Influences of temperature, upwelling intensity, and oceanic versus land precipitation 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 long-term time series of quarterly catches. Potentially influential variables examined included precipitation, upwelling intensity, sea surface temperature (SST), chlorophyll-a 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. Only two covariates explained catch variation and improved out of sample prediction: the 2.5-year average regional SST and precipitation over land during June-July. The most significant relationship was between the SST covariate and post-monsoon landings with an adjusted *R*2 = 72% and a 17-22% reduction in out-of-sample prediction error. This result is consistent with previous findings on multiyear average SST and sardine recruitment and suggests that this covariate successfully integrates a variety of factors that affect sardine catch. Models with the second best covariate, precipitation over land during the monsoon, had adjusted *R*2 = 70.5% and a 5-15% reduction in out-of-sample prediction error. The earth’s changing climate is associated with both rapid warming in the Western Indian Ocean and changes to southwest monsoon rainfall patterns. Our work highlights these as key variables important for understanding and forecasting impacts 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). At the same time, heavy monsoon rain over land causes high nutrient flux from rivers into the shallow nearshore regions which causes eutrophication and anoxia (Chauhan et al., 2011). 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 oceanic 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 monthly resolutions, which make them practical for operational forecasting using oceanic environmental variables. In addition to the oceanic environmental variables, we use one non-remote sensing variable: precipitation over land based on land-gauges. River discharge due to heavy precipitation over land has strong impacts on the nearshore ocean environment during the monsoon season (Chauhan et al., 2011).

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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; we are not modeling abundance rather catch. 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 abundance for our purposes, this relationship can be assumed to be strong for many reasons.

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). We used an autoregressive base catch model to capture smooth landing trends due to increased effort (or multiyear changes in biomass), and environmental covariates are used to explain variation that cannot be explained by this base model.

### 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 (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). The peak catches occur in October-December (Figure 3). Oil sardines remain inshore to feed in winter and catches remain high from January to March; in March–May, they move offshore to deeper waters due to considerable inshore warming (Chidambaram, 1950). Sardine catches are correspondingly lower during this period for all size classes (Figure 3). The sardines reach maturity (~150 mm long) within 1 year (Nair et al., 2016).

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. accounting for various boat and gear types (Srinath et al., 2005). We used CMFRI data from the Indian state of Kerala (Figure 1), 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 and to facilitate additive modeling.

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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. Since the AVHRR data are only available from 1981, we used the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST product, available from 1960 on a 1° × 1° grid, for the analysis involving catch prior to 1981. The nearshore (<80km) ICOADS SST measurements are not as accurate as AVHRR and could not be used to compute the nearshore-offshore SST used as an upwelling metric.

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 2). SSTs were obtained from the AVHRR remote-sensing data sets described above. The second index was the Bakun index (kg m-1 s-1), which is based on Ekman’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. The DMI and our regional SST data off the Kerala coast are correlated (Figure S7).

## 2.3 Hypothesized drivers

Our statistical tests were structured around tests of specific hypothesized drivers of catch variability (Table 1) based on the biological information concerning how environmental conditions affect sardine survival and recruitment and affect exposure of Indian oil sardines to the coastal fishery. These tests consisted of a specific response variable (catch either during the monsoon or after) and a covariate in a specific time-frame during the current or prior season. We hypothesized that variables affecting or correlated with the inshore movement of sardines would correlate with July–September (monsoon- and spawning-period) landings, and that variables correlated with spawning strength and larval/juvenile survival would correlate with October–March (post-monsoon, mixed-age catch–period) landings in the current year and subsequent 1–2 years. Our tests (Table 1) examined multiple indices of upwelling, known to drive productivity, and ocean temperature, which affects juvenile and larval growth and survival. We also tested

precipitation, historically considered to influence the timing of oil sardine landings but which when over land leads to high river discharge with high nutrient fluxes and accompanying nearshore anoxia, and those concerning the ONI and DMI, as the effects of the ENSO and the IOD on sardine fluctuation have received attention recently. Lastly, we tested models using the chlorophyll-a concentration, as this concentration correlates directly with sardine food availability and chlorophyll fronts influence sardine shoaling. The power for these analyses was low given the brevity of the chlorophyll-a 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: July-September or October-March 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 corrected for small sample size (AICc) and leave-one-out cross-validation (LOOCV) were applied to nested sets of models to evaluate support for the catch, and subsequently covariate, models. LOOCV involves model fitting with the omission of a data point, followed by prediction of that data point. 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, AICc 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 and non-linear effects were compared: and , where is the best catch model from the preliminary model fitting step described above.

All statistical analysis was completed in the R programming language (R Development Core Team, 2019). Data and code are provided in the Supporting Information.

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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 AICc 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 (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 (Tables 2, S4 and S5). The simpler model with only had the second lowest AICc but 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 AICc 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 AICc 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 (time-varying effects) performed poorly for the July–September catch, with high AICc and LOOCV RMSE values. One DLM for the October–March catch showed mixed performance, with a higher AICc 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 (adjusted *R*2 = 21.7%) was chosen for the July–September catch:

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

(adj. *R*2 = 45.9) and

(adj. *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 that may drive catch variability and improve out of sample prediction (Table 1). Below, the model numbers refer to the models listed in Table 1. 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 (models S1 and S3; Tables A1, A2, S7). 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 (models 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 (model A2). The fall DMI (model A3) 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 (model S2) and the 2.5-year average regional SST (model 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-March 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 other strong correlation and reduction in out of sample prediction error was found for the current season June-July precipitation over land. For the October-March catch, this covariate had lower AICc (relative to the base model) and reduced both LOOCV RMSE and MdAE (Tables 2, A2, S7).

Our examination of the chlorophyll-a 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 and October–December 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. 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.

Using the ICOADS SST data set does not capture the nearshore SST as accurately, and thus was not used for our main analyses. Nonetheless it is highly correlated with the AVHRR SST data (Figure S7) and extends almost the start of the catch time series (to 1960). The precipitation data also extends back to 1960. Using dynamic linear modeling and the October-March catch, we examined whether the ability of the multiyear average SST and June-July land precipitation to explain catch variation changed over time. Time-varying covariate models were fit to the residuals of the simpler base October-March catch model (Table 2); the results were very similar with the more complex October-March catch model thus only one model is shown. The covariates were z-scored (mean removed and variance standardized to 1) and included as third-order polynomials to allow a non-linear response. The models took the form where *r* is the residual and *V* is the covariate. The ** were allowed to evolve as an autoregressive process, , with *et* ~ N(0, **). The ** was chosen such that the model complexity (time-variation) did not increase out-sample-prediction error over the base catch model (with no environmental covariates).

The explanatory power of the covariates, even when allowed to be time-varying and thus flexible enough to fit local conditions, changed over time. Up to 1990, the land precipitation did not increase model fit but did afterwards. The 2.5-year average regional SST improved the model fit over the entire time series (the covariate RMSE line was below that of the model with no covariates), but especially so from the mid-1980s to late-1990s (Figure 7). Thus the relationship between the covariates and the catch residuals (the catch not explained by prior year catch) changed over time.

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# 4 DISCUSSION

Our results indicate that successful modeling of Indian oil sardine catch depends on the season of interest (monsoon versus post-monsoon) and selection of the environmental covariate to use in the model. All the covariates we tested were tied to environmental conditions known to impact key life- stages of the oil sardine. However only two covariates, the multiyear average regional SST and the monsoon rainfall levels over land improved model fit and out of sample prediction. However, the explanatory power of these two covariates varied over time (1956 to 2015) becoming more explanatory after 1990.

**4.1 Monsoon versus post-monsoon model performance**

The July-September catch (third quarter), which overlaps with the southwest monsoon and a seasonal fishery closure, is difficult to model. The best models with only prior catch as a covariate explained less than 30% of the variation, using either a non-linear or a time-varying effect of prior catch, while the best model with environmental covariates explained 45% of the variation with median out of sample prediction errors of +/-65% (of unlogged catch). We found no covariate that improved the root mean squared out of sample prediction error (although some improved the median prediction errors). In contrast variation in the post-monsoon catch (October-March) was much better explained. The best model with only prior catch as a covariate explained 57% of the variation and with the best covariate, explained 72%. The best environmental covariate reduced the prediction errors by more than 20% and explained two of the four recent catch collapses.

This result cautions against modeling all quarters of oil sardine catch together (as yearly catch). The July–September catch is difficult to model, 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 and the best forecasts have smaller predictive errors. Lumping all quarters together means that the high variability in the third quarter catch will hide the predictability of the October-March catch, which comprises 60-80% of the seasonal catch.

**4.2 Sea surface temperature**

In this study, the multiyear average regional SST explained the most variability in monsoon and post-monsoon oil sardine landings and improved out-of-sample catch prediction, reducing the out of sample prediction errors by 10-20%. Studies conducted in the California Current System have also found that the multiyear average SST 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). 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 in the SST effect was important. Both Jacobson and MacCall (1995) and Checkley et al. (2017) found a step-like response function for temperature: below a threshold value the effect of temperature was linear (and positive) and above the threshold, the effect was flat (no longer increased). In the linear portion of the effect curve, the point where the effect curve crosses from negative to positive represents an important biological threshold . Our analysis found a similar effect curve with a negative effect when the 2.5-year average temperature was below C and positive above and with the positive effect leveling off above C.

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. In some years, extreme heat events occur in March–May during the period of egg development which may affect spawning and thus the fall and future biomass. However, we found no correlation of these seasonal SST covariates with the July–September or October-March catch in the current or future seasons. Only the SST averaged over the lifespan of an oil sardine emerged as a consistently informative SST covariate.

**4.3 Precipitation**

From early studies of oil sardines, precipitation during the summer monsoon has been studied as a variable to explain catch fluctuations (Antony Raja, 1969, 1974; Murty & Edelman, 1966; Srinath, 1998). While correlations have been found, the identified correlations between precipitation and oil sardine landings have been positive in some studies and negative in others (Madhupratap, Shetye, Nair, & Nair, 1994) and varied depending on the time period studied. In general, the correlation was assumed to be positive as rainfall is correlated with monsoon intensity which is in turn correlated with upwelling and productivity. But heavy monsoon rain also has negative effects. During heavy rainfall, nutrient and sediments flow into the nearshore region from rivers, which leads to short-term eutrophication and anoxia (Chauhan et al., 2011).

In our study, we compared rainfall over the ocean (using remote-sensing data) and over the land (using land-gauge data). Though correlated, these are not identical. We found no correlation between rainfall over the ocean and catch in any combination of our statistical tests. Oceanic rainfall was uniformly disinformative—increasing both AICc and out-of-sample prediction errors—across all combinations of models tested. In contrast the June-July precipitation over land in the current season was strongly informative and was the only covariate besides the multiyear average SST that improved model fit and out-of-sample prediction. The effect of precipitation was non-linear; zero for low to moderate rain and then negative at high precipitation. This suggests that the negative effects of high rainfall was the dominant impact of precipitation on the catch. The effects were only seen on the current season catch and thus may reflect a temporary movement of fish offshore away from the fishery rather than causing lower cohort strength that would persist into the next season.

**4.4 Upwelling**

Despite the strong connections of upwelling with productivity which positively impacts sardine recruitment, growth, and survival, none of the prior-season upwelling indices examined in this study (SST-nearshore-offshore differential, Bakun index, nor nearshore SST) explained year-to-year variation in landings in any consistent pattern. When we did find a relationship with current-season upwelling intensity and catch, the effect was negative, rather than positive. The negative effect emerged at 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 we found no evidence of an optimal intermediate upwelling intensity, i.e. an effect curve with a peak at some intermediate level, as found for other sardines (Deyle et al., 2013).

The upwelling indices tested in this study capture only nearshore intensity, whereas other aspects of upwelling, such as its spatial extent along the coast and the timing of its initiation, also affect Indian oil sardines. We did find support for a more direct measure of productivity and food availability: the coastal surface chlorophyll-a concentration. Chlorophyll-a concentration in fall, the period of peak juvenile somatic growth, explained the October-March catch in the next season, reducing out of sample prediction errors by 10% to 20%. With chlorophyll data only available after 1997, the power of our tests was limited, but this suggests that fall chlorophyll-a concentration, when available, may prove useful for improving forecasts.

**4.5 Oil sardine collapses**

There were four years when October-March oil sardine landings were much lower than expected based on prior catches: 1986, 1991, 1994 and 2013. The 2.5-year average SST explained the collapses in 1986 and 1991 (Figure 6d). The largest collapse was in 1994 and the most recent, in our dataset, was 2013. The 2.5-year average SST did not successfully predict the 1994 nor 2013 collapses; although the prediction error was reduced for both years, it was still large. The same pattern was seen for the July-September catch, with the exception that 1991 was not unusually low (Figure 6b). The 2.5-year average SST reduced the prediction error for 1986, but did not (appreciably) for 1994 nor 2013. In fact, none of the covariates we tested explained the lower than expected 1994 catch; while only the precipitation over land in June-July explained the 2013 collapse (but not 1994, 1991, nor 1986). The causes of the unusual 1994 decline appear unrelated to the environmental factors we studied, suggesting either that other factors, biological or anthropogenic, drove this decline or that a particular combination of environmental factors was responsible.

# 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 ocean measurements, 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 regional 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, but it does integrate multiple influences (i.e., upwelling strength and temperature) over the average oil sardine lifespan. The second best covariate was the precipitation over land, not ocean, with a negative effect of high rainfall leading to lower catch in the current season.

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, monitoring of covariate performance in catch forecast models is crucial, as changes in the ocean environment may alter associations, such as that observed in this study when we examined the covariate explanatory power over the entire 1956 to 2015 catch time series.

Our study emphasizes a number of key points for developing catch forecast models. First, non-linear effects are common and important to include. All the informative covariates involved a non-linear effect curve which matched known covariate effects, e.g. a negative effect of a covariate at high levels. Second, covariate effects change over time. Fisheries exist within complex multi-species ecological systems. Forecast models will need to guard against changing effects least the forecast model become disinformative. Lastly) Model complexity comes at a price particularly when the goal is forecasting. Inclusion of out-of-sample forecast metrics is crucial as these can give a very different picture than the model fit metrics. Covariates that are supported by model fit, even using metrics that penalize extra complexity, may be still be uninformative or even disinformative for out-of-sample prediction. Nonetheless, including key environmental covariates can appreciably improve catch forecasts, and in particular, the multiyear average sea surface temperature has emerged as an informative covariate across multiple studies on sardine species.

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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), current-season upwelling intensity (average June-September SST-derived UPW index in box 4) and June-July precipitation over land 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** Predicted 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. The value to be predicted as left out in the model fitting. 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 only. d) October–March, modeled as in c with the addition of the 2.5-year average SST. LOOCV RMSE, leave one out root mean squared prediction error.

**FIGURE 7** Model fit over 10-year windows for dynamic linear models of October-March catch 1956-2015 using the 2.5-year average SST from the ICOADS data set and June-July precipitation over land (from land gauges) as covariates. These models allowed the covariate model to evolve over time. The models were fit to the residuals of the simpler base model (with only prior October-March catch as a covariate) with the 1994 residual was removed. The covariates were z-scored (mean removed and standardized to variance of 1) and included as a third-order polynomial to allow a non-linear effect. The plot shows the RMSE computed on a 10-year sliding window.

**TABLE 1** Hypothesized covariates and relationships for the July–September (*S*) and October–March (*N*) landings. The models are structured as response ∼ explanatory variable(s). The tests did not impose a direction (positive or negative) and some covariates have been hypothesized to have both positive and negative impacts on oil sardines. References for the description and justification appear in the main text introduction.

|  |  |
| --- | --- |
| **Model** | **Description and justification** |
| DD1: *St* ∼ *Nt-1* | *St* comprises fish aged ≥ 1 year. These fish would have appeared in *Nt*−1as aged 0–2 year age fish. |
| DD2: *St* and *Nt* ∼ *St-1* and *St-2* | *St* comprises predominantly post-spawned spent fish and is correlated with spawning stock abundance and cohort strength. If cohort strength persists over time, *St* and *Nt* should correlate with *St-1* and *St-2*. |
| DD3: *Nt* ∼ *Nt-1* | *Nt*−1comprises fish aged 0 to >2 years, which will appear one year older in the next season in *Nt* landings. |
| S1: *St* ∼Jun–Jul and Apr-Mar oceanic precipitation | The April-May and June–July precipitation over the ocean directly or indirectly prompts spawning, after which spent adults migrate inshore and are exposed to the fishery. |
| S2: *St* and *Nt* ∼Jun–Jul land precipitation | Precipitation over land during the monsoon leads to high nutrient input from river discharge which leads to eutrophication and anoxia in the nearshore areas during the monsoon, while at the same time supporting productivity post-monsoon. |
| S3: *Nt* ∼Apr–Mar precipitation | Spring precipitation is an indicator of climatic conditions during egg development, which aﬀect spawning success and thus the cohort strength in the current and future seasons. |
| S4: *St* ∼Jun–Sep upwelling | High upwelling drives by the offshore advection of phytoplankton biomass and brings hypoxic water to the surface. Both drive mature fish further oﬀshore, reducing fishery exposure. Conversely, moderate upwelling leads to phytoplankton blooms which bring fish closer to the coast and to the fishery. |
| S5: *St* and/or *Nt* ∼Mar–May r-SST | Extreme pre-monsoon heating events drive mature fish from spawning areas, resulting in poor recruitment and fewer 0-year fish in *Nt*. |
| L1: *St* and/or *Nt* ∼Oct–Dec ns-SST | Larval and juvenile growth and survival are aﬀected by temperature and October-November are peak somatic growth months. Thus post-monsoon nearshore SST can affect current and future abundance. |
| L2: *St* and/or *Nt* ∼Jun–Sep UPW | Upwelling drives phytoplankton productivity, which in turn leads to better larval and juvenile growth, and higher future landings, but extreme upwelling leads to hypoxic conditions and phytoplankton biomass advection. |
| L3: *St* and *Nt* ∼ Jul-Sep and Oct-Dec CHL | The surface chlorophyll concentration is a proxy for phytoplankton abundance which supports greater fish abundance and catches in the current and future years. Peak chlorophyll abundance is in July-September but October-December are critical months for juvenile growth and survival. |
| A1: *St* and *Nt* ∼2.5-year average r-SST and 2.5-year average DMI | Spawning, early survival, and recruitment depend on many cascading factors summarized by the average regional SST over the lifespan of an oil sardine. DMI is correlated with regional SST in the SE Asia Sea and is another proxy for the average SST. |
| A2: *St* and *Nt* ∼ONI | The El Niño–Southern Oscillation has impacts on precipitation, SST, frontal zones, wind and upwelling patterns which impact spawning and early survival and current and future abundance. |
| A3: *St* and *Nt* ∼Sep-Nov DMI | Negative DMI values in September–November are associated with anoxic events along the Kerala coast which could move fish offshore (and inaccessible to the fishery) or cause lower juvenile growth and survival. |
| *Notes.* Model codes: DD, density dependence–related; S, spawning-months catch–related; L, larval and juvenile growth and survival–related; A, affecting all ages. Environmental covariates: UPW, upwelling; r-SST, regional (0-160km) sea surface temperature; ns-SST, nearshore (0-80km) sea surface temperature; CHL, chlorophyll surface concentration; ONI, Oceanic Niño Index; DMI, Dipole Mode Index. | |

**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 1983-2015** |  |  |  |  |  |  |
| 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 |
|  |  |  |  |  |  |  |
| **October-March catch - simpler model 1983-2014** | | | |  |  |  |
| 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 |
| = Sep-Nov DMI prior year (A1) | 26.0 | 44 | 0.79 | 94.4 | 0.95 | 0.34 |
|  |  |  |  |  |  |  |
| **October-March catch - more complex model 1983-2014** | | | | | | |
| 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 |
| = Sep-Nov DMI prior year (A1) | 23.8 | 69 | 0.57 | 81.3 | 0.88 | 0.35 |
|  |  |  |  |  |  |  |

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).