Influences of changing temperature and upwelling intensity on Indian oil sardine landings

# Abstract

Commercial landings of sardines are known to show strong year-to-year fluctuations. A key driver is thought to be environmental variability, to which small forage fish are especially sensitive. We examined environmental drivers associated with Indian oil sardine landing fluctuations using a 32-year time series of quarterly catches. Potentially influential variables examined included precipitation, upwelling intensity, sea surface temperature (SST), chlorophyll concentration, and large-scale coupled atmosphere–ocean phenomena [El Niño–Southern Oscillation (ENSO) patterns]. Using the life history of the Indian oil sardine, we developed hypotheses concerning the effects of these variables on landings and tested them using generalized additive models, which allow for non-linear response curves, and dynamic linear models, which allow for time-varying responses. We found significant correlations of upwelling intensity, an ENSO index, and the multiyear average nearshore SST with landings. Upwelling had a positive effect (fueling higher food availability) at lower intensity, and a negative effect at extreme intensity (surface anoxia) for the monsoon and post-monsoon catches. The most significant correlation found was between the 2.5-year average nearshore SST and post-monsoon landings (adjusted *R*2 = 67.5%). This result is consistent with previous findings and suggests that the average SST over the sardine lifespan successfully captures a variety of factors that predict future abundance. The Western Indian Ocean has been warming steadily, and changes have been most extreme during the summer monsoon. Our work highlights the likelihood that these changes will affect oil sardine landings.

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# 1 INTRODUCTION

Environmental variability is known to be a key driver of population variability for small forage fish, such as sardine, anchovy, and herring (Alheit & Hagen, 1997; Checkley, Asch, & Rykaczewski, 2017; Cury et al., 2000). In particular, ocean temperature and upwelling dynamics, together with density-dependent feedback, substantially affect the recruitment success and biomass of European and Pacific sardines (*Sardina pilchardus* and *Sardinops sagax*, respectively; Alheit et al., 2012; Garza-Gil, Varela-Lafuente, Caballero-Míguez, & Torralba-Cano, 2015; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012; Lindegren, Checkley, Rouyer, MacCall, & Stenseth, 2013; Rykaczewski & Checkley, 2008). Upwelling, influenced by large-scale forces such as regimes shifts and El Niño–Southern Oscillation (ENSO) patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010), as well as by seasonal wind and current patterns, brings nutrient- and oxygen-rich waters to the surface, driving seasonal variability in phytoplankton resources and, in turn, sardine prey (Bakun, Roy, & Lluch-Cota, 2008). Local variability in temperature, salinity, and oxygen levels has direct and indirect effects on sardine reproduction, recruitment, and survival (Checkley et al., 2017). Sardines are also influenced by competition and predation by other species, and are known to be sensitive to overfishing, which has been linked to the collapse of many fisheries (Kripa et al., 2018).

Like other sardines, the Indian oil sardine (*Sardinella longiceps* Valenciennes, 1847) shows strong interannual fluctuations in abundance and larger decadal booms and busts. This fish can provide an instructive case study for investigation of the effects of environmental variability, as it lives in a warmer ocean system than do other sardines and has a strong seasonal cycle driven by the Indian summer monsoon. It is among the most commercially important fish resources along the southwestern coast of India; historically, it has comprised approximately 25% of the marine catch in Indian fisheries (Vivekanandan, Srinath, Pillai, Immanuel, & Kurup, 2003). Landings of this small pelagic finfish are highly seasonal, peaking in October–December, after the summer monsoon period, and reaching a nadir in April–June, before the monsoon. In addition to effects on biomass seen for all sardine species, environmental conditions affect the fishery exposure of the Indian oil sardine. Until recently, this fishery was artisanal, based on small human- and small motor–powered boats with no refrigeration. As it is confined to nearshore waters (Rohit et al., 2018), the migration of sardines into and out of the coastal zone has greatly affected exposure to the fishery and hence landings.

Correlations of various environmental variables with Indian oil sardine landings have been examined. Precipitation during the monsoon and the day of monsoon arrival are thought to act as direct or indirect cues for spawning (Antony Raja, 1969, 1974; Jayaprakash, 2002; Murty & Edelman, 1966; Pitchaikani & Lipton, 2012; Srinath, 1998; Xu & Boyce, 2009). Identified correlations between precipitation and landings, however, have been positive in some studies and negative in others (Madhupratap, Shetye, Nair, & Nair, 1994). Correlations have also been identified with various metrics of upwelling intensity (Jayaprakash, 2002; Longhurst & Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara, 2011); direct measures of productivity, such as nearshore zooplankton and phytoplankton abundance (George et al., 2012; Madhupratap et al., 1994; Menon et al., 2019; Nair, 1952; Nair & Subrahmanyan, 1955; Piontkovski, Al Oufi, & Al Jufaily, 2014; Pitchaikani & Lipton, 2012); and nearshore sea surface temperature (SST; Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed, 1970; Supraba et al., 2016). SST can affect somatic growth rates and juvenile survival; in the Indian system, it also can cause fish to move offshore. The multiyear average sea temperature is postulated to affect the recruitment and survival of larval and juvenile sardines, which affect subsequent overall abundance (Checkley et al., 2017; Takasuka, Oozeki, & Aoki, 2007). The ENSO has a cascading effect on SST, precipitation, and upwelling, and correlations have been found between ENSO indices and sardine landings (Rohit et al., 2018; Supraba et al., 2016), as well as coastal anoxic events that affect sardines (Vallivattathillam et al., 2017).

In this study, we examined the utility of environmental covariate data obtained by remote sensing in explaining year-to-year variability in Indian oil sardine landings using a lengthy quarterly time series derived from stratified surveys of fishery landing sites, first conducted in the 1950s (Srinath, Kuriakose, & Mini, 2005). The goal was to identify environmental covariates that explain catch variability and improve the accuracy of short-term catch forecasts. Landings are products of biomass, catchability, and effort. A traditional autocorrelated catch [autoregressive integrated moving average (ARIMA)] model can capture smooth changes in landings, such as those occurring due to changes in fleet size or multiyear biomass, but not the large environmental component of year-to-year variability. The environment has strong effects on catchability in the Indian oil sardine system, via effects on the inshore versus offshore distribution of the fish. The covariates examined in this study are linked to aspects of oil sardine life history that are expected to affect catch via catchability or biomass. We used remote sensing data due to their broad spatial extent and daily and monthly resolutions, which make them practical for operational forecasting. A better understanding of whether and how remote sensing data explain variation in seasonal catches will support future efforts to use satellite data to improve catch forecasts.

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## 1.1 Catch versus biomass modeling

The modeling and forecasting of landings using statistical models fit to annual and seasonal catch time series has long been performed in fisheries research on many species (Cohen & Stone, 1987; Farmer & Froeschke, 2015; Georgakarakos, Doutsoubas, & Valavanis, 2006; Hanson, Vaughan, & Narayan, 2006; Lawer, 2016; Lloret, Lleonart, & Sole, 2000; Mendelssohn, 1981; Nobel & Sathianandan, 1991; Prista, Diawara, Costa, & Jones, 2011; Stergiou & Christou, 1996), including oil sardines (Srinath, 1998; Venugopalan & Srinath, 1998). These models can be used to identity variables correlated with catch fluctuations and to provide landings forecasts, which are useful for fishery managers and the fishing industry. For example, catch forecasts that exceed the permitted limits can prompt the setting of or warning about seasonal fishery closures (Farmer & Froeschke, 2015). The annual Gulf and Atlantic menhaden landings forecast produced by the National Oceanic and Atmospheric Administration (NOAA) Fisheries, based on a multiple regression model, has been used for the last 45 years for planning in the industry, among fishers, fish sellers and buyers, businesses providing fishery gear, and banks providing financing (Hanson et al., 2006; Schaaf, Sykes, & Chapoton, 1975).

As this study was conducted to understand drivers of landing variability, the assumption of a close relationship between landings and abundance was not required. However, Indian oil sardine landings are often assumed to reflect total abundance for species- and fishery-specific reasons (cf. Kripa et al., 2018). The ring seine was introduced in this fishery in the 1980s, but widespread mechanization of the fleet is a very recent development. Fishers with small boats have limited ability to target stock, at least not to the degree that landings remain constant as stock declines, as seen with a large, mobile, highly mechanized fleet. As the fishery is unregulated, except for brief closure during the monsoon months, landings are not affected by area closures or catch limits. Finally, the fishery is dispersed along the entire coastline, rather than being focused from a few large ports. Thus, landings need not be a tight index of biomass, but this relationship can be assumed to be strong for many reasons.

Estimation of the Indian oil sardine’s historical biomass is not possible. Length- and age-structured models (e.g., for virtual population analyses) that produce biomass estimates cannot be constructed due to the lack of effort and catch-at-age information for the fishery. The available long-term effort data are indirect (i.e., fishery boat composition at multiyear intervals), and estimates of the numbers of trips and hours fishing are available for only a few recent years, and are approximate due to the diversity of fishery vessels and to sampling constraints. Nonetheless, the number and size of boats involved in the fishery have been increasing. Oil sardines are caught primarily by ring seines, different sizes of which are used on traditional small boats and large mechanized ships (Das & Edwin, 2018). Since 1985, the ring seine fishery has expanded steadily in terms of horsepower, boat size, and net length. Concern about overfishing has been spurred by recent (post-2015) oil sardine declines (Kripa et al., 2018). Steadily increasing effort is assumed to have increased landings, at least prior to 2015. We thus used an autoregressive base catch model to capture smooth landing trends due to increased effort (or multiyear changes in biomass).

### 1.2 Study area

The study area is located off the Kerala coast of India (Figure 1), where the majority of Indian oil sardines are landed and where this species comprises about 40% of the marine fish catch (Srinath, 1998; Vivekanandan et al., 2003). It is in the Southeast Arabian Sea, one of the world’s major upwelling zones (Habeebrehman et al., 2008; Madhupratap, Gopalakrishnan, Haridas, & Nair, 2001). The portion of the study area falling between 9N 13N has especially intense upwelling due to the combined effects of wind stress and remote forcing (BR, 2010; BR, Sanjeevan, Vimalkumar, & Revichandran, 2008). The results are a strong temperature differential between the nearshore and offshore, and high primary productivity and surface chlorophyll in June–September (BR, 2010; Chauhan et al., 2011; Habeebrehman et al., 2008; Jayaram, Chacko, Joseph, & Balchand, 2010; Madhupratap et al., 2001; Raghavan et al., 2010). Primary productivity subsides after September, whereas mesozooplankton abundances increase and remain high in the post-monsoon period (Madhupratap et al., 2001).

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### 1.3 Oil sardine life cycle and fishery

The Indian oil sardine fishery is restricted to the narrow strip of the western Indian continental shelf, <20 km offshore (Figure 1). The yearly cycle of these sardines begins with spawning in June and July (when the fishery is closed), corresponding to the onset of the summer monsoon (Antony Raja, 1969; Chidambaram, 1950) and much lower nearshore SSTs due to upwelling (Figure 2). Mature fish migrate from offshore to coastal spawning areas (outside of the traditional fishery range) (Antony Raja, 1964), and spawning begins when temperature, salinity, and food availability are conducive to larval survival (Chidambaram, 1950; Jayaprakash & Pillai, 2000; Krishnakumar et al., 2008; Murty & Edelman, 1966; Nair, Joseph, Kripa, Remya, & Pillai, 2016). After an initial peak, spawning continues into September (Antony Raja, 1969; Hornell, 1910; Hornell & Nayudu, 1924; Prabhu & Dhulkhed, 1970), and early- and late-spawning cohorts are evident in the length distributions of 0-year fish. After spawning, adults migrate closer to the coast, where the spent fish become exposed to the fishery.

Spawned sardine eggs develop rapidly into larvae (Nair, 1959). The phytoplankton bloom that provides food for the larvae depends on nutrient influx from coastal upwelling and runoff from rivers during the summer and early fall. Blooms start near the southern tip of India in June, then increase in intensity and spread northward (BR, 2010). Variation in the bloom initiation time and intensity leads to changes in the food supply, and thus in larval growth and survival and subsequent recruitment of 0-year sardines into the fishery (George et al., 2012). Oil sardines grow rapidly in the first few months of life, and 0-year fish from early spawning (40–100 mm in length) appear in the August and September catches in most years (Antony Raja, 1970; Nair et al., 2016). As the oil sardines follow the phytoplankton bloom northward, the fishery builds from south to north during the post-monsoon period. Oil sardines remain inshore to feed in winter; in March–May, they move offshore to deeper waters due to considerable inshore warming (Chidambaram, 1950). Sardine catches are correspondingly low during this period for all size classes. The sardines reach maturity (~150 mm long) within 1 year (Nair et al., 2016).

Catches along the Kerala coast are high throughout the year, except in April–June (Figure 3). The age distribution of fishery catches varies over the course of the year. When the fishery opens in mid-July, catches are dominated by 1–2.5-year-old fish (Antony Raja, 1969; Bensam, 1964; Nair et al., 2016). Spikes of 0-year fish are seen in August/September catches, and sometimes in the February catch (reflecting late spawning; Antony Raja, 1969; Nair et al., 2016; Prabhu & Dhulkhed, 1967, 1970). October–June catches are dominated by 120–180-mm-long fish aged 0–2 years (Antony Raja, 1970; Nair et al., 2016; Prabhu & Dhulkhed, 1970; Rohit et al., 2018).

# 2 MATERIALS AND METHODS

## 2.1 Sardine landing data

The Central Marine Fisheries Research Institute (CMFRI), Kochi, India, has collected quarterly fish landing data along the country’s southwestern coast since the early 1950s using a stratified multistage sampling design (e.g., accounting for various boat and gear types; Srinath et al., 2005). We used CMFRI data from Kerala, the longest and most sardine-centered time series available, in this study. Quarterly oil sardine landings data (in metric tons) for all gear types used in Kerala were obtained from CMFRI reports (1956–1984) and online databases (1985–2015; Appendix G). These data were log transformed to stabilize variance.

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## 2.2 Remote sensing data

We analyzed monthly composites of the following environmental data derived from satellite data: SST, chlorophyll-a concentration, upwelling, precipitation, the Oceanic Niño Index (ONI), and the Dipole Mode Index (DMI; Figure 4; Appendix G). SST and chlorophyll-a satellite data were retrieved from NOAA remote-sensing data servers and averaged across thirteen 1° × 1° boxes, which roughly parallel the bathymetry of the study area.

For SST, we used Advanced Very-High Resolution Radiometer data, which provides more accurate nearshore values than does the International Comprehensive Ocean-Atmosphere Data Set, but for a more limited time period. For 1981–2003, we used the Pathfinder (version 5.2) product on a 0.0417° grid with data developed by the Group for High Resolution Sea Surface Temperature and served by the US National Oceanographic Data Center. For 2004–2016, we used the CoastWatch SST products derived from NOAA’s Polar Operational Environmental Satellites.

For chlorophyll-a, we used the products developed by the Ocean Biology Processing Group of the Ocean Ecology Laboratory at the National Aeronautics and Space Administration (NASA) Goddard Space Flight Center. For 1997–2002, we used the chlorophyll-a 2014.0 reprocessing product from the Sea-viewing Wide Field-of-view Sensor on the Orbview-2 satellite, which contains data on a 0.1° grid. For 2003–2017, we used the Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua product, which contains data on a 0.05° grid obtained by MODIS on NASA’s Aqua Spacecraft.

For coastal upwelling, we used three indices. The first index is the SST differential between nearshore and 3° offshore, based on Naidu, Kumar, and Babu (1999) and BR et al. (2008). This index has been validated and shown to be more reliable than wind-based upwelling indices for the Kerala coast region (BR et al., 2008), and has a strong temporal association with chlorophyll-a blooms (Figure 2). SSTs were obtained from the remote-sensing data sets described above. The second index was the average nearshore SST along the Kerala coast (Figure 1, average of boxes 2–5). The third index was the Bakun index, which is based on wind stress and computed from the *x* and *y* components of Ekman transport.

Precipitation data were obtained from two sources: estimated monthly precipitation (in millimeters) over Kerala, obtained with land-based rain gauges and available from the Indian Institute of Tropical Meteorology from 1956; and estimated precipitation over the ocean since 1979 on a 2.5° grid from a remote-sensing product of the NOAA Global Precipitation Climatology Project. From the latter, we extracted data for the 2.5° × 2.5° box defined by latitude 8.75–11.25 and longitude 73.25–75.75. The land and nearshore ocean precipitation data were highly correlated (Appendix D).

The ONI is a measure of the SST anomaly in the east-central Pacific and a standard index of the ENSO cycle. More specifically, it is 3-month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region, based on centered 30-year base periods updated every 5 years. For this study, we downloaded the ONI from the NOAA National Weather Service Climate Prediction Center.

The DMI is defined by the SST anomaly difference between the western (10°S–10°N, 50°E–70°E) and southeastern (10°S–0°, 90°E–110°E) Indian Ocean. It has been shown to predict anoxic events in the study area (Vallivattathillam et al., 2017). DMI data were downloaded from the NOAA Earth System Research Laboratory.

## 2.3 Hypotheses

We developed hypotheses about correlations between quarterly landings and remote-sensing covariate data from specific months, based on information about the effects of environmental conditions presented above (Table 1). We hypothesized that variables affecting or correlated with the inshore movement of sardines would correlate with July–September (monsoon- and spawning-period) landings, that variables correlating with spawning strength would correlate with March–May (pre-spawning, accelerated adult growth–period) landings, and that variables correlated with spawning strength and larval/juvenile survival would correlate with October–May (post-monsoon, mixed-age catch–period) landings in the current year and subsequent 1–2 years. We focused on upwelling and SST as drivers. We also tested hypotheses concerning precipitation, historically considered to influence the timing of oil sardine landings, and those concerning the ONI and DMI, as the effects of the ENSO on sardine fluctuation have received attention recently. Lastly, we tested hypotheses concerning the chlorophyll-a concentration, as this concentration correlates directly with sardine food availability and chlorophyll fronts influence sardine shoaling, but the power for these analyses was low given the brevity of the chlorophyll time series.

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## 2.4 Statistical models

We modeled yearly series of July–September (late-monsoon) and October–March (post-monsoon) catches separately, meaning that seasonality was absent, for biological and statistical reasons. Unlike the October–March catch, the July–September catch contains a mixture of spawning-age fish, is affected by fishery closure, and is periodically inflated by 0-year fish from early spawning. In addition, covariates that affect the timing of spawning, post-spawning inshore movement of mature fish, and early egg and larval survival may differ from those that affect later growth, survival, and shoaling (and thus fishery exposure). The absence of seasonality also provided a statistical advantage, as it eliminated confounding influences and permitted a focus on year-to-year variability; a simple statistical model, by contrast, would “explain” much of the quarterly catch data because most yearly variability is due to seasonality and any environmental covariate with similar seasonality would correlate strongly with landings.

In preliminary testing of ARIMA models, we found little support for autoregressive errors (ARIMA models with MA components) based on diagnostic tests of the residuals and model selection. The best-supported ARIMA models were simple AR models (). Similar lack of strong autocorrelation in residuals has been found in other studies involving the testing of ARIMA models for the forecasting of small pelagic catches (Stergiou & Christou, 1996). We thus used AR-only models; however, we tested linear and non-linear models with generalized additive models (GAMs; Wood, 2017) of the form and time-varying linear models with dynamic linear models (DLMs). GAMs enable modeling of the effect of a covariate as a flexible non-linear function and permit estimation of the smoothing parameter for the response curve, and DLMs allow the effect of the covariate to vary over time. Our GAM approach is analogous to that taken by Jacobson and MacCall (1995) in a study of the effects of SST on Pacific sardine recruitment.

The first step in our analysis was to determine the model for current catch as a function of past catch. We explored four classes of model: naïve (null) models with a simple function of prior catch, linear regressive models with 1–2 years of prior catch data, DLMs (using the MARSS package in R; Holmes, Ward, & Wills, 2012), and GAMs. We fit GAMs with smooth terms represented by penalized regression splines (using the mgcv package in R; Wood, 2011) and fixed the smoothing term at an intermediate value (sp = 0.6) to obtain smooth responses, as multimodal or overly flexible response curves would not be realistic for our application. We thus compared the following catch models:

* naïve (null):
* random walk:
* linear AR-1:
* linear AR-2:
* DLM AR-1:
* GAM AR-1:
* GAM AR-2:

is the log catch in the current year in season and is a non-linear function estimated by the GAM algorithm. The models are primarily statistical, and should not be thought of as population growth models. We tested models with the inclusion of 1 and 2 prior years for the October–March ( and ) and July–September ( and ) catches as the explanatory catch variables. was not used as a predictor for because is the immediately preceding quarter, and data would not be available for forecast models due to processing time requirements. The catch models were fit to 1984–2015 catch data, as SST, upwelling, and precipitation data were available for this period. *F* tests, Akaike information criterion (AIC) calculation, and leave-one-out cross-validation (LOOCV) were applied to nested sets of models (Wood, Pya, & Säfken, 2016) to evaluate support for the catch, and subsequently covariate, models. LOOCV involves model fitting with the omission of a datapoint, followed by prediction of that datapoint. The root mean squared error is reported for the set of prediction errors (also known as the predicted residual error sum of squares). After selection of the best model using the 1984–2015 data, fitting was repeated with catch data from 1956–1983 to confirm the catch model form. An influential years test was performed by removing each year in the series sequentially and repeating the model selection analysis.

After establishment of the catch models, covariates from the study hypotheses were studied individually and then in pairs (correlated covariates were not entered into the same model). As with the catch models, support was evaluated using *F* tests, AIC calculation, and LOOCV with nested sets of models and the smoothing term was fixed at an intermediate value (sp = 0.6). Models with covariates (*V*) modeled as a linear, non-linear, and time-varying effects were compared: , , and , where is the best catch model from step 1.

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# 3 RESULTS

## 3.1 Catch model selection

For 1984–2015 July–September catches, models with the October–March catch in the prior year [] serving as the explanatory covariate were strongly supported over the naïve model and over models with the prior-year July–September catch [ serving as the explanatory variable (Tables A1 and A2). The use of 2 years of prior catch [ or ] was not supported by AIC or *F* values for the linear or non-linear models. In the comparison of GAMs with or included as a linear or non-linear effect, the use of a non-linear response reduced the residual error and LOOCV, but at the increased the degrees of freedom (Table A2). Three models had almost identical AICs and LOOCV: linear and non-linear models with , and a non-linear model with and . We choose the non-linear model with as the base catch model based on further diagnostic tests (described below) and to minimize the loss of degrees of freedom. The adjusted value for this model was 24.4.

Similar model selection results were obtained for the October–March landings, but these models explained much more variance (maximum adjusted ). The best-supported model based on AIC and *F* values, was the non-linear model with and , and this model exhibited more out-of-sample prediction accuracy (LOOCV) than did the naïve model (Tables A3 and A4). The simpler model with only had the second lowest AIC (lower than the naïve model) and lowest LOOCV values. This model was also included as a base model for the October–March catch.

Repeated model comparison using 1956–1983 data yielded the same results for the July–September catch, with the non-linear model with having the lowest AIC and LOOCV values (Table A5). For the October–March catch, the results were very similar, but not identical. The non-linear model with had the lowest LOOCV value, and the models with and or had the lowest AICs [although the difference from the AIC for the model was <1;Table A6]. The influential years analysis supported the base models selected using the 1984–2015 data (Appendix F). The DLMs performed poorly for the July–September catch, with high AIC and LOOCV values. One DLM for the October–March catch showed mixed performance, with a higher AIC and lower LOOCV value.

Ultimately, the following non-linear base model (weakly explanatory: *R*2 < 30%) was chosen for the July–September catch:

Two non-linear base models were chosen for the October–March catch:

(*R*2 = 45.3) and

(*R*2 = 56.6).

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## 3.2 Environmental covariate selection

Our analyses provided no support for the use of April–May or June–July precipitation (in the current or prior season, or as a linear or non-linear effect) as an explanatory variable for the July–September or October–March catch (hypotheses S1 and S2; Tables B1–B3). We also found no support for the use of March–May (current or prior year) or October–December SST as an explanatory variable for the July–September catch, and only weak support (based on the AIC) for the use of the current-season March–May SST as an explanatory variable for the October–March catch (hypotheses S4, S5, and L1; Tables B4–B6). The prior fall average SST did not explain variability in the July–September or October–March catch. In addition, we found no correlation between the ONI and the July–September or October–March catch (hypothesis A2; Tables B7–B9).

The two indices of upwelling in the current season (June–September average nearshore SST and average nearshore/offshore SST differential) correlated with the July–September and October–March catches (Tables 2 and B4–B6). Better support was found for non-linear models including the June–September average nearshore SST (July–September catch, adjusted = 41.0 vs. 24.4 for the model with no covariate; October–March catch, adjusted = 61.8 vs 56.6; Tables B4 and B5).

Our examination of the chlorophyll covariate was limited, as the simplest model including the chlorophyll-a concentration required five degrees of freedom, and catch size varied little in the period for which we had chlorophyll data (1998–2014: July–September, 10–11 metric tons; October–June, 11–12 metric tons). The fitting of second-degree polynomial models to the average log chlorophyll-a concentrations in July–September, October–December, and January–March of the current and prior years yielded no significant result for the July–September catch, and a significant effect of the prior-year October–December chlorophyll-a concentration on the October–March catch (Tables C1–C3).

The strongest correlations were found between a non-linear model with the average nearshore SST for 2.5 prior years and the July–September (adjusted *R*2, 41.0 versus 24.4 for the model without the covariate) and October–March (a, 67.5 vs. 56.6; Tables 2 and B7–B9) catches. The response curve was step-like, with a negative effect at low temperatures (<28.35°C) and a flat positive effect at higher temperatures (>28.5°C; Figure 5). This covariate can be used for forecasting because it does not overlap with the July–September or October–March catch. The only other strong correlation found was between the prior-season DMI with and and the October–March catch.

We identified four outlier years in which October–March oil sardine landings were much lower than expected based on prior catches: 1986, 1991, 1994, and 2013 (Figure 6c). The 2.5-year average SST explained the collapses in 1986 and 1991; the catch sizes predicted with the model including this covariate were much closer to the observed catches (Figure 6d). The 2.5-year average SST did not explain the 1994 collapse, the largest during the study period, or the 2013 collapse, as the sizes of the residuals did not differ in models with and without this covariate. The same pattern was seen for the July–September catch, with the exception that this catch was not unusually low in 1991. The 2.5-year average SST reduced the prediction error for this catch in 1986, but did not (appreciably) reduce it for 1994 or 2013. No covariate tested in this study explained the lesser-than-expected 1994 and 2013 catches.

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# 4 DISCUSSION

In this study, the multi-season average nearshore SST explained the most variability in monsoon and post-monsoon Indian oil sardine landings off the Kerala coast. Similarly, studies conducted in the California Current System have shown that SST, and more specifically the multi-season average nearshore temperature, explains at least a portion of the year-to-year variability in Pacific sardine recruitment (Checkley, Alheit, Oozeki, & Roy, 2009; Checkley et al., 2017; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012). This covariate has also been found to correlate with southern African sardine recruitment (Boyer, Boyer, Fossen, & Kreiner, 2001). In contrast, McClatchie, Goericke, Auad, and Hill (2010) found no relationship between SST and Pacific sardine recruitment, but they examined this relationship linearly; in the present study, allowance of non-linearity yielded significant results. Moreover, we found a step-like response function for temperature. Jacobson and MacCall (1995) and Checkley et al. (2017) reported similar patterns, with linear negative effects below threshold values and flat positive effects above these values.

All GAM catch models tested in this study showed better predictive performance than did the naïve models. We found that the addition of the 2.5-year average SST improved prediction the most for the October–March catch (by 22.1% with M1 and 17.5% with M2). For the July–September catch, only the current-season June–September SST reduced the prediction error (by 8.2%). Given the temporal overlap, models including this covariate cannot be used to forecast the July–September catch, and they give only a 1-month-prior forecast for the October–March catch; these results, however, do help us to understand which factors potentially influence catches. The July–September catch is difficult to forecast, as it exhibits high variability that is poorly explained by past catches or environmental factors. In contrast, the October–March catch is much better explained by prior catches, with smaller predictive errors.

Although the March–May SST has been speculated to correlate with successful egg development and spawning behavior, and extreme heat events in the pre-spawning period have been associated with low recruitment, we found no correlation of this covariate with the July–September catch. The SST in October–December, the period of larval and early juvenile development, may affect survival and growth in multiple ways and thus correlate with biomass in future years. However, we found no such correlation in this study. Instead, we found support for (current-year) upwelling intensity and (prior-year) surface chlorophyll-a concentrations, which are associated directly and indirectly with productivity and food availability. We also found that the prior-season DMI, which has been shown to correlate with nearshore anoxia off the Kerala coast (Vallivattathillam et al., 2017), with the October–March catch.

Despite the strong connections of upwelling with sardine recruitment, growth, and survival, none of the prior-season upwelling indices examined in this study explained the year-to-year variation in landings. We did find that the current-season upwelling intensity explained variability in current-season landings, but this effect was negative, rather than positive, and emerged only with extremely high upwelling. This negative effect is not surprising. Extremely high upwelling transports larval sardines offshore and creates regions of low oxygen that sardines avoid (Gupta et al., 2016). What was surprising is that the effect was not unimodal; it was positive with low to moderate upwelling and became negative for extremely high upwelling.

Although the July–September catch overlaps with the late spawning period and precipitation is often thought to trigger spawning, we found no association with precipitation for either catch in this study. Our precipitation data may have been at too coarse a temporal scale; Antony Raja (1974) posited that rainfall effects occur in the weeks before and after the new moon, when spawning is postulated to occur, and such effects would not be captured by the examination of total rainfall during the monsoon season.

The unusual declines in July–September landings observed in 1994 and 2013 in this study appear unrelated to the environmental factors we studied, suggesting that they were driven by biological or anthropogenic factors, or by particular combinations of environmental factors. In addition, the upwelling indices tested in this study captured only nearshore intensity, whereas other aspects of upwelling, such as its spatial extent along the coast and offshore and the timing of its initiation, also affect Indian oil sardines.

# 5 CONCLUSIONS

Satellite remote sensing can be used to detect changes in physical, biological, and chemical properties of the ocean, such as surface temperature, wind, surface height, surface waves, rainfall, and surface salinity, as well as ecosystem and water-quality changes. Unlike in-situ measurement, remote sensing enables the rapid acquisition of environmental measurements over large regions. In the case of the Indian oil sardine, however, the life history of the fish alone does not clarify which environmental covariates can improve landing forecasts. In this study, we tested many covariates that are known or have been postulated to affect sardine spawning, growth, and survival. We found that the multiyear average nearshore ocean temperature explained the most variability in landings and best improved out-of-sample prediction. This covariate is not tied to stages of the oil sardine life cycle as directly as are other covariates we tested, although it does integrate multiple influences (i.e., upwelling strength and temperature).

The temperature of the Western Indian Ocean, of which the Southeast Arabian Sea is a part, has been increasing over the last century at a greater rate than in any other tropical ocean (Roxy, Ritika, Terray, & Masson, 2014), and warming has been most extreme during the summer monsoon months. This ocean climate change is affecting the oil sardine distribution, with significant landings now occurring north of Goa (Vivekanandan, Rajagopalan, & Pillai, 2009). Continued warming is expected to affect the productivity of the region via multiple pathways, including direct effects of temperature change on the physiology and behavior of organisms and multiple indirect effects, including changes in salinity, oxygen concentrations, currents, wind patterns, ocean stratification, and upwelling spatial patterns, phenology, and intensity (Moustahfid, Marsac, & Grangopadhyay, 2018). The incorporation of environmental covariates into landings forecasts has the potential to improve fishery management for small pelagic species, such as oil sardines, in the face of a changing ocean environment (Haltuch et al., 2019; Tommasi et al., 2016). However, the monitoring of model covariate and overall forecast performance is crucial, as changes in the ocean environment may alter associations, such as that observed between landings and average SST in this study.

# REFERENCES

Alheit, J., & Hagen, E. (1997). Long-term climate forcing of European herring and sardine populations. *Fisheries Oceanography*, *6*(2), 130–139. [https://doi.org/10.1046/j.1365-2419.1997.00035.x](https://doi.org/https://doi.org/10.1046/j.1365-2419.1997.00035.x)

Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., … Wagner, C. (2012). Climate variability drives anchovies and sardines into the North and Baltic Seas. *Progress in Oceanography*, *96*(1), 128–139. [https://doi.org/10.1016/j.pocean.2011.11.015](https://doi.org/https://doi.org/10.1016/j.pocean.2011.11.015)

Annigeri, G. G. (1969). Fishery and biology of the oil sardine at Karwar. *Indian Journal of Fisheries*, *16*(1/2), 35–50.

Antony Raja, B. T. (1964). Some aspects of spawning biology of Indian oil sardine Sardinella longiceps Valenciennes. *Indian Journal of Fisheries*, *11*(1), 45–120.

Antony Raja, B. T. (1969). Indian oil sardine. *CMFRI Bulletin*, *16*, 1–142.

Antony Raja, B. T. (1970). Estimation of age and growth of the Indian oil sardine, Sardinella longiceps Val. *Indian Journal of Fisheries*, *17*(1/2), 26–42.

Antony Raja, B. T. (1974). Possible explanation for the fluctuation in abundance of the Indian oil sardine, Sardinella longiceps Valenciennes. *Proceedings of the Indo-Pacific Fisheries Council*, *15*(3), 241–252.

Bakun, A., Roy, C., & Lluch-Cota, S. (2008). Coastal upwelling and other processes regulating ecosystem productivity and fish production in the western Indian Ocean. In K. Sherman, E. N. Okemwa, & M. J. Ntiba (Eds.), *Large marine ecosystems of the Indian ocean : Assessment, sustainability and management* (pp. 103–141). Londres: Blackwell.

Bensam, P. (1964). Growth variations in the Indian oil sardine, Sardinella longiceps Valenciennes. *Indian Journal of Fisheries*, *11 A*(2), 699–708.

Boyer, D. C., Boyer, H. J., Fossen, I., & Kreiner, A. (2001). Changes in abundance of the northern Benguela sardine stock during the decade 1990 to 2000 with comments on the relative importance of fishing and the environment. *South African Journal of Marine Science*, *23*(1), 67–84. [https://doi.org/10.2989/025776101784528854](https://doi.org/https://doi.org/10.2989/025776101784528854)

BR, S. (2010). *Coastal upwelling of the south eastern Arabian Sea — an integrated approach*. Kerala, India: PhD Thesis. Physical Oceanography. Cochin University of Science; Technology.

BR, S., Sanjeevan, V. N., Vimalkumar, K. G., & Revichandran, C. (2008). On the upwelling of the southern tip and along the west coast of India. *Journal of Coastal Research*, *24*(sp3), 95–102. [https://doi.org/10.2112/06-0779.1](https://doi.org/https://doi.org/10.2112/06-0779.1%20)

Chauhan, O. S., Raghavan, B. R., Singh, K., Rajawat, A. S., Kader, U., & Nayak, S. (2011). Influence of orographically enhanced SW monsoon flux on coastal processes along the SE Arabian Sea. *Journal of Geophysical Research. Oceans*, *116*(12), C12037. [https://doi.org/10.1029/2011JC007454](https://doi.org/https://doi.org/10.1029/2011JC007454)

Checkley, D. M., Alheit, J., Oozeki, Y., & Roy, C. (2009). *Climate change and small pelagic fish*. Cambridge: Cambridge University Press.

Checkley, D. M., Asch, R. G., & Rykaczewski, R. R. (2017). Climate, anchovy, and sardine. *Annual Review of Marine Science*, *9*, 469–493. [https://doi.org/10.1146/annurev-marine-122414-033819](https://doi.org/https://doi.org/10.1146/annurev-marine-122414-033819)

Chidambaram, K. (1950). Studies on the length frequency of oil sardine, Sardinella longiceps Cuv. & Val. And on certain factors influencing their appearance on the Calicut coast of the Madras Presidency. *Proceedings of Indian Academy of Sciences*, *31*, 352–286.

Cohen, Y., & Stone, N. (1987). Multivariate time series analysis of the Canadian fisheries system in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, *44*(S2), 171–181. [https://doi.org/10.1139/f87-321](https://doi.org/https://doi.org/10.1139/f87-321)

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. [https://doi.org/10.1006/jmsc.2000.0712](https://doi.org/https://doi.org/10.1006/jmsc.2000.0712)

Das, P. H. D., & Edwin, L. (2018). Temporal changes in the ring seine fishery of Kerala, India. *Indian Journal of Fisheries*, *65*(1), 47–54. [https://doi.org/10.21077/ijf.2018.65.1.69105-08](https://doi.org/https://doi.org/10.21077/ijf.2018.65.1.69105-08)

Farmer, N. A., & Froeschke, J. T. (2015). Forecasting for recreational fisheries management: What’s the catch? *North American Journal of Fisheries Management*, *35*(4), 720–735. [https://doi.org/10.1080/02755947.2015.1044628](https://doi.org/https://doi.org/10.1080/02755947.2015.1044628)

Garza-Gil, M. D., Varela-Lafuente, M., Caballero-Míguez, G., & Torralba-Cano, J. (2015). A study on economic impact on the European sardine fishery due to continued global warming. In B. R. Singh (Ed.), *Global warming: Causes, impacts and remedies* (pp. 115–136). [https://www.doi.org/10.5772/58877](https://doi.org/https://www.doi.org/10.5772/58877)

Georgakarakos, S., Doutsoubas, D., & Valavanis, V. (2006). Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. *Fisheries Research*, *78*(1), 55–71. [https://doi.org/10.1016/j.fishres.2005.12.003](https://doi.org/https://doi.org/10.1016/j.fishres.2005.12.003)

George, G., Meenakumari, B., Raman, M., Kumar, S., Vethamony, P., Babu, M. T., & Verlecar, X. (2012). Remotely sensed chlorophyll: A putative trophic link for explaining variability in Indian oil sardine stocks. *Journal of Coastal Research*, *28*(1A), 105–113. [https://doi.org/10.2112/JCOASTRES-D-10-00070.1](https://doi.org/https://doi.org/10.2112/JCOASTRES-D-10-00070.1)

Gupta, G. V. M., Sudheesh, V., Sudharma, K. V., Saravanane, N., Dhanya, V., Dhanya, K. R., … Naqvi, S. W. A. (2016). Evolution to decay of upwelling and associated biogeochemistry over the southeastern Arabian Sea shelf. *Journal of Geophysical Research: Biogeosciences*, *121*(1), 159–175. [https://doi.org/10.1002/2015JG003163](https://doi.org/https://doi.org/10.1002/2015JG003163)

Habeebrehman, H., Prabhakaran, M. P., Jacob, J., Sabu, P., Jayalakshmi, K. J., Achuthankutty, C. T., & Revichandran, C. (2008). Variability in biological responses influenced by upwelling events in the eastern Arabian Sea. *Journal of Marine Systems*, *74*(1-2), 545–560. [https://doi.org/10.1016/j.jmarsys.2008.04.002](https://doi.org/https://doi.org/10.1016/j.jmarsys.2008.04.002)

Haltuch, M. A., Brooks, E. N., Brodziak, J., Devine, J. A., Johnson, K. F., Klibansky, N., … Wells, B. K. (2019). Unraveling the recruitment problem: A review of environmentally-informed forecasting and management strategy evaluation. *Fisheries Research*, *217*, 198–216. [https://doi.org/10.1016/j.fishres.2018.12.016](https://doi.org/https://doi.org/10.1016/j.fishres.2018.12.016)

Hanson, P. J., Vaughan, D. S., & Narayan, S. (2006). Forecasting annual harvests of Atlantic and Gulf menhaden. *North American Journal of Fisheries Management*, *26*(3), 753–764. [https://doi.org/10.1577/M04-096.1](https://doi.org/https://doi.org/10.1577/M04-096.1)

Holmes, E. E., Ward, E. J., & Wills, K. (2012). MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *R Journal*, *4*(1), 11–19. [https://doi.org/10.32614/RJ-2012-002](https://doi.org/https://doi.org/10.32614/RJ-2012-002)

Hornell, J. (1910). Report on the results of a fishery cruise along the Malabar coast and to the Laccadive Islands in 1908. *Madras Fishery Bulletin*, *4*(4), 76–126.

Hornell, J., & Nayudu, M. R. (1924). A contribution to the life history of the Indian sardine with notes on the plankton of the Malabar coast. *Madras Fishery Bulletin*, *17*(5), 129–197.

Jacobson, L. D., & MacCall, A. D. (1995). Stock-recruitment models for Pacific sardine (Sardinops sagax). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(3), 566–577. [https://doi.org/10.1139/f95-057](https://doi.org/https://doi.org/10.1139/f95-057)

Jayaprakash, A. A. (2002). Long term trends in rainfall, sea level and solar periodicity: A case study for forecast of Malabar sole and oil sardine fishery. *Journal of the Marine Biological Association of India*, *44*(1/2), 163–175.

Jayaprakash, A. A., & Pillai, N. G. K. (2000). The Indian oil sardine. In V. N. Pillai & N. G. Menon (Eds.), *Marine fisheries research and management* (pp. 259–281). Kerala, India: Central Marine Fisheries Research Institute.

Jayaram, C., Chacko, N., Joseph, K. A., & Balchand, A. N. (2010). Interannual variability of upwelling indices in the southeastern Arabian Sea: A satellite based study. *Ocean Science Journal*, *45*(1), 27–40. [https://doi.org/10.1007/s12601-010-0003-6](https://doi.org/https://doi.org/10.1007/s12601-010-0003-6)

Kripa, V., Mohamed, K. S., Koya, K. P. S., Jeyabaskaran, R., Prema, D., Padua, S., … Vishnu, P. G. (2018). Overfishing and climate drives changes in biology and recruitment of the Indian oil sardine Sardinella longiceps in southeastern Arabian Sea. *Frontiers in Marine Science*, *5*, Article 443. [https://doi.org/10.3389/fmars.2018.00443](https://doi.org/https://doi.org/10.3389/fmars.2018.00443)

Krishnakumar, P. K., Mohamed, K. S., Asokan, P. K., Sathianandan, T. V., Zacharia, P. U., Abdurahiman, K. P., … Durgekar, N. R. (2008). How environmental parameters influenced fluctuations in oil sardine and mackerel fishery during 1926-2005 along the south-west coast of India? *Marine Fisheries Information Service, Technical and Extension Series*, *198*, 1–5.

Lawer, E. A. (2016). Empirical modeling of annual fishery landings. *Natural Resources*, *7*(3), 193–204. [http://dx.doi.org/10.4236/nr.2016.74018](https://doi.org/http://dx.doi.org/10.4236/nr.2016.74018)

Lindegren, M., & Checkley, D. M. (2012). Temperature dependence of Pacific sardine (Sardinops sagax) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(2), 245–252. [https://doi.org/10.1139/cjfas-2012-0211](https://doi.org/https://doi.org/10.1139/cjfas-2012-0211)

Lindegren, M., Checkley, D. M., Rouyer, T., MacCall, A. D., & Stenseth, N. C. (2013). Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proceedings of the National Academy of Sciences*, *110*(33), 13672–13677. [https://doi.org/10.1073/pnas.1305733110](https://doi.org/https://doi.org/10.1073/pnas.1305733110)

Lloret, J., Lleonart, J., & Sole, I. (2000). Time series modelling of landings in Northwest Mediterranean Sea. *ICES Journal of Marine Science*, *57*(1), 171–184. [https://doi.org/10.1006/jmsc.2000.0570](https://doi.org/https://doi.org/10.1006/jmsc.2000.0570)

Longhurst, A. R., & Wooster, W. S. (1990). Abundance of oil sardine (Sardinella longiceps) and upwelling on the southwest coast of India. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(12), 2407–2419. [https://doi.org/10.1139/f90-268](https://doi.org/https://doi.org/10.1139/f90-268)

Madhupratap, M., Gopalakrishnan, T. C., Haridas, P., & Nair, K. K. C. (2001). Mesozooplankton biomass, composition and distribution in the Arabian Sea during the fall intermonsoon: Implications of oxygen gradients. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(6), 1345–1368. [https://doi.org/10.1016/S0967-0645(00)00142-9](https://doi.org/https://doi.org/10.1016/S0967-0645(00)00142-9)

Madhupratap, M., Shetye, S. R., Nair, K. N. V., & Nair, S. R. S. (1994). Oil sardine and Indian mackerel: Their fishery, problems and coastal oceanography. *Current Science*, *66*(5), 340–348. [https://doi.org/10.1029/2004GL019652](https://doi.org/https://doi.org/10.1029/2004GL019652)

McClatchie, S., Goericke, R., Auad, G., & Hill, K. (2010). Re-assessment of the stock–recruit and temperature–recruit relationships for Pacific sardine (Sardinops sagax). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(11), 1782–1790. [https://doi.org/10.1139/F10-101](https://doi.org/https://doi.org/10.1139/F10-101)

Mendelssohn, R. (1981). Using Box-Jenkins models to forecast fishery dynamics: Identification, estimation and checking. *Fishery Bulletin*, *78*(4), 887–896.

Menon, N. N., Sankar, S., Smitha, A., George, G., Shalin, S., Sathyendranath, S., & Platt, T. (2019). Satellite chlorophyll concentration as an aid to understanding the dynamics of Indian oil sardine in the southeastern Arabian Sea. *Marine Ecology Progress Series*, *617-618*, 137–147. [https://doi.org/10.3354/meps12806](https://doi.org/https://doi.org/10.3354/meps12806)

Moustahfid, H., Marsac, F., & Grangopadhyay, A. (2018). Climate change impacts, vulnerabilities and adaptations: Western Indian ocean marine fisheries. In M. Barange, T. Bahri, M. C. M. Beveridge, K. L. Cochrane, S. Funge-Smith, & F. Poulain (Eds.), *Impacts of climate change on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options* (pp. 251–280). Rome: FAO Fisheries; Aquaculture Technical Paper No. 627.

Murty, A. V. S., & Edelman, M. S. (1966). On the relation between the intensity of the south-west monsoon and the oil-sardine fishery of India. *Indian Journal of Fisheries*, *13*(1/2), 142–149.

Naidu, P. D., Kumar, M. R. R., & Babu, V. R. (1999). Time and space variations of monsoonal upwelling along the west and east coasts of India. *Continental Shelf Research*, *19*(4), 559–572. [https://doi.org/10.1016/S0278-4343(98)00104-6](https://doi.org/https://doi.org/10.1016/S0278-4343(98)00104-6)

Nair, P. G., Joseph, S., Kripa, V., Remya, R., & Pillai, V. N. (2016). Growth and maturity of Indian oil sardine Sardinella longiceps (Valenciennes, 1847) along southwest coast of India. *Journal of Marine Biological Association of India*, *58*(1), 64–68. [https://doi.org/10.6024/jmbai.2016.58.1.1899-07](https://doi.org/https://doi.org/10.6024/jmbai.2016.58.1.1899-07)

Nair, R. V. (1952). Studies on the revival of the Indian oil sardine fishery. *Proceedings of Indo-Pacific Fisheries Council*, *2*, 1–15.

Nair, R. V. (1959). Notes on the spawning habits and early life-history of the oil sardine, Sardinella longiceps Cuv. & Val. *Indian Journal of Fisheries*, *6*(2), 342–359.

Nair, R. V., & Subrahmanyan, R. (1955). The diatom, Fragilaria oceanica Cleve, an indicator of abundance of the Indian oil sardine, Sardinella longiceps Cuv. And Val. *Current Science*, *24*(2), 41–42.

Nobel, A., & Sathianandan, T. V. (1991). Trend analysis in all-India mackerel catches using ARIMA models. *Indian Journal of Fisheries*, *38*(2), 119–122.

Pillai, V. N. (1991). Salinity and thermal characteristics of the coastal waters off southwest coast of India and their relation to major pelagic fisheries of the region. *Journal of the Marine Biological Association of India*, *33*(1/2), 115–133.

Piontkovski, S., Al Oufi, H., & Al Jufaily, S. (2014). Seasonal and interannual changes of Indian oil sardine, Sardinella longiceps, landings in the governorate of Muscat (the Sea of Oman). *Marine Fisheries Review*, *76*(3), 50–59. [https://dx.doi.org/10.7755/MFR.76.3.3](https://doi.org/https://dx.doi.org/10.7755/MFR.76.3.3)

Pitchaikani, J. S., & Lipton, A. P. (2012). Impact of environmental variables on pelagic fish landings: Special emphasis on Indian oil sardine off Tiruchendur coast, Gulf of Mannar. *Journal of Oceanography and Marine Science*, *3*(3), 56–67. [https://doi.org/10.5897/JOMS](https://doi.org/https://doi.org/10.5897/JOMS)

Prabhu, M. S., & Dhulkhed, M. H. (1967). On the occurrence of small-sized oil sardine Sardinella longiceps Val. *Current Science*, *35*(15), 410–411.

Prabhu, M. S., & Dhulkhed, M. H. (1970). The oil sardine fishery in the Mangalore zone during the seasons 1963-64 and 1967-68. *Indian Journal of Fisheries*, *17*(1/2), 57–75.

Prista, N., Diawara, N., Costa, M. J., & Jones, C. (2011). Use of SARIMA models to assess data-poor fisheries: A case study with a sciaenid fishery off Portugal. *Fisheries Bulletin*, *109*(2), 170–185. [https://doi.org/10.7755/FB](https://doi.org/https://doi.org/10.7755/FB)

Raghavan, B. R., Deepthi, T., Ashwini, S., Shylini, S. K., Kumarswami, M., Kumar, S., & Lotliker, A. A. (2010). Spring inter monsoon algal blooms in the Eastern Arabian Sea: Shallow marine encounter off Karwar and Kumbla coast using a hyperspectral radiometer. *International Journal of Earth Sciences and Engineering*, *3*(6), 827–832. [https://doi.org/10.21276/ijee](https://doi.org/https://doi.org/10.21276/ijee)

Rohit, P., Sivadas, M., Abdussamad, E. M., Rethinam, A. M. M., Koya, K. P. S., Ganga, U., … Supraba, V. (2018). *Enigmatic Indian oil sardine: An insight*. CMFRI Special Publication No. 130. p156. ICAR-Central Marine Fisheries Research Institute.

Roxy, M. K., Ritika, K., Terray, P., & Masson, S. (2014). The curious case of Indian Ocean warming. *Journal of Climate*, *27*(22), 8501–8509. [https://doi.org/10.1175/JCLI-D-14-00471.1](https://doi.org/https://doi.org/10.1175/JCLI-D-14-00471.1)

Rykaczewski, R. R., & Checkley, D. M. (2008). Influence of ocean winds of the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Science*, *105*(6), 1965–1970. [https://doi.org/10.1073/pnas.0711777105](https://doi.org/https://doi.org/10.1073/pnas.0711777105)

Schaaf, W. E., Sykes, J. E., & Chapoton, R. B. (1975). Forecasts of Atlantic and Gulf menhaden catches based on the historical relation of catch and fishing effort. *Marine Fisheries Review*, *37*(10), 5–9. [https://doi.org/10.7755/MFR](https://doi.org/https://doi.org/10.7755/MFR)

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., … Zuzunaga, J. Z. (2010). Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, *21*(1), 289–347. [https://doi.org/10.2989/025776199784125962](https://doi.org/https://doi.org/10.2989/025776199784125962)

Srinath, M. (1998). Exploratory analysis on the predictability of oil sardine landings in Kerala. *Indian Journal of Fisheries*, *45*(4), 363–374.

Srinath, M., Kuriakose, S., & Mini, K. G. (2005). Methodology for estimation of marine fish landings in India. In *CMFRI Special Publications No. 86. p57.* Central Marine Fisheries Research Institute.

Stergiou, K. I., & Christou, E. D. (1996). Modeling and forecasting annual fisheries catches: Comparison of regression, univariate and mulivariate time series methods. *Fisheries Research*, *25*(2), 105–138. [https://doi.org/10.1016/0165-7836(95)00389-4](https://doi.org/https://doi.org/10.1016/0165-7836(95)00389-4)

Supraba, V., Dineshbabu, A. P., Thomas, S., Rohit, P., Rajesh, K. M., & Zacharia, P. U. (2016). Climate influence on oil sardine and Indian mackerel in southeastern Arabian Sea. *International Journal of Development Research*, *6*(8), 9152–9159.

Takasuka, A., Oozeki, Y., & Aoki, I. (2007). Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(5), 768–776. [https://doi.org/10.1139/f07-052](https://doi.org/https://doi.org/10.1139/f07-052)

Thara, K. J. (2011). *Response of eastern Arabian Sea to extreme climatic events with special reference to selected pelagic fishes*. Kerala, India: PhD Thesis. Department of Physical Oceanography. Cochin University of Science; Technology.

Tommasi, D., Stock, C. A., Pegion, K., Vecchi, G. A., Methot, R. D., Alexander, M. A., & Checkley, D. M. (2016). Improved management of small pelagic fisheries through seasonal climate prediction. *Ecological Applications*, *27*(2), 378–388. [https://doi.org/10.1002/eap.1458](https://doi.org/https://doi.org/10.1002/eap.1458)

Vallivattathillam, P., Iyyappan, S., Lengaigne, M., Ethé, C., Vialard, J., Levy, M., … Naqvi, W. (2017). Positive Indian Ocean Dipole events prevent anoxia off the west coast of India. *Biogeosciences*, *14*(6), 1541–1559. [https://doi.org/10.5194/bg-14-1541-2017](https://doi.org/https://doi.org/10.5194/bg-14-1541-2017)

Venugopalan, R., & Srinath, M. (1998). Modelling and forecasting fish catches: Comparison of regression, univariate and multivariate time series methods. *Indian Journal of Fisheries*, *45*(3), 227–237.

Vivekanandan, E., Rajagopalan, M., & Pillai, N. G. K. (2009). Recent trends in sea surface temperature and its impact on oil sardine. In P. K. Aggarwal (Ed.), *Global climate change and Indian agriculture* (pp. 89–92). New Delhi: Indian Council of Agricultural Research.

Vivekanandan, E., Srinath, M., Pillai, V. N., Immanuel, S., & Kurup, K. N. (2003). Marine fisheries along the southwest coast of India. In G. Silvestre, L. Garces, I. Stobutzki, C. Luna, M. Ahmad, R. A. Valmonte-Santos, … D. Pauly (Eds.), *Assessment, management, and future directions for coastal fisheries in Asian countries* (pp. 759–792). WorldFish Center, Penang.: WorldFish Center Conference Proceedings 67.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, *73*(1), 3–36. [https://doi.org/10.1111/j.1467-9868.2010.00749.x](https://doi.org/https://doi.org/10.1111/j.1467-9868.2010.00749.x)

Wood, S. N. (2017). *Generalized additive models: An introduction with R*. Boca Raton, FL: CRC Press.

Wood, S. N., Pya, N., & Säfken, B. (2016). Smoothing parameter and model selection for general smooth models (with discussion). *Journal of the American Statistical Association*, *111*(516), 1548–1563. [https://doi.org/10.1080/01621459.2016.1180986](https://doi.org/https://doi.org/10.1080/01621459.2016.1180986)

Xu, C., & Boyce, M. S. (2009). Oil sardine (Sardinella longiceps) off the Malabar coast: Density dependence and environmental effects. *Fisheries Oceanography*, *18*(5), 359–370. [https://doi.org/10.1111/j.1365-2419.2009.00518.x](https://doi.org/https://doi.org/10.1111/j.1365-2419.2009.00518.x)

# FIGURE LEGENDS

**FIGURE 1** The study area, located off the southwestern coast of India, as indicated by latitude/longitude boxes used for the satellite data. Kerala State is shaded gray.

**FIGURE 2** Key oil sardine life history events, overlaid on the monthly nearshore and offshore sea surface temperatures (SSTs) and nearshore chlorophyll-a (Chl-a) concentrations.

**FIGURE 3** Quarterly catch data for 1956–2014 from Kerala. Note that the fishery is closed July 1–mid-August, meaning that the quarter 3 catch represents only 1.5 months. Mean catches in quarters 1–4 were 38, 19.2, 30.9, and 59.9 metric tons, respectively.

**FIGURE 4** Remote sensing covariates used in the analysis. All data are monthly averages over box 4 in Figure 1. The upwelling index was defined as the difference between the nearshore and 3° latitude offshore sea surface temperatures (SSTs). Surface chlorophyll-a data were available only from 1997 onward. SSTs were obtained from the Advanced Very High Resolution Radiometer.

**FIGURE 5** Effects of 2.5-year average nearshore sea surface temperature (SST; over boxes 2–5 in Figure 1) and current-season upwelling intensity on July–September and October–March catches. As the upwelling index reflects the difference between offshore and inshore SST, negative values indicate that coastal surface waters are warmer than offshore waters.

**FIGURE 6** Fitted versus observed catches obtained with models with and without the 2.5-year average nearshore sea surface temperature (SST) included as a covariate. The lines indicate predicted = observed values. a) July–September catch, modeled with only the prior-season October–March catch: . b) July–September catch, modeled with the prior-season October–March catch and 2.5-year average SST: . c) October–March catch, modeled with the prior-season October–March catch and two prior seasons of the July–September catch: . d) October–March, modeled as in c with the addition of the 2.5-year average SST (): . RMSE, root mean squared error.

**TABLE 2** Best-performing models for the July–September ( and October–March () catches

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | Residual df | Adj.R2 | RMSE | AIC | LOOCV |
| Jul-Sep catch models with covariates |  |  |  |  |  |
| = Jun-Sep SST current season |  |  |  |  |  |
| = Jun-Sep Bakun-UPW current season |  |  |  |  |  |
| = 2.5-year ave nearshore SST |  |  |  |  |  |
| M0: | 28.6 | 24 | 1.184 | 109.52 | 1.299 |
|  | 25.9 | 41 | 1.007 | 103.43 | 1.192 |
|  | 27.6 | 28 | 1.133 | 108.66 | 1.404 |
|  | 26.2 | 41 | 1.011 | 103.26 | 1.338 |
|  |  |  |  |  |  |
| Oct-Mar catch models with covariates |  |  |  |  |  |
| = Mar-May SST current season |  |  |  |  |  |
| = Jun-Sep SST current season |  |  |  |  |  |
| = 2.5-year ave nearshore SST |  |  |  |  |  |
| = fall DMI prior season |  |  |  |  |  |
| M1: | 24.8 | 57 | 0.713 | 79.53 | 1.062 |
|  | 22 | 63 | 0.628 | 76.01 | 1.002 |
|  | 23.8 | 63 | 0.648 | 75.57 | 1.042 |
|  | 22.7 | 67 | 0.597 | 71.88 | 0.827 |
|  | 21.1 | 68 | 0.58 | 72.69 | 0.89 |
|  |  |  |  |  |  |
| M2: | 27.6 | 45 | 0.836 | 84.75 | 0.966 |
|  | 24.8 | 47 | 0.791 | 85.9 | 0.981 |
|  | 26.6 | 52 | 0.772 | 81.79 | 0.927 |
|  | 25.3 | 60 | 0.688 | 76.34 | 0.796 |
|  | 23.7 | 43 | 0.8 | 88.43 | 0.969 |

Notes. The full set of covariate models and the results of testing of nested model sets are provided in Appendix B. Null model leave-one-out cross-validation (LOOCV) root mean square errors (RMSEs), 1.599 for the July–September catch and 1.015 for the October–March catch.