Influences of changing temperature and upwelling intensity on Indian oil sardine (*Sardinella longiceps*) landings

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# 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 landings 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. 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 responses, and dynamic linear models, which allow for time-varying responses. We found significant correlations of upwelling intensity, an Indian Ocean Dipole index, and the multiyear average SST with landings. Upwelling had a positive effect at lower intensity and a negative effect at high intensity. This is consistent with expectations since upwelling fuels productivity but at high levels leads to surface anoxia and advection of larvae offshore. However, the most significant relationship was found between the 2.5-year average SST and post-monsoon landings with an adjusted *R*2 = 67.5% and a 17-22% reduction in out-of-sample prediction error. 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 more rapidly than other oceans. Our work highlights key variables important for forecasting the impacts of these changes on sardine landings.

# 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 the El Niño–Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) (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 an unusually 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 the effects on biomass seen for all sardine species, environmental conditions also affect the catchability 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.

A variety of environmental variables have been studied to explain the variability in the landings of the Indian oil sardine. 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 oil sardine landings, however, have been positive in some studies and negative in others (Madhupratap, Shetye, Nair, & Nair, 1994). Seasonal upwelling is thought to be a key driver of oil sardine abundance. Correlations have been identified with landings and 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 (ns-SST), another index of upwelling intensity (Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed, 1970; Supraba et al., 2016). Coastal upwelling is linked to productivity but at high levels brings low oxygen water to the surface which can cause fish to move offshore where they are inaccessible to the fishery. Large-scale ocean climate modes (ENSO and IOD) have cascading effects on SST, precipitation, and upwelling. Correlations have been found between ENSO and IOD indices and oil sardine landings (Rohit et al., 2018; Supraba et al., 2016), as well as coastal anoxic events (Vallivattathillam et al., 2017) and chlorophyll blooms (Currie et al., 2013) in the southeastern Indian Ocean. For other sardine species, a multiyear average SST has been found to explain variability in recruitment and survival of larval and juvenile sardines, which affect subsequent overall abundance (Checkley et al., 2017; Takasuka, Oozeki, & Aoki, 2007).

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, along the southwest Indian coast and first implemented 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 affects food resources which affects recruitment through spawning and survival, and thus the biomass available to the fishery. In addition, catchability is strongly affected by the environment, 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 (Table 1). 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 landings 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, while landings need not be a tight index of biomass for our purposes, 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 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, which has the longest and most complete time series and where the overwhelming majority of oil sardines are landed (Figure 3). 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). See the Supporting Information for data references. 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). SST and chlorophyll-a satellite data were retrieved from NOAA remote-sensing data servers and averaged across thirteen 1° × 1° boxes, which parallel the bathymetry of the study area. See the Supporting Information for data sources and references.

For SST, we used Advanced Very-High Resolution Radiometer (AVHRR) data, which provides accurate nearshore SST values. 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 provided by the US National Oceanographic Data Center. For 2004–2016, we used the CoastWatch AVHRR SST products derived from NOAA’s Polar Operational Environmental Satellites. The SST data are in °C.

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. Satellite-derived chlorophyll-a data are only available since September 1997. 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 2003–2015, 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. Both products are in mg m-3.

For coastal upwelling, we used three indices. The first index is the SST differential between nearshore and 3° longitude 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 3). SSTs were obtained from the remote-sensing data sets described above. The second index was the Bakun index (kg m-1 s-1), which is based on Erkman’s theory of mass transport and computed from the *x* and *y* components of Ekman transport off the Kerala coast. The last index was the average nearshore SST along the Kerala coast during June-September (Figure 1, average of boxes 2–5).

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 daily precipitation (averaged monthly) over the ocean 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 off the Kerala coast. The land and nearshore ocean precipitation data are correlated (Supporting Information; Figure S6).

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 and is an index for the IOD cycle. It has been shown to predict anoxic events in the study area (Vallivattathillam et al., 2017) and seasonal chlorophyll blooms in the southeastern Indian Ocean (Currie et al, 2013). DMI data were downloaded from the NOAA Earth System Research Laboratory.

## 2.3 Hypotheses

Our statistical tests were structured around specific hypotheses (Table 1) concerning which remote sensing covariates in which months should correlate with landings in specific quarters. These hypotheses were based on biological information concerning how environmental conditions affect sardine survival and recruitment and affect exposure of Indian oil sardines to the coastal fishery. 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. Our hypotheses (Table 1) focus mainly on two drivers, upwelling and ocean temperature. 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 influence of seasonality and permitted a focus on year-to-year variability rather than seasonal variation.

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 where *s*() is non-linear spline smoothing function, 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 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 thin-plate 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 catch models with the following forms:

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

are the log catches. t, t-1 and t-2 denote current, prior year and two years prior. i, j and k denote the season might be July-September or October-May catch depending on the model. is a non-linear spline based smoothing function (with fixed smoothing level) 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 the October–March ( and ) and July–September ( and ) catches 1 and 2 prior years for as the explanatory catch variables (the and ). 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) 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 (RMSE) and median absolute error (MdAE) is reported for the set of prediction errors. After selection of the best model using the 1984–2015 data, fitting was repeated with catch data from 1956–1983 to confirm the base catch model form (with no covariates). An influential years test was performed by removing each year in the series sequentially and repeating the model selection analysis (Supporting Information).

Once the catch models were determined, the covariates were studied. 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 the preliminary model fitted step described above.

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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 S1 and S2). 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 RMSE, but at the cost of reduced degrees of freedom (Table S2). Three models had almost identical AICc and LOOCV RMSE: 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 (*Validation of catch base models*; Supporting Information) and to minimize the loss of degrees of freedom from an additional covariate . The adjusted value for this model was 21.7.

Similar model selection results were obtained for the October–March landings (Tables S4 and S5), but these models explained much more variance (maximum adjusted ). The best-supported model based on AICc and *F* values, was the non-linear model with and , less this model exhibited less out-of-sample prediction accuracy (LOOCV RMSE) than did the naïve model (Tables 2, S4 and S5). The simpler model with only had the second lowest AIC and lowest LOOCV RMSE values. Both models were included as base models for the October–March catch.

Repeating the model selection 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 RMSE values (Table S3). For the October–March catch, the results were very similar, but not identical. The non-linear model with had the lowest LOOCV RMSE value, and the models with and or had the lowest AICs [although the difference from the AIC for the model was <1;Table S6]. The influential years analysis supported the base models selected using the 1984–2015 data (Supporting Information; Figures S1-S5). The DLMs performed poorly for the July–September catch, with high AIC and LOOCV RMSE values. One DLM for the October–March catch showed mixed performance, with a higher AIC and lower LOOCV RMSE value. Overall the model selection indicated that a catch model with a time-varying effect of prior catch did not improve either model fit or out of sample prediction, but inclusion of a non-linear effect was important.

Ultimately, the following non-linear base model (weakly explanatory: adjusted *R*2 = 21.7%) was chosen for the July–September catch:

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

(*R*2 = 45.9) and

(*R*2 = 57.3).

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## 3.2 Environmental covariate selection

The covariate analysis was able to rule out a number of the hypothesized covariates (Table 1) as explanatory variables for catch variation and as covariates which would improve out of sample prediction. Specifically, we found no support for the use of April–May or June–July precipitation over the ocean (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 A1 and A2). 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 or October–March catch (hypotheses S4, S5, and L1; Tables A1 and A2). In general the indices of upwelling in the current season or prior season were not or only weakly supported (based on AICc) and did not improve out of sample prediction (LOOCV RMSE or MdAE) (Tables A1, A2, S7). The one exception was the June-September nearshore SST upwelling index and the July-September catch. This reduced AICc and reduced both the LOOCV RMSE and MdAE prediction errors (Table 2 and A1). The Bakun upwelling index had a lower AICc (Table 2) but did not reduce the prediction errors. Lastly, we found no support for using the ONI to explain either the July–September or October–March catch variation (hypothesis A2). The fall DMI was weakly supported. It reduced AICc and LOOCV RMSE and MdAE but only for October-March catch with the more complex model (Table 2 and S7).

Only two covariates emerged as explanatory variables that both explained catch variance and reduced out of sample predictions errors: the June-July precipitation over land (hypothesis S1) and the 2.5-year average regional (0-160km) SST (hypothesis A1). The strongest correlations were found using a non-linear response with the 2.5-year average regional SST with both the July–September (adjusted *R*2, 37.3 versus 21.7 for the model without the covariate) and October–March (a, 72.0 vs. 57.3; Tables 2 and A2, S7) catches. This covariate reduced the out of sample prediction error (LOOCV RMSE or MdAE) for the October-May and July-September catch by over 20% relative to the base model without environmental covariates (Table 2). The response curve for this covariate 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). The DMI is correlated with the regional SST and the 2.5-year average DMI showed similar, though less strong, support and reduction in out of sample prediction errors. The other strong correlation and reduction in out of sample prediction error found was for the current season June-July precipitation over land. For the October-May catch, this covariate had lower AICc (relative to the base model) and reduced both LOOCV RMSE and MdAE (Table 2).

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 (1998–2015: 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 A1, A2 and S7).

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.

Both the 2.5-year average DMI and the June-July precipitation over land covariates were available for the full catch time series from 1956 onward. Using dynamic linear modeling and the October-May catch, we examined whether the effect sizes of these covariates changed over time and whether the mean and median errors over time (Figure 7). The models were fit to the residuals of the simpler base October-May catch model (with no environmental covariates) and the covariates were z-scored (mean removed and variance standardized to 1). The models took the form with one or both covariates. The effect size of DMI was positive and non-zero for the entire time-series, while the effect size of precipitation was negative and strongly negative in the 1990s in the (Figure 7a). Up to the mid-1980s, the covariates, either together or alone, did not reduce the mean square error (RMSE) but did reduce the median error (MdAE) computed in 10-year moving windows (Figure 7b). The y-axis for the errors is the percent of the unlogged catch; thus 25 = 25% over or under the unlogged catch. The RMSE is strongly influenced by outlier events while the median captures the central behavior of the errors. After 1990, the model with both covariates had the lowest errors, with RMSE falling from 75% errors to 25% and MdAE fluctuating around 25% (Figure 7b and 7c). Which covariate reduced the errors the most varied across the time series.

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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 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, as in the other cited studies, 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.

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# 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 (top colored bars), overlaid on the monthly nearshore and offshore sea surface temperatures (SSTs; °C) and nearshore chlorophyll-a (Chl-a) concentrations (mg/m3).

**FIGURE 3** Quarterly catch data for 1956–2015 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. The upwelling index was defined as the difference between the nearshore and 3° longitude offshore sea surface temperatures (SSTs). Surface chlorophyll-a data are available only from September 1997 onward. SSTs were obtained from Advanced Very High Resolution Radiometer (AVHRR) products which provide high resolution nearshore measurements.

**FIGURE 5** Effects of 2.5-year average regional sea surface temperature (SST; over boxes 2–10 in Figure 1) and current-season upwelling intensity (average June-September SST-derived UPW index in box 4) on July–September and October–March catches. As the upwelling index reflects the difference between offshore and nearshore SST, positive values indicate that coastal surface waters are colder than offshore waters. The more positive the difference, the stronger the upwelling intensity.

**FIGURE 6** Fitted versus observed catches obtained with models with and without the 2.5-year average sea surface temperature (SST) included as a covariate. The lines indicate a perfect prediction where observed catch equals the predicted catch. Values above the line are cases where the prediction was too high and values below the line are cases where the prediction was too low. a) July–September catch, modeled with only the prior-season October–March catch as a covariate: . 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.

**FIGURE 7** Effect sizes and error sizes for dynamic linear models of October-May catch 1956-2015 using the 2.5-year average DMI and June-July precipitation over land as covariates with a time-varying effect size. The models were fit to the residuals of the simpler base model (with only prior October-May catch as a covariate) fit to the whole time series. The covariates were z-scored (mean removed and standardized to variance of 1). a) Effect size. b) RMSE computed on a 10-year sliding window with a 10% trim (remove the most extreme error). The trim prevented one error from dominating the 10-year window. d) Median absolute error computed on a 10-year sliding window.

**TABLE 2** Best-performing GAM models for the July–September ( and October–March () catches. M is the base models with only prior catch as covariates. To the base models, the environmental covariates are added. ns-SST is nearshore (0-80km) and r-SST is regional (0-160km). The full set of nested covariate models and tests are given in the appendices.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Model | Residdf | Adj R2 | RMSE | AICc | LOOCV  RMSE | LOOCV  MdAE |
| **July-Sept catch** |  |  |  |  |  |  |
| null model: | 33 |  | 1.60 | 126.6 | 1.60 | 0.56 |
| M0: | 30 | 22 | 1.20 | 115.2 | 1.31 | 0.69 |
| covariate model: = M0 + | | |  |  |  |  |
| = Jun-Sep ns-SST (L2) | 27.9 | 35 | 1.06 | 112.7 | 1.24 | 0.64 |
| = Jun-Sep Bakun-UPW (L2) | 27.6 | 43 | 0.98 | 109.1 | 1.35 | 0.73 |
| = Jun-Jul Precip - land gauges (S1) | 28 | 30 | 1.10 | 115.3 | 1.33 | 0.62 |
| = 2.5-year average r-SST (A1) | 27.8 | 37 | 1.04 | 111.8 | 1.29 | 0.49 |
| = DMI 2.5-year average (A3) | 28.2 | 36 | 1.05 | 111.5 | 1.34 | 0.59 |
|  |  |  |  |  |  |  |
| **October-March catch - simpler model** | | | |  |  |  |
| null model: | 32 |  | 1.00 | 92.9 | 1.00 | 0.26 |
| M1: | 29.1 | 46 | 0.82 | 87.7 | 0.95 | 0.32 |
| covariate model: = M1 + | | | |  |  |  |
| = Jun-Jul Precip - land gauges (S1) | 26.9 | 60 | 0.69 | 82.1 | 0.91 | 0.25 |
| = 2.5-year average r-SST (A1) | 26.9 | 65 | 0.64 | 78.1 | 0.76 | 0.35 |
| = DMI 2.5-year average (A1) | 27.2 | 60 | 0.69 | 81.5 | 0.82 | 0.36 |
|  |  |  |  |  |  |  |
| **October-March catch - more complex model** | | |  |  |  |  |
| M2: | 26.6 | 57 | 0.70 | 84.6 | 1.05 | 0.35 |
| covariate model: = M2 + | | | |  |  |  |
| = Jun-Jul Precip - land gauges (S1) | 24.6 | 70 | 0.56 | 77.5 | 0.97 | 0.29 |
| = 2.5-year average r-SST (A1) | 24.7 | 72 | 0.55 | 75.6 | 0.75 | 0.28 |
| = DMI 2.5-year average (A1) | 24.9 | 62 | 0.64 | 84.5 | 0.93 | 0.43 |
|  |  |  |  |  |  |  |

Notes: The nested F-tests are given in Supporting Information. LOOCV = Leave one out cross-validation. RMSE = root mean square error. MdAE = median absolute error. AICc = Akaike Information Criterion corrected for small sample size. and = AICc greater than 2 and greater than 5 below base catch model (M). , , and = LOOCV RMSE and MdAE 5%, 10% and 20% below model M, respectively. indicates current season (Jul-Jun). For covariates that are multiyear, is the current calendar year. The equations with s() are GAM models where the covariates has a non-linear response (defined by a spline based smoothing function).