 \times 10^{-5}$ for the slope and $p = 0.00032$ for the intercept of the updated series). Although the stock recruitment relationship was consistent for both time periods, the SIO pier temperatures were cooler in the early period. There were no years where the SIO pier temperatures were higher than 18 °C in the early data (Fig. 3*a*).

Both the SR anomalies and the R/S anomalies were linearly related to 3-year SIO pier temperature in the early years, in agreement with Jacobson and MacCall (1995) (Figs. 3*c* and 3*e*). For both anomalies the relationship broke down when more recent data from 1991 to 2008 were added (Figs. 3*d* and 3*f*). In addition, the linear relationship between SR anomaly and offshore SCB temperatures was weak ($p = 0.156$, adj. $R^2 = 0.021$). There was also no linear relationship between R/S anomalies and offshore SCB temperatures ($p = 0.521$, adj. $R^2 = -0.012$). This indicates that both the SIO pier temperatures and the offshore SCB temperatures are not linearly related to sardine recruitment.

Autocorrelation

There is an additional problem with the temperature–recruit relationship that affects the significance of the correlation between the variables. Both the 3-year mean SIO pier temperature and the stock–recruit anomaly time series are significantly autocorrelated at a one year lag (Figs. 4*a* and 4*c*). Further, the residuals of the SR anomaly – SIO pier temperature model and the updated version of this model are also significantly autocorrelated (Figs. 4*e* and 4*g*). The autocorrelation in the variables artificially inflates the coefficient of variation and the confidence limits, causing the temperature–recruit relationship to appear stronger than it actually is. This problem is common in relationships between environmental variables and fisheries catches (Drinkwater and Myers 1987) or recruits (Pyper and Peterman 1998). There are several ways of adjusting for the autocorrelation (Pyper and Peterman 1998), but it is common to find that the correlations are no longer significant after adjustments are made (Drinkwater and Myers 1987). The effect of autocorrelation was also observed in the SR anomaly – SIO pier temperature model. While the original relationship

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Fig. 3. (*a*) Spawning stock biomass–recruit (age-2 Pacific sardine) relationship using data from Jacobson and MacCall (1995; Table 1, Erratum) for years 1935–1963 and 1985–1990. Black line is a fitted Ricker curve and gray lines are 95% confidence intervals. Data points are color-coded by SIO pier temperature (°C) (*b*) Same as (*a*) updated with data from and Hill et al. (2008; data from 1991–2008). (*c*) Stock–recruit (SR) anomaly calculated from (*a*) in relation to SIO pier temperature for years 1935–1963 and 1985–1990; *p* is the probability that the slope of the linear regression is not different from zero. Grey lines are the 95% confidence intervals (*d*) SR anomaly calculated from (*b*) in relation to updated SIO pier temperature, updated with recent years (1991–2008). (*e*) Recruitment success (R/S) anomaly based on numbers of age-2 sardines in relation to the 3-year mean SIO pier surface temperature using data from Jacobson and MacCall (1995) (1935–1963, 1985–1990). (*f*) Same as (*e*), but updated with recent years (1991–2008). Grey circles are the data from (*e*).
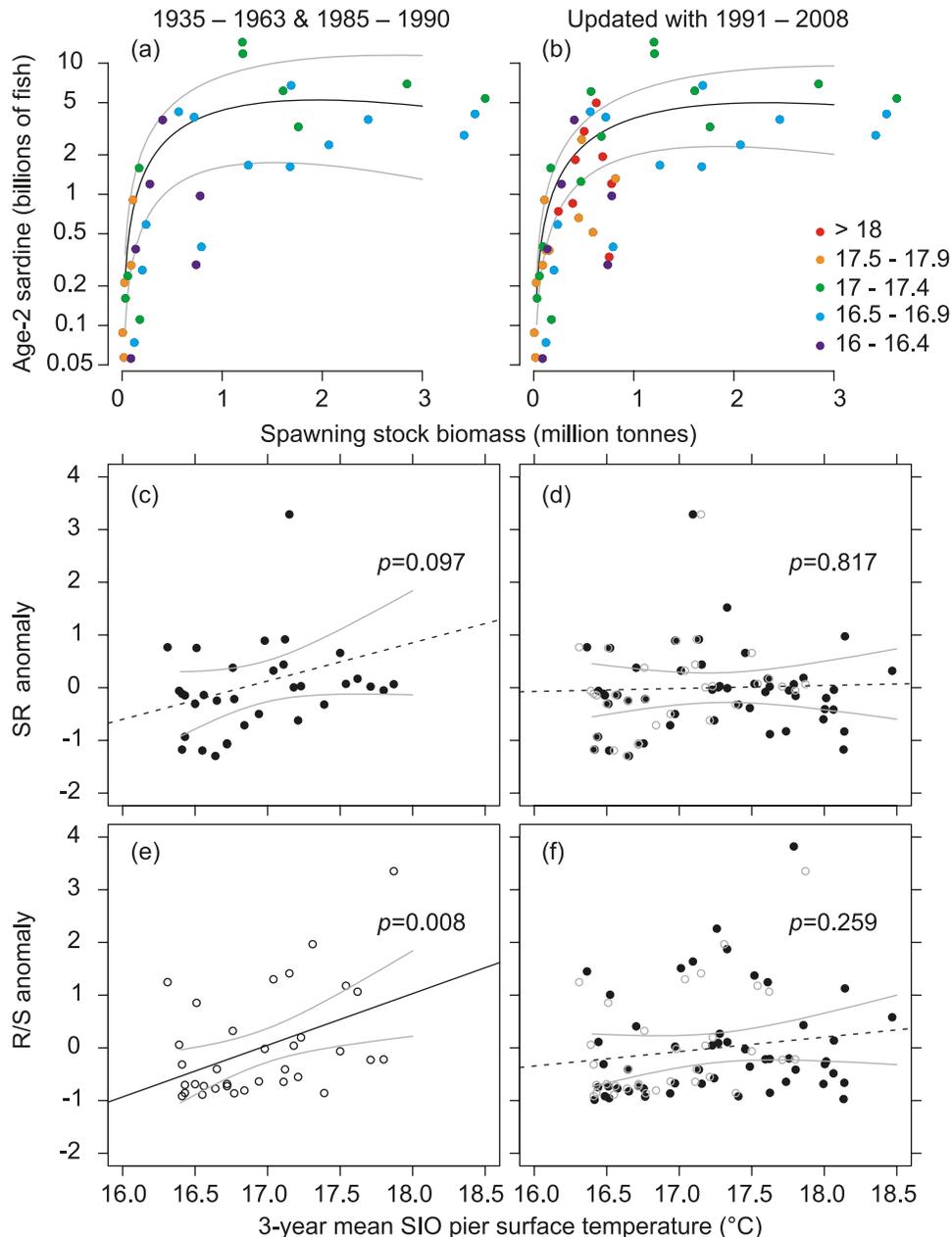
showed a fairly strong, but not a significant correlation (significance of the slope, *p* = 0.097, Fig. 3*c*) when autocorrelation was removed by first differencing the variables (Figs. 4*b* and 4*d*), the correlation all but disappeared, with non-significant slope in the regression (*p* = 0.82). The effect of autocorrelation on the updated SR anomaly – SIO pier temperature model (Fig. 3*d*) was less drastic where significance of the slope coefficient was *p* = 0.817 for the autocorrelated variables and *p* = 0.86 after autocorrelation was removed by differenc-

ing. Averaging monthly data over three years changes the pattern of autocorrelation by reducing the seasonal signal (Figs. 5*a* and 5*b*). Averaging to a yearly value reduces but does not eliminate significant autocorrelation (Fig. 5*c*). The sign of the autocorrelation changes in the original temperature series because of the gap between 1963 and 1985 (Fig. 5*d*). The remaining autocorrelation suggests that the original relationship may well have been spurious and was due to the autocorrelation of the variables in the regression.

Fig. 4. (*a*) Autocorrelation of the 3-year mean SIO pier temperature series for 1935–1963 and 1985–1990. Bars extending beyond broken lines indicate significant autocorrelation (*p* < 0.05). (*b*) Same as (*a*) after first differencing the series. (*c*) Autocorrelation of the stock–recruit (SR) anomaly series for 1935–1963 and 1985–1990. (*d*) Same as (*c*) after first differencing the series. (*e*) Autocorrelation of the residuals of the SR anomaly – SIO pier temperature model in Fig. 3*c*. (*f*) Same as (*e*) using first-differenced variables. (*g*) Autocorrelation of the residuals of the updated (1991–2008) SR anomaly – SIO pier temperature model in Fig. 3*d*. (*h*) Same as (*g*) using first-differenced variables.
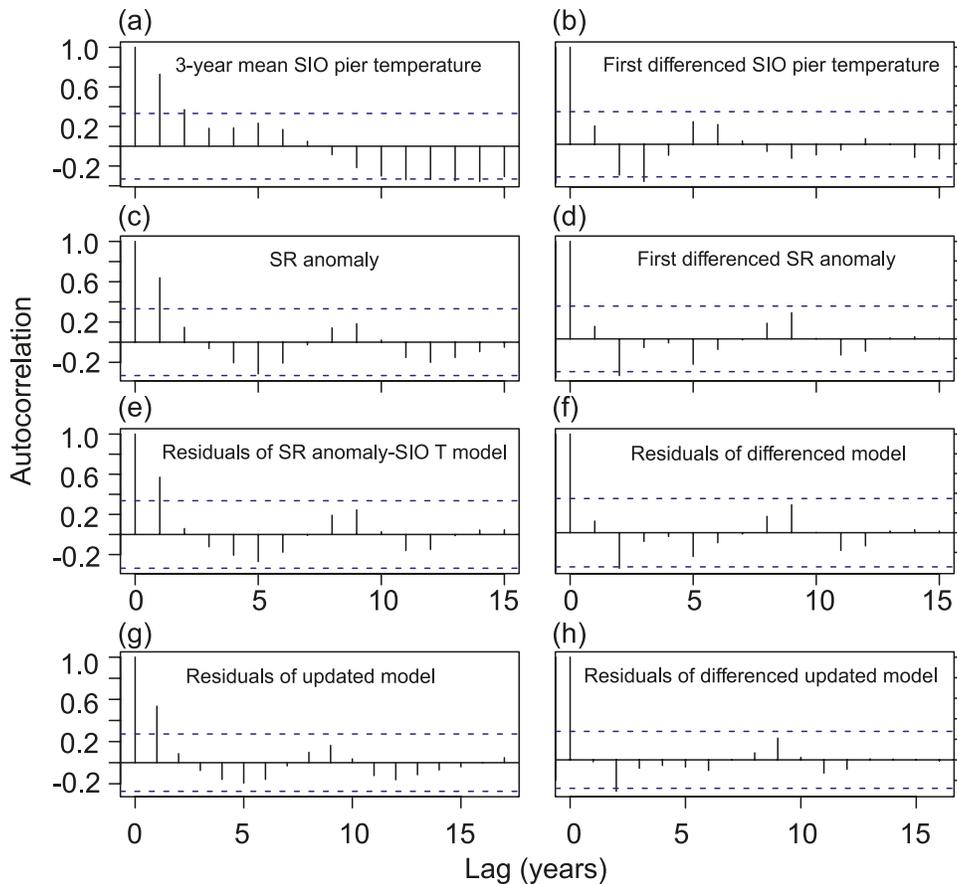
The failure of the temperature–recruit relationship is perhaps to be expected (Myers 1998). That being the case, the basis for the current decision rule in the Coastal Pelagic Species Fishery Management Plan based on the SIO pier temperature index is no longer justifiable, although temperature may affect the growth, fecundity, or later survival of sardines. In addition, we found no relationship between the offshore SCB temperatures and sardine SR anomalies or R/S anomalies, which means that we cannot simply substitute offshore SCB temperatures for the SIO pier temperatures. We need a new index, based on other environmental parameters. A cautionary note might be that any new index should be frequently re-assessed to determine if the underlying relationships can withstand adding new data.

Discussion

Addition of new data causes the temperature–recruit relationship (Jacobson and MacCall 1995) to fail using either the SIO pier temperatures or the offshore temperatures from areas where the sardine currently spawn. Our results show that one of the fundamental relationships (the temperature–recruit relationship) underpinning the stock–recruit-environment relationship does not fit the more recent data. The other fundamental relationship underpinning the original model (the

stock–recruit relationship) remains valid when tested with more recent data. Why should this be the case? By matching the early data points to the updated data points it is apparent that many of the more recent recruitment estimates are associated with warmer SIO pier temperatures. In fact, all of the years from 1991 to 2008 except 2001 had 3-year SIO pier temperatures ≥ 17.3 °C. Further, all of the years from 1991 to 2008 except 1998, 2002, 2007 and 2008 had negative SR anomalies, indicating that recruit numbers were lower than the mean after accounting for stock size. After removing the effect of SSB, low recruitment in the warmest years reduced the correlation between between age-2 recruits and temperature, causing the failure of the temperature–recruit relationship. This runs counter to the current theory that warm years are better for sardine recruitment.

The SIO pier temperatures no longer show the same trend as the offshore SCB temperatures where sardine are currently spawning. The explanation for the increasing difference between SIO pier and offshore SCB temperatures is not simple, because the SIO pier is more exposed to waters of tropical origins (e.g., through coastally trapped waves at the surface (Auad and Hendershott 1997) and through the California Undercurrent at deeper levels) while a good deal of the water masses present in the center of the SCB have a

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Fig. 5. (*a*) Autocorrelation of the monthly SIO pier temperature series before 3-year averaging. (*b*) Autocorrelation of the same monthly series after averaging. (*c*) Autocorrelation of 3-year mean SIO pier temperature yearly series. (*d*) Autocorrelation of 3-year mean SIO pier temperature yearly series for the years 1935–1963 and 1985–1990 used in Jacobson and MacCall (1995).
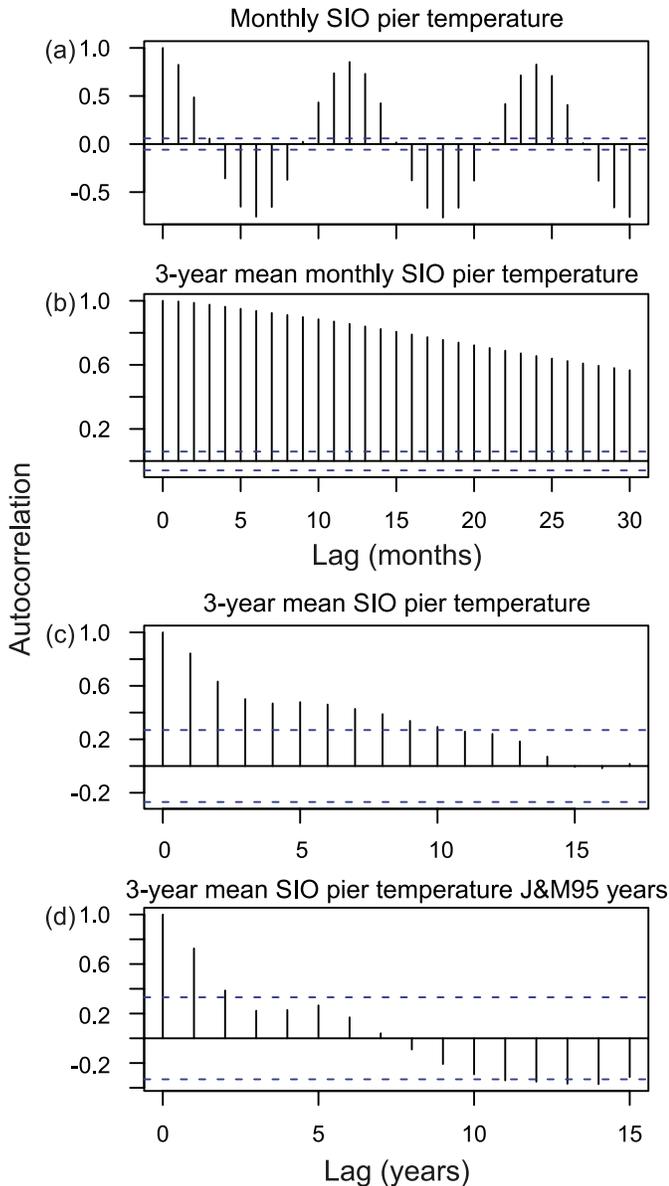
sub-arctic origin. Thus, depending on how the sources vary, the SIO pier to offshore SCB gradient will also vary. Warm, saline, low oxygen poleward flows characterize the coastal location of the SIO pier, but the offshore SCB is dominantly exposed to waters with lower temperature and salinity and higher oxygen content. The atmospheric forcing of these two areas is also different as wind speeds are significantly faster over the offshore SCB (Dorman and Winant 2000) than at the SIO pier.

In past sardine assessments based on the CANSAR model (Deriso et al. 1996; Hill et al. 1999), the approach to accounting for environmental effects on recruitment was to use the data in the direct calculation of the expected level of recruitment via an explicit term in the stock–recruit model. The approach currently preferred is to use the environmental data as if it were a survey observation of the recruitment deviation (Methot 2009; Schirripa et al. 2009). The environmental index is treated as if it were a survey of age-0 recruitment abundance because by focusing on the fit to the deviations it removes the effect of spawning stock biomass on recruitment. In this alternative, the recruitment variance (σ_R) would not be changed by the environmental data; instead the environmental data would be used to explain some of the total variability represented by σ_R. Moreover, this approach allows the environmental time series to be input with measurement error.

There is now considerable evidence that relationships between stock, recruitment, and environment may prove to be illusory (Myers 1998). In most cases where statistical relationships have been found between environmental variables and either the biomass of commercially exploited fishes or some index of recruitment, the relationships were not robust when further data were added to the original dataset (Myers 1998). The observation that stock–recruit-environment relationships generally fail has not prevented a burgeoning literature presenting newly discovered relationships. One emergent generalization from Myers (1998) is that stock–recruit-environment relationships tend to be more robust at the margins of a species geographical range. This is presumably because the physiological tolerances of species are approached and so the impact of climate change on environment has greater effect.

Interactions between environmental effects and the impacts of fishing on species biomass or recruitment are also affected by geographical location and species biogeographic range. Because environmental indices may show greater correlations with stock and recruitment at the margins of species range, the effects of environment alone could induce population collapse (Beaugrand and Kirby 2009). In the center of the species range, the effects of environment may be less, and the relative impact of fishing correspondingly greater. It is consequently difficult to develop environmental indices using data over an entire species range. This was shown by Beaugrand and Kirby (2009) where their plankton index was correlated with the decline of Atlantic cod (*Gadus morhua*) in the North Sea, but had low explanatory power for fluctuations of Atlantic cod biomass off Iceland. For the Pacific sardine, the modeled estimates of recruitment are derived from the SCB which is near the center of the species geographic range. We do not have data that would allow us to test stock–recruit-environment relationships at the margins of the range.

The effect of geographical range and the regional differences on the explanatory power of environmental indices is complicated by the evidence that populations and communities are modifying their geographical ranges with climate change (Hsieh et al. 2009). Developing indices necessarily requires time series, but if ranges are shifting latitudinally with climate change, the movement in the margins of the range will tend to obscure the relationship between environmental indices and biomass or recruitment by increasing variability in the relationship.

These considerations; that stock–recruit-environment relationships are strongest at the margins of a species biogeographic range, and that the ranges of populations shift with climate change indicate that stock–recruit-environment relationships are both spatially and temporally dynamic. Recent studies show that the search for stock–recruit-environment relationships that apply over the full spatial domain of a fish species or near the center of the geographic range using long time series of indices are doomed to temporary success at best.

There is some evidence that the most consistent explanatory variables are those that exert both direct effects on physiological tolerances and that affect food web processes such as energy allocation, predator–prey interactions and benthic–pelagic coupling (Kirby and Beaugrand 2009). Temperature is one such variable (Beaugrand and Kirby 2009; Kirby and Beaugrand 2009). Kirby and Beaugrand (2009) used partial correlation and path analysis to reveal consistent correlative relationships between the relative abundance of *Calanus finmarchicus* (an important prey item for larval Atlantic cod), and the biomass and recruitment of Atlantic cod. They interpreted these non-linear correlations as trophic amplification of the effects of temperature through the food web. The observation that the correlations are greatest with a time lag was used to infer that the amplification acts on sensitive life history stages, namely the larval phase of development. Although temperature exerted both direct and food web amplification effects on Atlantic cod larvae, temperature exerts a noisier effect on Pacific sardine. This raises the distinct possibility that the most consistent explanatory variables in stock–recruit-environment relationships is different between species.

What might a new environmental index for Pacific sardine recruitment look like? There have been studies addressing the effect of temperature, salinity, chlorophyll, mesoscale features, advection and wind on the spawning habitat, biomass, growth, survival and recruitment variability of Pacific sardine (Reiss et al. 2008; Rykaczewski and Checkley 2008; MacCall 2009, and references therein), but there are fewer studies on the effects of production, predators and prey. We plan to develop a new environmental index incorporating both physical variables and measures of larval predators and prey to replace the SIO pier temperature index. Given what we know about communities shifting geographic range under climate change and the sensitivity to environmental variability at the edges of a species range, spatial modeling is expected to play an important role in producing a more robust environmental index.

Acknowledgments

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