Example journal article on oil sardine (*Sardinella longiceps*)

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Running title: An example article

Acknowledgements

We thank the U.S. National Marine Fisheries Service for support, and we acknowledge the many researchers involved in collecting and maintaining the long-term data set.

This shows you a realistic Rmd for a journal article. This was an early version and I've cut out many paragraphs here and there to shorten it, but it is still has all the parts.

Note that the repository is a self-contained paper with all the data and the analyses are redone completely whenever Main.Rmd is re-knit. So if the data change, all the analyses will be updated.

Abstract

Commercial landings of sardine are known for strong year-to-year fluctuations. A key driver is thought to be environmental variability, to which small forage fish are especially sensitive. We examined the environmental drivers associated with landings fluctuations in the Indian oil sardine using a 32-year time series of quarterly catch. Past research suggested a variety of influential variables: precipitation, upwelling intensity, ocean temperature (SST), chlorophyll concentration and large-scale coupled atmosphere–ocean phenomena (ENSO). Using the life history of the Indian oil sardine, we developed hypotheses concerning how these variables might affect landings and tested them using generalized additive models which allow non-linear response curves and dynamic linear models which allow time-varying responses. We found significant correlation for three variables: upwelling intensity, an ENSO index, and the multi-year average nearshore SST. Upwelling intensity can have both a positive effect (fueling higher food availability) and a negative effect at extreme intensity (surface anoxia). The negative effect was apparent for both monsoon and post-monsoon catch. However, the most significant correlation (adjusted R^2 of 67.5%) was between the 2.5 year average nearshore SST and post-monsoon landings. The multi-year average SST also been identified as a predictor for Pacific and southern African sardine fluctuations, suggesting that the average SST over the sardine lifespan successfully captures a variety of factors which predict future abundance.

Keywords: Indian oil sardine, catch prediction, GAM modeling, climate, sea surface temperature, remote sensing, Southeast Arabian Sea

Introduction

Environmental variability is known to be a key driver of population variability of small forage fish such as sardines, anchovy and herring (Alheit & Hagen, 1997; Checkley et al., 2017; Cury et al., 2000). In particular, ocean temperature and upwelling dynamics, along with density-dependent feedback, have been identified as important in affecting recruitment success and biomass of European and Pacific sardines (*Sardina pilchardus* and *Sardinops sagax*) (Alheit et al., 2012; Garza-Gil et al., 2015; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012; Lindegren et al., 2013; Rykaczewski & Checkley, 2008). Like other sardines, the Indian oil sardine (*Sardinella longiceps* Valenciennes, 1847) shows strong inter-annual fluctuations and larger decadal booms and busts. The Indian oil sardine offers an instructive case study to investigate the effects of environmental variability, particularly temperature and upwelling dynamics, as they occupy an ocean system that is warmer than that occupied by other sardines and have a strong seasonal cycle driven by the Indian summer monsoon.

The Indian oil sardine is one of the most commercially important fish resources along the southwest coast of India (Figure 1) and historically has comprised approximately 25% of the marine catch in the Indian fisheries (Vivekanandan et al., 2003). Landings of the Indian oil sardine are highly seasonal, peaking after the summer monsoon period in October-December and reaching a nadir in spring before the summer monsoon in April-June (Figure 2). At the same time, the landings of this small pelagic finfish are highly variable from year to year. Small pelagics are well known to exhibit high variability in biomass due to the effects of environmental conditions on survival and recruitment, but in this fishery, environmental conditions also affect exposure of sardines to the fishery. Until recently, the Indian oil sardine fishery was artisanal and based on small human or low powered boats with no refrigeration. The fishery was confined to nearshore waters, and thus migration of sardines in and out of the coastal zone greatly affected exposure to the fishery and hence landings.

Researchers have examined a variety of environmental variables for their correlation with landings of the Indian oil sardine. Precipitation during the monsoon and the day of the monsoon arrival are thought to act as either a direct or indirect cue for spawning (Antony Raja, 1969, 1974; Jayaprakash, 2002; Murty & Edelman, 1966; Pitchaikani & Lipton, 2012; Srinath, 1998; Xu & Boyce, 2009). Although many studies have looked for and some have found correlations between precipitation and landings, the reported relationships are positive in some studies and negative in others (Madhupratap et al., 1994). Researchers have also looked for and found correlations with various metrics of upwelling intensity (Jayaprakash, 2002; Longhurst

& Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara, 2011), with 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 et al., 2014; Pitchaikani & Lipton, 2012), and with nearshore sea surface temperature (SST) (Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed, 1970; Supraba et al., 2016).

Catch modeling versus biomass modeling

Modeling and forecasting landings data using statistical models fit to annual or seasonal catch time series has a long tradition in fisheries and has been applied to many species (Cohen & Stone, 1987; Farmer & Froeschke, 2015; Georgakarakos et al., 2006; Hanson et al., 2006; Lawer, 2016; Lloret et al., 2000; Mendelssohn, 1981; Nobel & Sathianandan, 1991; Prista et al., 2011; Stergiou & Christou, 1996), including oil sardines (Srinath, 1998; Venugopalan & Srinath, 1998). These models can be used to identity the variables correlated with catch fluctuations and can be used to provide landings forecasts which are useful for fishery managers and the fishing industry. An example of the former is using catch forecasts to set or give warnings of seasonal fishery closures if the forecasted catch is higher than the allowed catch limits (Farmer & Froeschke, 2015). An example of the latter is the annual Gulf and Atlantic menhaden forecast produced by NOAA Fisheries (Hanson et al., 2006; Schaaf et al., 1975). This multiple regression model has been used for the last 45 years to produce an annual forecast of menhaden landings, which is used for planning purposes by the industry, not only the fishers but also fish catch sellers and buyers, businesses which provide fisheries gear, and banks which provide financing (Hanson et al., 2006).

Study Area

Our analysis focuses on the Kerala coast (Figure 1) region of India, where the majority of the Indian oil sardines are landed and where oil sardines comprise ca. 40% of the marine fish catch (Srinath, 1998; Vivekanandan et al., 2003). This area is in the Southeast Arabian Sea, one of world's major upwelling zones, with seasonal peaks in primary productivity driven by upwelling caused by winds during the Indian summer monsoon (Habeebrehman et al., 2008; Madhupratap et al., 2001) between June and September. Within the study area, the coastal zone off Kerala between 9°N to 13°N has especially intense upwelling due to the combined effects of wind stress and remote forcing (BR, 2010; BR et al., 2008). The result is a strong temperature differential between the nearshore and offshore and high primary productivity and surface chlorophyll concentration in this region during summer and early fall (BR, 2010; Chauhan et al., 2011; Habeebrehman et al., 2008; Jayaram et al., 2010; Madhupratap et al., 2001; Raghavan et al., 2010). The primary productivity peaks subside after September while mesozooplankton abundances increase and remain high in the post-monsoon period (Madhupratap et al., 2001).

Oil sardine life cycle and fishery

The Indian oil sardine fishery is restricted to the narrow strip of the western India continental shelf, within 20 km from the shore (Figure 1). The yearly cycle of the fishery begins at the start of spawning during June to July, corresponding with the onset of the summer monsoon (Antony Raja, 1969; Chidambaram, 1950) and the initiation of strongly cooler nearshore SST due to upwelling (Figure 3). At this time, the mature fish migrate from offshore to coastal spawning areas, and the spawning begins during the summer monsoon period when temperature, salinity and suitable food availability are conducive for larval survival (Chidambaram, 1950; Jayaprakash & Pillai, 2000; Krishnakumar et al., 2008; Murty & Edelman, 1966; Nair et al., 2016). Although peak spawning occurs in June to July, 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 the 0-year fish. Spawning occurs in waters outside of the traditional range of the fishery (Antony Raja, 1964), and after spawning the adults migrate closer to the coast where the spent fish become exposed to the fishery.

After eggs are spawned, they develop rapidly into larvae (Nair, 1959). The phytoplankton bloom that provide sardine larvae food is dependent upon nutrient influx from coastal upwelling and runoff from rivers during the summer monsoon and early fall. The blooms start in the south near the southern tip of India in June, increase in intensity and spread northward up the coast (BR, 2010). Variation in the bloom initiation time and intensity leads to changes in the food supply and to corresponding changes in the growth and survival of larvae and in the later recruitment of 0-year sardines into the fishery (George et al., 2012). Oil sardines grow rapidly during their first few months, and 0-year fish (40mm to 100mm) from early spawning appear in the catch in August and September in most years (Antony Raja, 1970; Nair et al., 2016). As the phytoplankton bloom spreads northward, the oil sardines follow, and the oil sardine fishery builds from south to north during the post-monsoon period. Oil sardines remain inshore feeding throughout the winter months, until March to May when the inshore waters warm considerably and sardines move offshore to deeper waters (Chidambaram, 1950). Catches of sardines are correspondingly low during this time for all size classes. The age at first maturity occurs at approximately 150 mm size (Nair et al., 2016), which is reached within one year. When the summer monsoon returns, the oil sardine cycle begins anew.

Materials and Methods

Sardine landing data

Quarterly fish landing data have been collected by the Central Marine Fisheries Research Institute (CMFRI) in Kochi, India, since the early 1950s using a stratified multi-stage sample design (Srinath et al., 2005). The survey visits the fish landing centers along the entire southwest coast of India and samples the catch from the variety of boat types and gear types used in the coastal fishery. Landings estimates are available for all the coastal states, however we model the catch for the state of Kerala only, where the longest time series is available and the overwhelming majority of oil sardines are landed (Figure 2).

Remote sensing data

We analyzed monthly composites of the following environmental data derived from satellite data: sea surface temperature (SST), chlorophyll-a (CHL), upwelling (UPW), the Oceanic Niño Index (ONI), the Dipole Mode Index (DMI) and precipitation. The monthly time series and means of the covariates are shown in Figure 4.

We used the chlorophyll-a products developed by the Ocean Biology Processing Group in the Ocean Ecology Laboratory at the NASA Goddard Space Flight Center. For 1997 to 2002, we used the chlorophyll-a 2014.0 Reprocessing (R2014.0) product from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite. These data are on a 0.1 degree grid. For 2003 to 2017, we used the MODIS-Aqua product on a 0.05 degree grid. These CHL data are taken from measurements by the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua Spacecraft. The SST and CHL data were averaged across thirteen 1 degree by 1 degree boxes which roughly parallel the bathymetry (Figure 1). The SST and

CHL satellite data were retrieved from NOAA remote-sensing data servers; see Appendix G for data sources and references.

For an index of coastal upwelling, we used three indices. The first was the sea surface temperature differential between near shore and 3 degrees offshore based on the index described by Naidu et al. (1999) and BR et al. (2008). For SST, we used the remote sensing sea surface temperature data sets described above. This SST-based upwelling index has been validated as a more reliable metric of upwelling off the coast of Kerala compared to wind-based upwelling indices (BR et al., 2008).

The Oceanic Niño Index (ONI) is a measure of the SST anomaly in the east-central Pacific and is a standard index of the El Niño/Southern Oscillation (ENSO) cycle. The ONI index 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. The ONI was downloaded from the NOAA National Weather Service Climate Prediction Center. The Dipole Mode Index (DMI) is defined by the SSTA difference between the western Indian Ocean (10°S–10°N, 50°E–70°E) and the southeastern Indian Ocean (10°S–0°, 90°E–110°E). The DMI has been shown to predict anoxic events in our study area (Vallivattathillam et al., 2017). The DMI data were downloaded from the NOAA Earth System Research Laboratory. See Appendix G for the data servers where the ENSO data were downloaded and computation notes and references.

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. The Jul-Sep catch overlaps the summer monsoon and the main spawning months. This is also the quarter where small 0-year fish from early spawning often appear in the catch, sometimes in large numbers. Variables that affect or are correlated with movement of sardines inshore should be correlated with Jul-Sep landings. In addition, pre-spawning (Mar-May) environmental conditions should be correlated with the spawning strength as adult oil sardines experience an acceleration of growth during this period along with egg development. The post-monsoon catch (Oct-May) is a mix of 0-year fish (less than 12 months old) and mature fish (greater than 12 months old). Variables that are correlated with spawning strength and larval and juvenile survival should correlate with the post-monsoon catch both in the current year and in future years, one to two years after.

Statistical models

Preliminarily, we tested ARIMA models on both the Jul-Sep and Oct-Mar catch time series and found little support for auto-regressive errors (ARIMA models with a MA component) based on diagnostic tests of the residuals and model selection. The best supported ARIMA models were simple AR models ($x_t = bx_{t-1} + \varepsilon_t$). This lack of strong auto-correlation in residuals has been found in other studies that tested ARIMA models for forecasting small pelagic catch (Stergiou & Christou, 1996). We thus used AR-only models, however we tested both linear and non-linear models using generalized additive models (GAMs, Wood, 2017) of the form $x_t = s(x_{t-1}) + \varepsilon_t$ and tested time-varying linear models with dynamic linear models (DLM). GAMs allow one to model the effect of a covariate as a flexible non-linear function while 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.

We compared the following catch models:

- null: $ln(C_{i,t}) = ln(C_{j,t-1})$
- random walk: $ln(C_{i,t}) = \alpha + ln(C_{j,t-1})) + \varepsilon_t$
- linear AR-1: $ln(C_{i,t}) = \alpha + \beta ln(C_{j,t-1})) + \varepsilon_t$
- linear AR-2: $ln(C_{i,t}) = \alpha + \beta_1 ln(C_{j,t-1})) + \beta_2 ln(C_{k,t-2})) + \varepsilon_t$
- DLM AR-1: $ln(C_{i,t}) = \alpha_t + \beta_t ln(C_{j,t-1})) + \varepsilon_t$
- GAM AR-1: $ln(C_{i,t}) = \alpha + s(ln(C_{j,t-1})) + \varepsilon_t$
- GAM AR-2: $ln(C_{i,t}) = \alpha + s_1(ln(C_{j,t-1})) + s_2(ln(C_{k,t-2})) + \varepsilon_t$

$ln(C_{i,t})$ is the log catch in the current year t in season i. We modeled two different catches: S_t (Jul-Sep) and N_t (Oct-Jun). The catches were logged to stabilize and normalize the variance. $s()$ is a non-linear function estimated by the GAM algorithm. The model is primarily statistical, meaning it should not be thought of as a population growth model. We tested models with prior year and two years prior Oct-Mar catch (N_{t-1} and N_{t-2}) and Jul-Sep catch (S_{t-1} and S_{t-2}) as the explanatory catch variable. S_t was not used as a predictor for N_t because S_t is the quarter immediately prior to N_t and would not be available for a forecast model since time is required to process landings data. The catch models were fit to 1984 to 2015 catch data, corresponding to the years when the SST, upwelling and precipitation data were available.

Once the catch models were determined, the covariates were studied individually and then jointly. As with the catch models, F-tests, AIC and LOOCV (leave-one-out cross-validation) on nested sets of models were used to evaluate the support for models with covariates. The smoothing term was fixed at an intermediate value (sp=0.6) instead of being treated as an estimated variable. Our models for catch with covariates took the form $ln(C_{i,t}) = M + \alpha + s_1(V_{1,t}) + s_2(V_{2,t-1}) + \varepsilon_t$, $ln(C_{i,t}) = M + \alpha + \beta_1 V_{1,t} + \beta_2 V_{2,t-1} + \varepsilon_t$, and $ln(C_{i,t}) = M + \alpha + \beta_t V_{1,t} + \varepsilon_t$ where M was the best catch model from step 1 and V is a covariate. Thus models with covariates modeled as a linear, non-linear and time-varying effect were compared.

Results

Catches in prior seasons as explanatory variables

Using the 1984-2015 catch data, the time-period that overlaps our available environmental data, the Jul-Sep catch models were compared against a "naive" model in which the forecasted Jul-Sep catch is the Jul-Sep catch in the prior year. The "naive" model has no estimated parameters and is a standard null model for time series modeling. Models with $ln(N_{t-1})$ (Oct-Mar catch in prior year) as the explanatory covariate were strongly supported over the naive model and over models with $ln(S_{t-1})$ (Jul-Sep catch in prior year) as the explanatory variable (Tables A1 and A2). Addition of the catch two years prior, $ln(N_{t-2})$ or $ln(S_{t-2})$, was not supported (by AIC or F-tests) for either the linear or non-linear models. We tested the support for non-linearity in the effect of the prior year catch by comparing models with $ln(N_{t-1})$ or $ln(S_{t-1})$ included as a linear effect or as a non-linear effect using GAMs.

As diagnostic checks, we repeated the model comparisons with the landings data set from 1956 to 1983. The results were the same for the Jul-Sep catch (Table A3) with the model with $ln(N_{t-1})$ included as a non-linear covariate giving the lowest AIC and LOOCV. For the Oct-Mar catch (Table A4), the results were very similar but not identical. The model with $ln(N_{t-1})$ included as a non-linear covariate had the lowest LOOCV while the models with $ln(N_{t-1})$ and $ln(S_{t-2})$ or $ln(S_{t-2})$ had the lowest AIC (though less than 1 from the AIC of the $ln(N_{t-1})$ model). We also did an influential years test using leave-one-out cross-validation (Appendix F). This test involved leaving out one year and repeating the model selection tests. This analysis supported the selected base models using the 1984-2015 data. The dynamic linear models (allowing a time-varying effect of prior catch) performed poorly for the Jul-Set catch with high AIC and LOOCV. For the Oct-Mar catch, the performance was mixed with higher AIC but lower LOOCV for one of the DLMs.

Based on the model selection tests, the following non-linear model was chosen as the base model for Jul-Sep (S_t) catch:

$$M0 : ln(S_t) = \alpha + s(ln(N_{t-1})) + \varepsilon_t.$$

Two base non-linear models were chosen for Oct-Mar (N_t) catch:

$$M1 : ln(N_t) = \alpha + s_1(ln(N_{t-1})) + s_2(ln(S_{t-2})) + \varepsilon_t$$

$$M2 : ln(N_t) = \alpha + s(ln(N_{t-1})) + \varepsilon_t$$

Note that although M0 was the best model for Jul-Sep catch, it was only weakly explanatory. The maximum adjusted R^2 was less than 30% (Table A2). For the Oct-Mar catch, M1 and M2 were more explanatory with an adjusted R^2 of 45.3% for M1 and 56.6% for M2 (Table A5).

Environmental covariates as explanatory variables

There was no support for using precipitation during the summer monsoon (June-July) or pre-monsoon period (April-May) as an explanatory variable for the Jul-Sep or Oct-Mar catch (hypotheses S1 and S2; Tables B1, B2 and B3). This was the case whether precipitation in the current or previous season was used, if precipitation was included as a non-linear or linear effect, and if either precipitation during early monsoon (June-July) or pre-monsoon (April-May) was used as the covariate. Jul-Sep catch overlaps with the late spawning period and precipitation is often thought to trigger spawning, however we were unable to find any consistent association of catch with precipitation. Raja (1974) posited that the appropriate time period for the effect of rainfall is the weeks before and after the new moon when spawning is postulated to occur and not the total rainfall during the monsoon season. Thus the lack of correlation may be due to using too coarse of a time average for the precipitation.

Instead we found support for the covariates indirectly and directly associated with productivity and food availability: upwelling intensity and surface chlorophyll. The correlation between landings and upwelling was only found for upwelling in the current season. No correlation was found when we used the upwelling index from the prior season. The correlation between landings and upwelling was found for both Jul-Sep and Oct-Mar landings and with either SST-based upwelling index: average nearshore SST along the Kerala coast during

June-September or the average SST nearshore versus offshore differential (UPW) off Kochi in June-September (Table 2, B4, B5 and B6). These two upwelling indices are correlated but not identical. The model with average June-September nearshore SST was more supported than the model using the SST differential off Kochi. For Jul-Sep catch, this model with a non-linear response had an adjusted R^2 of 41.0 versus an adjusted R^2 of 24.4 for the model with no covariates (Table B4), and for Oct-Mar catch, the adjusted R^2 was 61.8 versus 56.6 (Table B5). Note, that this covariate is June-September in the current season and overlaps with the July-September catch. Thus this model cannot be used to forecast Jul-Sep catch and gives only a month-prior forecast for Oct-Mar, but it does help us understand what factors may be influencing catch.

Discussion

Sardines in all the world's ecosystems exhibit large fluctuations in abundance (Checkley et al., 2017). These small forage fish are strongly influenced by natural variability in the ocean environment. Upwelling, influenced by both large-scale forces such as regimes shifts and El Niño/Southern Oscillation patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010) and by seasonal wind and current patterns, brings nutrient rich and oxygen rich waters to the surface. This drives the seasonal variability in phytoplankton resources and in turn sardine prey (Bakun et al., 2008). Local variability in temperature, salinity, and oxygen levels have both 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 well-known for their sensitivity to over-fishing which has been linked to many fishery collapses (Kripa et al., 2018).

Many studies on Pacific sardines have looked at the correlation between ocean surface temperature (SST) and recruitment. Temperature can have direct effect on larval survival and growth and an indirect effect on food availability. Studies in the California Current System, have found that SST explains (a portion of) year-to-year variability in Pacific sardine recruitment (Checkley et al., 2009, 2017; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012) and that the average nearshore temperature over multiple seasons is the relevant explanatory variable. Similar to these studies, we found that the average nearshore SST over multiple seasons was the covariate that explained the most variability in catch both in the monsoon and post-monsoon months. McClatchie et al. (2010) found no relationship with SST and Pacific sardine recruitment, however their analysis used a linear relationship while the other studies, and ours, that found a relationship allowed non-linearity. 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 above the threshold, the effect was flat and at lower temperatures the effect was negative and became positive as temperature increased. Our analysis found a similar pattern with a negative effect when the 2.5-year average temperature was below 28.35°C and positive above and with the positive effect leveling off above 28.5°C (Figure 5).

Conclusions

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 rate higher than any other tropical ocean (Roxy et al., 2014) and the warming has been most extreme during the summer monsoon months. This ocean climate change is affecting oil sardine distributions, with significant landings now occurring north of Goa (Vivekanandan et al., 2009). Continued warming is expected to affect the productivity of the region via multiple pathways, including both the direct effects of temperature change on the physiology and behavior of organisms and multiple of indirect effects (Moustahfid et al., 2018). These indirect effects include changes to salinity, oxygen concentrations, currents, wind patterns, ocean stratification and upwelling spatial patterns, phenology, and intensity. Incorporating environmental covariates into landings forecasts has the potential to improve fisheries management for small pelagics such as oil sardines in the face of a changing ocean environment (Haltuch et al., 2019; Tommasi et al., 2016). However, monitoring forecast performance and covariate performance in models will be crucial as a changing ocean environment may also change the association between landings and average sea surface temperature.

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Figure Legends

Figure 1. Southwest coast of India with the latitude/longitude boxes used for the satellite data. Kerala State is marked in grey and the oil sardine catch from this region is being modeled. For the SST covariate, ‘nearshore’ SST (ns-SST) was the average of boxes 2 to 5 (0 to 80km offshore), and ‘regional’ SST (r-SST) was the average of boxes 2 to 5 and 7 to 10 (0 to 160km offshore).

Figure 2. Quarterly catch data 1956-2014 from Kerala. The catches have a strong seasonal pattern with the highest catches in quarter 4 (Oct-Dec). Note that the fishery is closed July 1 to mid-August, thus the fishery is only open 1.5 months in quarter 3 (Jul-Sep). The mean catch (metric tonnes) in quarters 1 to 4 are 37.4, 22.3, 33.7, and 53.7 metric tonnes respectively.

Figure 3. Key oil sardine life history events overlaid on the monthly sea surface temperature in the nearshore and offshore and the nearshore chlorophyll-a concentration.

Figure 4. Remote sensing covariates used in the analysis. All data are monthly averages over Box 4 in Figure 1 on the Kerala coast off of Kochi. Panel A) Upwelling Index. The upwelling index is the difference between the nearshore sea surface temperature (SST) and the offshore SST defined as 3 degrees longitude offshore. Panel B) Nearshore surface chlorophyll-a (CHL). The CHL data are only available from 1997 onward. Panel C) Sea surface temperature from Advanced Very High Resolution Radiometer (AVHRR). Panel D) Average daily rainfall (mm/day) off the Kerala coast.

Figure 5. Effects of the two most influential covariates estimated from the GAM models: 2.5 year average nearshore (boxes 2-5) SST and upwelling intensity in June-September (spawning months). Panel A) Effect of the 2.5 year average nearshore SST on Jul-Sep catch (late spawning and early post-spawning months). Panel B) Effect of upwelling (nearshore/offshore SST differential) during June-September in the current season on Jul-Sep catch. The index is the difference between offshore and inshore SST, thus a negative value indicates warmer coastal surface water than offshore. Panel C) Effect of the 2.5 year average nearshore SST on Oct-Mar catch (post-monsoon, age-0, -1, -2 year fish). Panel D) Effect of upwelling (nearshore/offshore SST differential) during June-September in the current season on Oct-Mar catch.

Figure 6. Fitted versus observed catch with models with and without the 2.5 year average nearshore SST included as a covariate. The line is the one-to-one line (prediction equals observed). Panel A) Fitted versus observed log catch in Jul-Sep (late monsoon) with only Oct-

Mar catch in the previous season as the covariate: $S_t = s(N_{t-1}) + \varepsilon_t$. Panel B) Fitted versus observed log catch in Jul-Sep with the 2.5-year average SST added as a covariate to the model in panel A. This model was: $S_t = s(N_{t-1}) + s(V_t) + \varepsilon_t$. Panel C) Fitted versus observed log Oct-Mar catch with only Oct-Mar catch in the previous season and Jul-Sep catch two seasons prior as the covariates: $N_t = s(N_{t-1}) + s(S_{t-2}) + \varepsilon_t$. Panel D) Fitted versus observed log Oct-Mar catch with 2.5-year average SST (V) added. This model was $N_t = s(N_{t-1}) + s(S_{t-2}) + s(V_t) + \varepsilon_t$.

Table 2. Top covariates for the monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch (S_t and N_t) models. 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	Resid. df	Adj. R^2	RMSE	AICc	LOOCV RMSE
July-Sept catch 1983-2015					
null model: $ln(S_t) = ln(S_{t-1}) + \varepsilon_t$	33		1.6	126.6	1.6
base (M): $ln(S_t) = \alpha + s(ln(N_{t-1})) + \varepsilon_t$	30	21.7	1.2	115.2	1.31
nonlinear covariate model: $ln(S_t)$ = M + $s(V_t)$					
V_t = Jun-Sep ns-SST (L2)	27.9	35.3	1.06	112.7†	1.24‡
V_t = Jun-Sep Bakun-UPW (L2)	27.6	43.1	0.98	109.1††	1.35
V_t = Jun-Jul Precipitation - land gauges (S1)	28	29.9	1.1	115.3	1.33
V_t = 2.5-year average r-SST - AVHRR (A1)	27.8	37.3	1.04	111.8†	1.29
October-March catch - simpler model 1983-2014					
null model: $ln(N_t) = ln(N_{t-1}) + \varepsilon_t$	32		1	92.9	1
base (M): $ln(N_t) = \alpha + s(ln(N_{t-1})) + \varepsilon_t$	29.1	45.9	0.82	87.7	0.95
nonlinear covariate model: $ln(N_t)$ = M + $s(V_t)$					
V_t = Jun-Jul Precipitation - land gauges (S1)	26.9	59.6	0.69	82.1††	0.91‡
V_t = 2.5-year average r-SST - AVHRR (A1)	26.9	64.5	0.64	78.1††	0.76‡‡‡
V_t = Sep-Nov DMI (A3)	26	44.3	0.79	94.4	0.95
October-March catch - more complex model					
null model: $ln(N_t) = ln(N_{t-1}) + \varepsilon_t$	32		1	92.9	1
base (M): $ln(N_t) = \alpha + s(ln(N_{t-1})) + s(ln(S_{t-2})) + \varepsilon_t$	26.6	57.3	0.7	84.6	1.05
nonlinear covariate model: $ln(N_t)$ = M + $s(V_t)$					
V_t = Jun-Jul Precipitation - land gauges (S1)	24.6	70.5	0.56	77.5††	0.97‡
V_t = 2.5-year average r-SST - AVHRR (A1)	24.7	72	0.55	75.6††	0.75‡‡‡
V_t = Sep-Nov DMI (A3)	23.8	68.9	0.57	81.3†	0.88‡‡

Notes: The nested F-tests are given in Supporting Information. LOOCV = Leave one out cross-validation. RMSE = root mean square error. AICc = Akaike Information Criterion corrected for small sample size. † and †† = AICc greater than 2 and greater than 5 below model M (base catch model). ‡, ‡‡, and ‡‡‡ = LOOCV RMSE 5%, 10% and 20% below model M, respectively. *t* indicates current season (Jul-Jun). For covariates that are multiyear, *t* is the current calendar year.

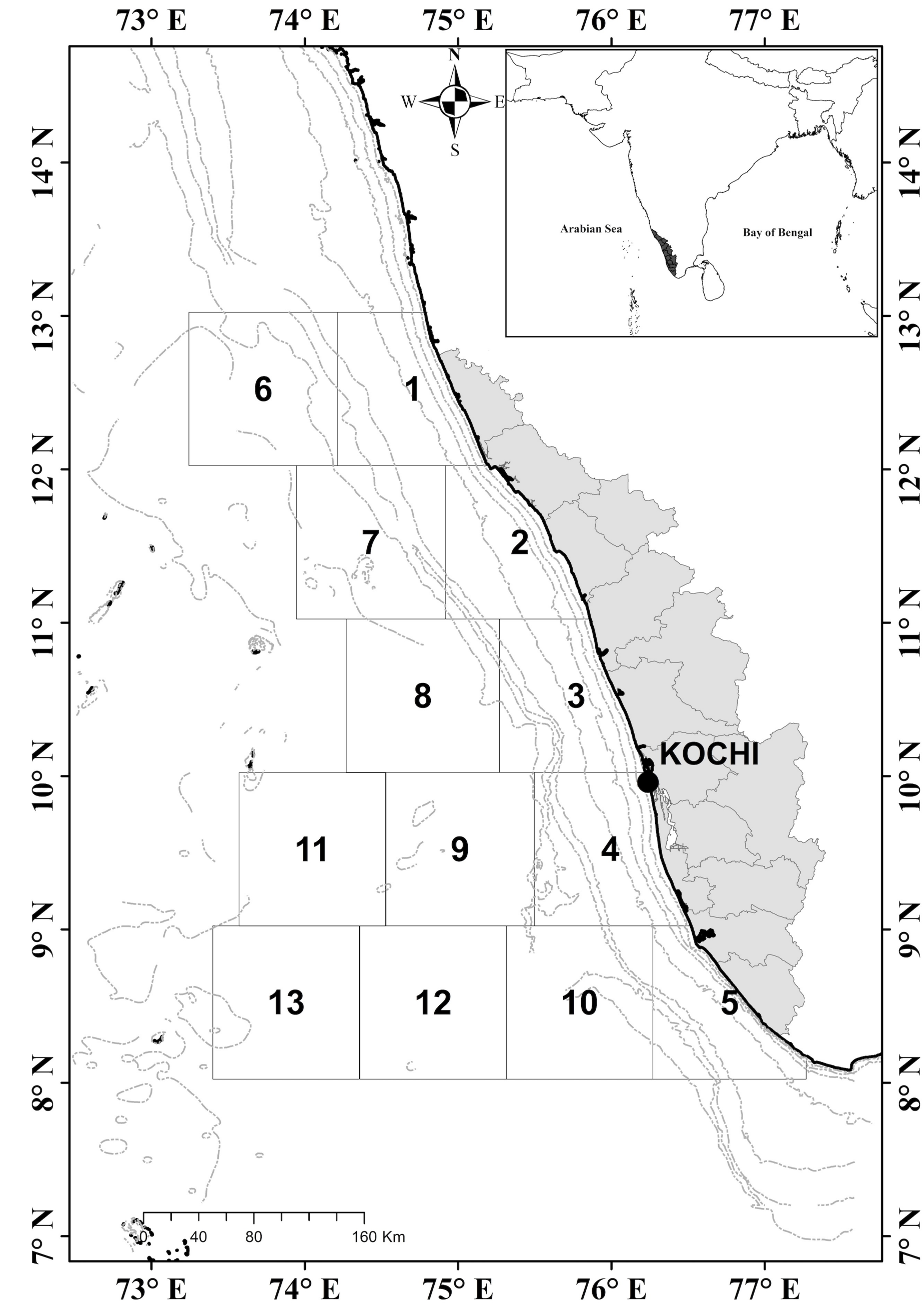
73° E
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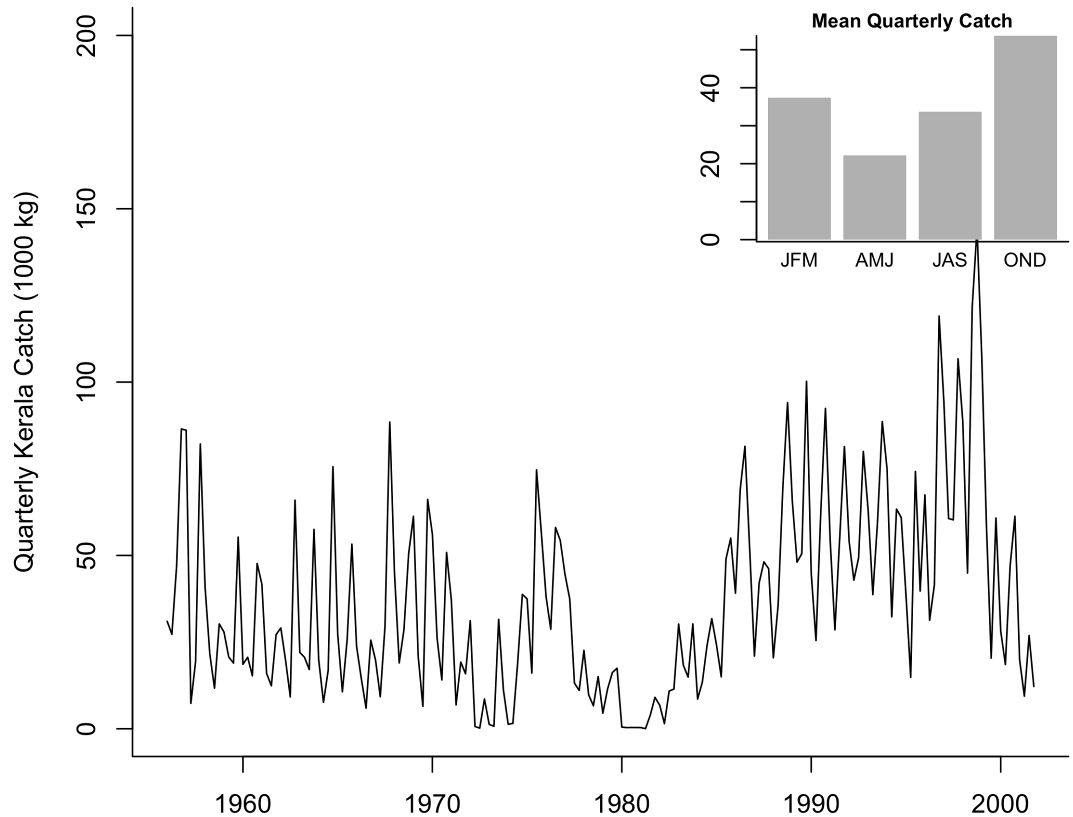
Figure 1


Mean Quarterly Catch
0
20
40
JFM
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OND
Quarterly Kerala Catch (1000 kg)
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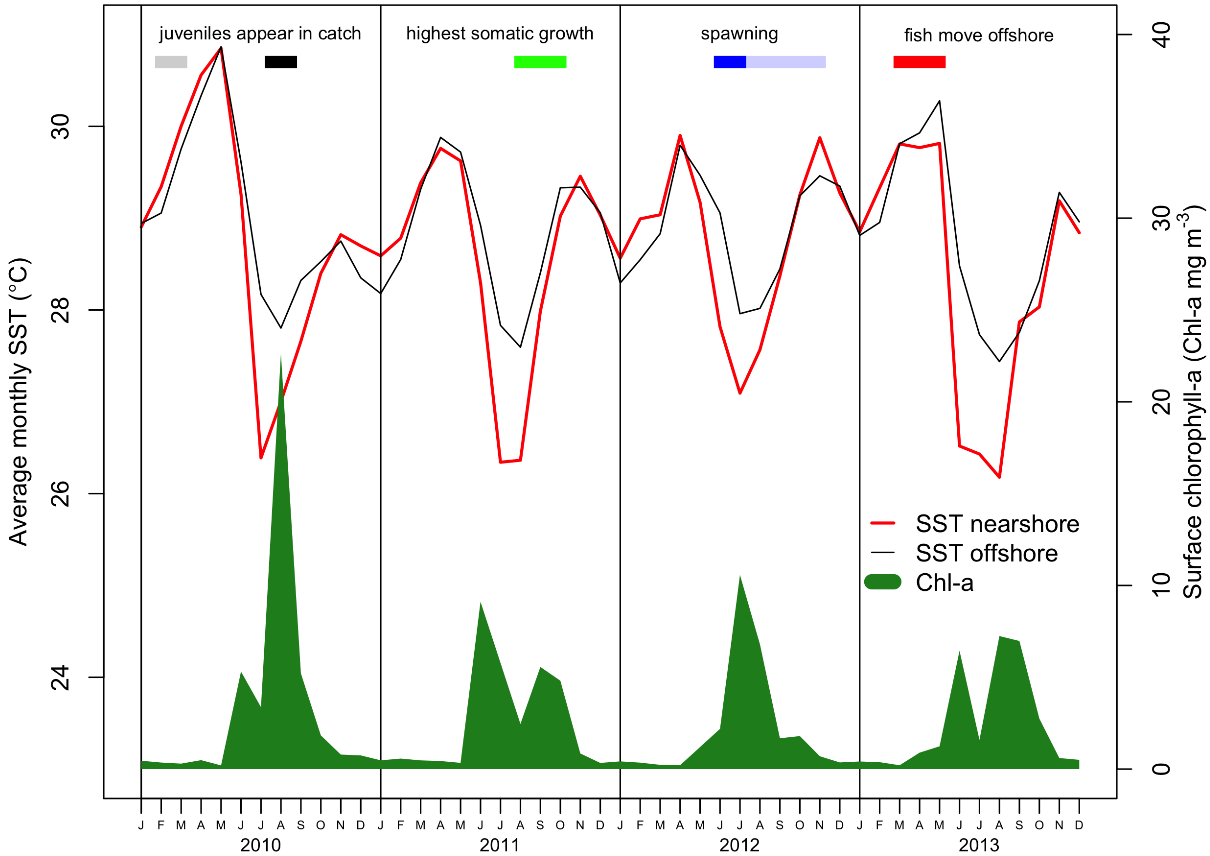
50
100
150
200
1960
1970
1980
1990
2000

Figure 2



juveniles appear in catch
highest somatic growth
spawning
fish move offshore
Average monthly SST (°C)
Surface chlorophyll-a (Chl-a mg m^{-3})
SST nearshore
SST offshore
Chl-a
24
26
28
30
0
10
20
30
40
J F M A M J J A S O N D
2010
2011
2012
2013

Figure 3

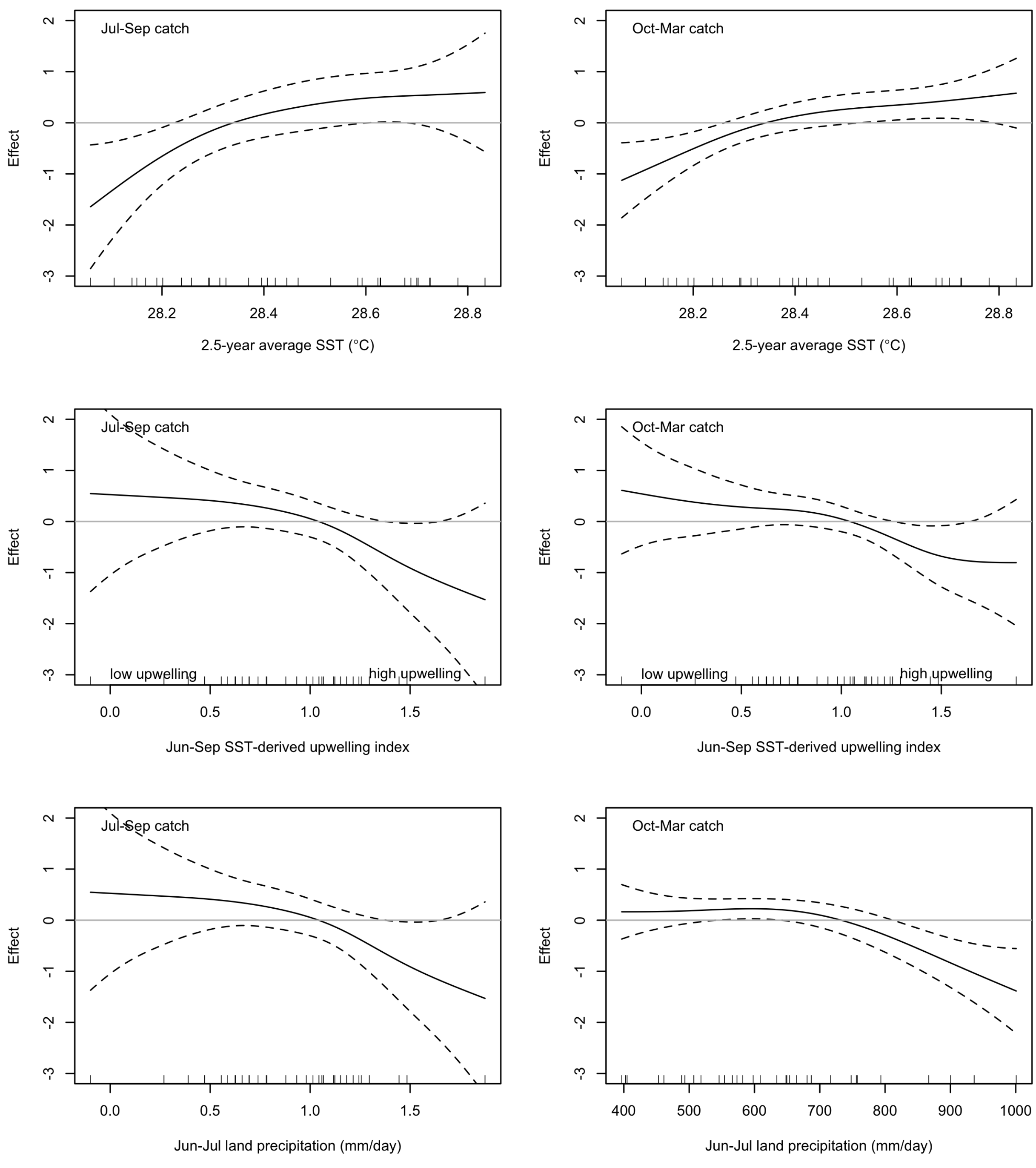

Jul-Sep catch
Oct-Mar catch
Effect
2.5-year average SST (°C)
Jun-Sep SST-derived upwelling index
low upwelling
high upwelling
Jun-Jul land precipitation (mm/day)

Figure 5