

¹ Fishing in a warming ocean: influence of changing temperature
² and upwelling intensity on Indian oil sardine (*Sardinella*
³ *longiceps*) landings

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¹² **Running title:** Modeling Indian oil sardine landings

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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 off Kerala state. Past research suggested a variety of influential variables: precipitation, upwelling intensity, ocean temperature (SST), chlorophyll density and large-scale coupled atmosphere–ocean phenomena (ENSO). Using the life-history of the Indian oil sardine, we developed hypotheses concerning how these environmental 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 only two variables: upwelling intensity and the multi-year average nearshore SST. Both monsoon and post-monsoon landings were correlated with upwelling intensity in June–September. Upwelling intensity has both a positive effect (fueling higher food availability) and a negative effect at extreme intensity (bringing poorly oxygenated water to the surface). 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 sardine and southern African sardine fluctuations, suggesting that the average SST over the sardine life-span successfully captures a variety of factors which predict future abundance. The temperature in the Western Indian Ocean has been increasing faster than in other tropical oceans and the warming has been most extreme during the summer monsoon. Our work highlights that these changes in summer upwelling intensity and sea temperature are likely to affect future landings.

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

51 **Introduction**

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

64 The Indian oil sardine (*Sardinella longiceps* Valenciennes, 1847) is one of the most com-
65 mercially important fish resources along the southwest coast of India (Figure 1) and historically
66 has comprised approximately 25% of the catch biomass (Vivekanandan et al., 2003). Land-
67 ings of the Indian oil sardine are highly seasonal, peaking after the summer monsoon period in
68 October-December and reaching a nadir in spring before the summer monsoon in April-June
69 (Figure 2). At the same time, the landings of this small pelagic finfish are highly variable
70 from year to year. Small pelagics are well known to exhibit high variability in biomass due
71 to the effects of environmental conditions on survival and recruitment (Alheit & Hagen, 1997;
72 Checkley et al., 2017; Cury et al., 2000). In this fishery, environmental conditions also affect
73 exposure of sardines to the fishery. Until recently, the Indian oil sardine fishery was artisanal
74 and based on small human or low powered boats with no refrigeration. The fishery was con-
75 fined to nearshore waters, and thus migration of sardines in and out of the coastal zone greatly
76 affected exposure to the fishery.

77 Researchers have examined a variety of environmental variables for their correlation with
78 landings of the Indian oil sardine. Precipitation during the monsoon and the day of the mon-
79 soon arrival are thought to act as either a direct or indirect cue for spawning (Antony Raja,
80 1969, 1974; Jayaprakash, 2002; Murty & Edelman, 1966; Pitchaikani & Lipton, 2012; Sri-
81 nath, 1998; Xu & Boyce, 2009). Although many studies have looked for and some have found
82 correlations between precipitation and landings, the reported relationships are positive in some
83 studies and negative in others (Madhupratap et al., 1994). Researchers have also looked for and

84 found correlations with various metrics of upwelling intensity (Jayaprakash, 2002; Longhurst
85 & Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara,
86 2011), with direct measures of productivity such as nearshore zooplankton and phytoplank-
87 ton abundance (George et al., 2012; Hornell, 1910; Madhupratap et al., 1994; Menon et al.,
88 2019; Nair, 1952; Nair & Subrahmanyam, 1955; Piontovski et al., 2015; Pitchaikani & Lip-
89 ton, 2012), and with near-shore sea surface temperature (SST) (Annigeri, 1969; Pillai, 1991;
90 Prabhu & Dhulkhed, 1970; Supraba et al., 2016). SST can affect both somatic growth rates
91 and juvenile survival but also can cause fish to move off-shore and away from the shore-based
92 fishery. The multi-year average sea temperature is postulated to have effects on recruitment and
93 the survival of larval and juvenile sardines, which affect the later overall abundance (Checkley
94 et al., 2017; Takasuka et al., 2007). The El Niño/Southern Oscillation (ENSO) has a cascad-
95 ing effect on all the aforementioned environmental parameters (SST, precipitation, upwelling)
96 which in turn impact oil sardines, and correlations have been found between ENSO indices and
97 landings (Rohit et al., 2018; Supraba et al., 2016) and coastal anoxia events (Vallivattathillam
98 et al., 2017).

99 In this paper, we study the utility of environmental covariates from remote sensing to ex-
100 plain year-to-year variability in oil sardine landings using the time series of quarterly Indian oil
101 sardine landings from the southwest coast of India. This time series is derived from a stratified
102 sampling design that surveys the fishery landing sites along the southeast Indian coast and was
103 first implemented in the 1950s (Srinath et al., 2005). This is purely a landings time series.
104 Catch-at-length data are not available prior to 2001. Effort data are indirect (boat composition
105 of the fishery) and appropriate effort data (estimates of number of trips or hours fishing) are
106 only available in a few recent years. In addition, stock size estimates and fisheries independent
107 data are unavailable. Thus traditional length- or age-structured models (e.g. virtual population
108 analysis) which produce biomass estimates are not possible. Instead we use statistical models
109 with covariates to model and produce a one-year ahead forecast of landings. Unlike prior work
110 on landings models with covariates, we use non-linear time-series models and dynamic linear
111 models to allow a flexible effect of covariates and past catch on current landings. We also focus
112 on environmental covariates measured via remote sensing. Remote sensing data provide long
113 time series of environmental data over a wide spatial extent at a daily and monthly resolution.
114 A better understanding of how and whether remote sensing data explains variation in seasonal
115 catch will support future efforts to use satellite data to improve catch forecasts.

116 Modeling and forecasting landings data using statistical models fit to annual or seasonal
117 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; Mendelsohn, 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 identify 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; the report is titled, “Forecast for the 20XX Gulf and Atlantic purse-seine fisheries and review of the 20XX fishing season”. A multiple regression model with environmental covariates, similar to the model used in our paper, was developed by NOAA Fisheries in the 1970s (Schaaf et al., 1975). This model has been used for the last 45 years to produce an annual forecast of menhaden landings. This forecast was requested by the menhaden fishing industry and has been 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).

The goal of the work presented here is to determine the environmental covariates which explain catch variability and improve the accuracy of catch forecasts. Landings of oil sardines are determined by biomass, catchability, and effort. Catchability is mainly determined by the inshore versus offshore distribution of the sardine. The fishery is restricted to the nearshore < 50 km offshore (Rohit et al., 2018) and when the sardines move offshore to spawn or to avoid hypoxic or excessive warm water, they are no longer available to the fishery. Thus the environment has a strong impact on catchability. Recruitment and survival tied to the environmental factors which determine food resources. The covariates studied are directly linked to known and conjectured connections between the environment and oil sardine that are expected to affect catch. This work is part of a joint research project between US and Indian research agencies: the National Marine Fisheries Service, NOAA, USA and the Indian National Centre for Ocean Information Services and the Centre for Marine Living Resources and Ecology, in the Ministry of Earth Sciences, India. The project objective is to develop a operational forecast of sardine landings, to be used by the Indian fishery industry for planning.

¹⁴⁸ **Study Area**

¹⁴⁹ Our analysis focuses on the Kerala coast (Figure 1) region of India, where the majority of the
¹⁵⁰ Indian oil sardines are landed and where oil sardines comprise ca. 40% of the marine fish catch
¹⁵¹ (Srinath, 1998; Vivekanandan et al., 2003). This area is in the Southeast Arabian Sea (SEAS),
¹⁵² one of world's major upwelling zones, with seasonal peaks in primary productivity driven by
¹⁵³ upwelling caused by winds during the Indian summer monsoon (Habeebrehman et al., 2008;
¹⁵⁴ Madhupratap et al., 2001) between June and September. Within the SEAS, the coastal zone off
¹⁵⁵ Kerala between 9°N to 13°N has especially intense upwelling due to the combined effects of
¹⁵⁶ wind stress and remote forcing (BR, 2010; BR et al., 2008). The result is a strong temperature
¹⁵⁷ differential between the near-shore and off-shore and high primary productivity and surface
¹⁵⁸ chlorophyll in this region during summer and early fall (BR, 2010; Chauhan et al., 2011;
¹⁵⁹ Habeebrehman et al., 2008; Jayaram et al., 2010; Madhupratap et al., 2001; Raghavan et
¹⁶⁰ al., 2010). The primary productivity peaks subside after September while mesozooplankton
¹⁶¹ abundances increase and remain high in the post-monsoon period (Madhupratap et al., 2001).

¹⁶² **Oil sardine life cycle and fishery**

¹⁶³ The Indian oil sardine fishery is restricted to the narrow strip of the western India continental
¹⁶⁴ shelf, within 20 km from the shore (Figure 1). The yearly cycle of the fishery begins at the
¹⁶⁵ start of spawning during June to July, corresponding with the onset of the southwest monsoon
¹⁶⁶ (Antony Raja, 1969; Chidambaram, 1950) and the initiation of strongly cooler nearshore SST
¹⁶⁷ due to upwelling (Figure 3). At this time, the mature fish migrate from offshore to coastal
¹⁶⁸ spawning areas, and the spawning begins during the southwest monsoon period when temper-
¹⁶⁹ ature, salinity and suitable food availability are conducive for larval survival (Chidambaram,
¹⁷⁰ 1950; Jayaprakash & Pillai, 2000; Krishnakumar et al., 2008; Murty & Edelman, 1966; Nair et
¹⁷¹ al., 2016). Although peak spawning occurs in June to July, spawning continues into Septem-
¹⁷² ber (Antony Raja, 1969; Hornell, 1910; Hornell & Nayudu, 1923; Prabhu & Dhulkhed, 1970)
¹⁷³ and early- and late-spawning cohorts are evident in the length distributions of the 0-year fish.
¹⁷⁴ Spawning occurs in shallow waters outside of the traditional range of the fishery (Antony Raja,
¹⁷⁵ 1964), and after spawning the adults migrate closer to the coast and the spent fish become ex-
¹⁷⁶ posed to the fishery.

¹⁷⁷ After eggs are spawned, they develop rapidly into larvae (Nair, 1959). The phytoplankton
¹⁷⁸ bloom that provide sardine larvae food is dependent upon nutrient influx from coastal up-
¹⁷⁹ welling 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 off-shore 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.

Catches along the Kerala coast are high throughout the year except during quarter 2, April-June (Figure 2). The age-distribution caught by the fishery varies through the year. The fishery is closed during June to mid-July during the monsoon and peak spawning, and when it resumes in mid-July, it is first dominated by 1-2.5 year old mature fish (Antony Raja, 1969; Bensam, 1964; Nair et al., 2016). In August or September a spike of 0-year (40mm) juveniles from the June spawning typically appears in the catch (Antony Raja, 1969; Nair et al., 2016) and another spike of 0-year fish is sometimes seen in February from the late fall spawning (Prabhu & Dhulkhed, 1967, 1970). From October through June, the catch is dominated by fish from 120mm-180mm (Antony Raja, 1970; Nair et al., 2016; Prabhu & Dhulkhed, 1970) which is a mix of 0-year, 1-year and 2-year fish (Nair et al., 2016; Rohit et al., 2018).

Contrast between catch modeling versus biomass modeling

Detailed yearly effort data for the individual gears is not available for the entire catch time series and the data available on size of the fleet are a coarse metric of effort and thus are difficult to use to compute catch-per-unit effort statistics. Nonetheless the number of boats and fishers involved in the fishery has been increasing as the population in Kerala has increased. Oil sardines are caught primarily by ring seines, which were introduced in the early 1980s. Ring seines of different sizes are used both by traditional small boats with a small outboard motor and large mechanized ships (Das & Edwin, 2018). Since 1985, the ring seine fishery has expanded steadily in terms of horsepower, size of boats, length of nets. There are concerns

212 that overfishing and especially catch of juveniles, which are at times discarded (Das & Edwin,
213 2018) is a factor in the most recent oil sardine declines (Kripa et al., 2018).

214 The relationship between the oil landings and the stock abundance is complex. It depends
215 both on the fleet size and composition, but also depends on the proximity of the stock to the
216 shore-based fishery. Although the landings are not a direct proxy for the overall abundance of
217 oil sardines, landings are often assumed to reflect the total abundance in most years for reasons
218 specific to the species and the fishery (Kripa et al., 2018): For most of the period of analysis,
219 the fishery was artisanal: small boats with small motors, no refrigeration, and limited to the
220 near shore. The ring seine was introduced but widespread mechanization of the fleet is a recent
221 development. The artisanal fisherman have limited ability to target the stock, at least not to the
222 degree that landings can remain constant as a stock declines, a pattern than can be observed in
223 a large, mobile, highly mechanized fleet. The fishery is unregulated, except for a brief closure
224 during the monsoon months. Unlike some species, oil sardine shoals do not perform long
225 distance migrations that take them out of contact with the fishery. However for the purpose
226 of our study, the assumption of a tight relationship between landings and abundance is not
227 necessary. The objective is to understand what drives landings variability, whether it be due to
228 abundance variability or due to exposure to the fishery (by being closer to shore).

229 Materials and Methods

230 Sardine landing data

231 Quarterly fish landing data have been collected by the Central Marine Fisheries Research In-
232 stitute (CMFRI) in Kochi, India, since the early 1950s using a stratified multi-stage sample
233 design (Srinath et al., 2005). The survey visits the fish landing centers along the entire south-
234 east coast of India and samples the catch from the variety of boat types and gear types used
235 in the coastal fishery. Landings estimates are available for all the coastal states, however we
236 model the catch for the state of Kerala only, where the longest time series is available and the
237 overwhelming majority of oil sardines are landed (Figure 2). Kerala contributes a remarkable
238 14.4% of the total marine production (CMFRI, 2017) and Major resources contributing to the
239 pelagic landings were oilsardine (57.4%). The quarterly landings (metric tons) for oil sardine
240 landed from all gears in Kerala were obtained from CMFRI reports (1956-1984) and online
241 databases (1985-2015) (CMFRI, 1969, 1995, 2016; Jacob et al., 1987; Pillai, 1982). The quar-
242 terly landing data were log-transformed to stabilize the variance. Yearly effort data for the

243 individual gears is not available for the entire catch time series and the data available on size of
244 the fleet are a coarse metric of effort and thus are difficult to use to compute catch-per-unit ef-
245 fort stastistics. However the goal in this study is to describe and forecast landings, not biomass,
246 and our analysis uses landings data as is standard in landings modeling.

247 **Remote sensing data**

248 We analysed monthly composites of the following environmental data derived from satellite
249 data: sea surface temperature (SST), chlorophyll-a (CHL), upwelling (UPW), the Oceanic
250 Niño Index (ONI) and precipitation. The monthly means of the covariate time series are shown
251 in Figure 4.

252 For sea surface temperature, we used Advanced Very-High Resolution Radiometer
253 (AVHRR) data, which provides accurate nearshore SST values. Although the ICOADS
254 product provides SST values for earlier years, ICOADS does not provide accurate nearshore
255 temperatures. For 1981 to 2003, we used the Pathfinder Version 5.2 product on a 0.0417
256 degree grid. These data were developed by the Group for High Resolution Sea Surface
257 Temperature (GHRSSST) and served by the US National Oceanographic Data Center. For
258 2004 to 2016, we used the NOAA CoastWatch SST products derived from NOAA's Polar
259 Operational Environmental Satellites (POES).

260 For chlorophyll-a, we used the chlorophyll-a products developed by the Ocean Biology
261 Processing Group in the Ocean Ecology Laboratory at the NASA Goddard Space Flight Cen-
262 ter. For 1997 to 2002, we used the chlorophyll-a 2014.0 Reprocessing (R2014.0) product from
263 the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite. These data
264 are on a 0.1 degree grid. For 2003 to 2017, we used the MODIS-Aqua product on a 0.05 de-
265 gree grid. These CHL data are taken from measurements by the Moderate Resolution Imaging
266 Spectroradiometer (MODIS) on NASA's Aqua Spacecraft. The SST and CHL data were aver-
267 aged across thirteen 1 degree by 1 degree boxes which roughly parallel the bathymetry (Figure
268 1). The SST and CHL satellite data were retrieved from the NOAA ERDDAP server (Simons,
269 2017).

270 For an index of coastal upwelling, we used the sea-surface temperature differential be-
271 tween near shore and 3 degrees offshore as described by Naidu et al. (1999) and Smitha et
272 al. (2008). The index was computed as the average SST in box 4 off Kochi (Figure 1) minus
273 the average SST in box 13. 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 SST-based upwelling index and chlorophyll-a blooms are strongly correlated (Figure 3).

Precipitation data were obtained from two different sources. The first was an estimate of the monthly precipitation (in mm) over Kerala from land-based rain gauges (Kothawale & Rajeevan, 2017); these data are available from the Indian Institute of Tropical Meteorology and the data are available from the start of our landing data (1956). The second was a remote sensing precipitation product from the NOAA Global Precipitation Climatology Project (Adler et al., 2016). This provides estimate of precipitation over the ocean using a global 2.5 degree grid. We used the 2.5 by 2.5 degree box defined by latitude 8.75 to 11.25 and longitude 73.25 to 75.75 for the precipitation off the coast of Kerala. These data are available from 1979 forward (NCEI, 2017). The land and nearshore ocean precipitation data are highly correlated (Appendix E), supporting the use of the land time series as a proxy for the precipitation over the ocean off the Kerala coast.

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.

Hypotheses

Our statistical analyses 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 as reviewed in the introduction. The quarter 3 (Jul-September) catch overlaps the summer monsoon and the main spawning months. This is also the quarter where small 0-year fish from early spawning (June) often appear in the catch, sometimes in large numbers. Variables that affect or are correlated with movement of sardines inshore should be correlated with quarter 3 landings. In addition, pre-spawning (March-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

306 (October-May) is a mix of 0-year fish (less than 12 months old) and mature fish (greater than
307 12 months old). Variables that are correlated with spawning strength and larval and juvenile
308 survival should correlate with the post-monsoon catch both in the current year and in future
309 years, one to two years after.

310 Our hypotheses (Table 1) focus mainly on two drivers: upwelling and ocean tempera-
311 ture. We also test hypotheses concerning precipitation as this has historically been an envi-
312 ronmental covariate considered to influence the timing of oil sardine landings. More recently,
313 researchers have highlighted the influence of large-scale ocean processes, specifically the El
314 Niño/Southern Oscillation, on sardine fluctuations; therefore we test the Ocean Niño Index
315 (ONI) also. Chlorophyll density is directly correlated with sardine food availability and chloro-
316 phyll fronts are known to influence sardine shoaling. However our chlorophyll time series is
317 short (1997-2015) and the statistical power for testing correlation with landings is low. Tests
318 of chlorophyll are shown in the appendices but are not the focus of our analyses.

319 Statistical models

320 We modeled the catches during the late-monsoon season (quarter 3, July-September) separately
321 from the post-monsoon season (October-March). Thus there is no seasonality in our catch time
322 series, as we analyzed a yearly time series of quarter 3 catches separately from a yearly time
323 series of post-monsoon catches. We divided the catch in this way for biological and statistical
324 reasons. Catch in quarter 3 (July-September) captures a mix of spawning age fish as it overlaps
325 with the tail end of the spawning season, is affected by a fishery closure from July to mid-
326 August during the summer monsoon, and is periodically inflated by the appearance of small
327 0-year fish from early summer spawning. In addition, the covariates that affect the timing of
328 spawning, movement of post-spawning mature fish inshore, and early egg and larval survival
329 may be different than those that affect later growth, survival and shoaling that exposes fish
330 to the inshore fishery. Analyzing catch and covariate time series without seasonality also had
331 an important statistical benefit—we removed the problem of seasonality in the catch and all
332 the covariates. The oil sardine life-cycle is seasonal and driven by the strong seasonality in
333 this monsoon influenced system. A simple statistical model with quarters will explain much
334 of the quarterly catch data since most of the yearly variability is due to seasonality and any
335 environmental covariate with a similar seasonality will also show high correlation with the
336 landings. Our goal was to explain year-to-year variability thus eliminating the confounding
337 effect of seasonality in the data was important.

338 We tested ARIMA models on both monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch
 339 time series and found little support for auto-regressive errors (ARIMA models with a MA
 340 component) based on diagnostic tests of the residuals and model selection. The best supported
 341 ARIMA models were simple AR models ($x_t = bx_{t-1} + \varepsilon_t$). This lack of strong autocorrelation
 342 in residuals has been found in other studies that tested ARIMA models for forecasting small
 343 pelagic catch (Stergiou & Christou, 1996). We thus used AR-only models, however we tested
 344 both linear and non-linear models using generalized additive models (GAMs, Wood, 2017) of
 345 the form $x_t = s(x_{t-1}) + \varepsilon_t$ and tested time-varying linear models with dynamic linear models
 346 (DLM). GAMs allow one to model the effect of a covariate as a flexible non-linear function
 347 while DLMs allow one to allow the effect of the covariate to vary over time. It was known that
 348 the effects of the environmental covariates were likely to be non-linear, albeit in an unknown
 349 way. Our GAM approach is analogous to that taken by Jacobson and MacCall (1995) in a study
 350 of the effects of SST on Pacific sardine recruitment.

351 The first step in our analysis was to determine the catch model: the model for current
 352 catch as a function of the past catch. We explored four classes of models: null models with a
 353 simple function of prior catch, linear regressive models with one to two years of prior catch,
 354 dynamic linear models (DLM) which allow the regression parameters to vary (Holmes et al.,
 355 2012, using the MARSS package in R), and GAMs to allow the effect of prior catch to be
 356 non-linear. One feature of GAMs is that they allow the smoothing parameter of the response
 357 curve to be estimated. We fixed the smoothing parameter at an intermediate value so that
 358 smooth responses were achieved. Multi-modal or overly flexible response curves would not
 359 be realistic for our application. We fit GAMs with smooth terms represented by penalized
 360 regression splines (Wood, 2011, using the mgcv package in R) and fixed the smoothing term
 361 at an intermediate value (sp=0.6).

362 We compared the following catch models:

- 363 • null: $\ln(C_{i,t}) = \ln(C_{j,t-1})$
- 364 • random walk: $\ln(C_{i,t}) = \alpha + \ln(C_{j,t-1}) + \varepsilon_t$
- 365 • linear AR-1: $\ln(C_{i,t}) = \alpha + \phi \ln(C_{j,t-1}) + \varepsilon_t$
- 366 • linear AR-2: $\ln(C_{i,t}) = \alpha + \phi_1 \ln(C_{j,t-1}) + \phi_2 \ln(C_{k,t-2}) + \varepsilon_t$
- 367 • DLM AR-1: $\ln(C_{i,t}) = \alpha_t + \phi_t \ln(C_{j,t-1}) + \varepsilon_t$
- 368 • GAM AR-1: $\ln(C_{i,t}) = \alpha + s(\ln(C_{j,t-1})) + \varepsilon_t$
- 369 • GAM AR-2: $\ln(C_{i,t}) = \alpha + s_1(\ln(C_{j,t-1})) + s_2(\ln(C_{k,t-2})) + \varepsilon_t$

370 $\ln(C_{i,t})$ is the log catch in the current year t in season i . We modeled two different catches:

monsoon catch S_t (July-September), which is during the late part of the summer monsoon, and post-monsoon catch N_t (October-June). 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 being a population growth model. We tested models with prior year post-monsoon catch (N_{t-1}) and 3rd quarter catch (S_{t-1}) as the explanatory catch variable. S_t was not used as a predictor for N_t ; 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 1982 to 2015 catch data, corresponding to the years where the SST, upwelling and precipitation data were available. F-tests and AIC on nested sets of models (Wood et al., 2016) were used to evaluate the support for the catch models and later for the covariate models. After selection of the best model with the 1982-2015 data, the fitting was repeated with the 1956-1981 and 1956-2015 catch data to confirm the form of the catch models.

Once the catch models were determined, the covariates were studied individually and then jointly. As with the catch models, F-tests, AIC and LOO (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 treated as an estimated variable. Our models for catch with covariates typically took the form $\ln(C_{i,t}) = M + s_1(V_{1,t}) + s_2(V_{2,t-1}) + \varepsilon_t$ or $\ln(C_{i,t}) = M + \beta_1 V_{1,t} + \beta_2 V_{2,t-1} + \varepsilon_t$ where M was the best catch model from step 1. Thus models with covariates modeled both as a linear and non-linear effect were compared. The covariates tested are those discussed in the section on covariates that have been hypothesized to drive the size of the sardine biomass exposed to the fishery. We tested both models with one and two covariates, and did not use correlated covariates in the same model.

Results

Catches in prior seasons as explanatory variables

Using the 1984-2015 catch data, which is 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 was simply 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), whether linear or non-linear, as the explanatory covariate were strongly supported over the naive model and over models with $\ln(S_{t-1})$ (Jul-

402 Sep catch in prior year) as the explanatory variable (Tables A1 and A2). Addition of the catch
 403 two years prior, $\ln(N_{t-2})$ or $\ln(S_{t-2})$, did not reduce AIC or LOOCV for either the linear or
 404 non-linear models. We tested the support for non-linearity in the effect of the prior year catch
 405 by comparing models with $\ln(N_{t-1})$ or $\ln(S_{t-1})$ included as a linear term or as a non-linear
 406 function $s()$ using GAMs (Table A2). The residual error decreased using a non-linear response
 407 at the cost increased degrees of freedom. The result was only weak (non-significant) support
 408 for allowing a non-linear response based on AIC and LOOCV.

409 The results on model structure were similar for models of the Oct-Mar landings (N_t),
 410 but the models explained much more of the variance (with a maximum adjusted $R^2 = 56.6$).
 411 The most supported model for N_t (Tables A3 and A4) based on AIC and F-tests used a non-
 412 linear response to Oct-Mar catch of the previous season $\ln(N_{t-1})$ plus a non-linear response
 413 to Jul-Sep catch two years prior $\ln(S_{t-2})$. However the simpler model with only $\ln(N_{t-1})$ had
 414 the lowest LOOCV (out of sample prediction accuracy). Thus this simpler model was also
 415 included as one of the base models for the Oct-Mar catch. Models with Jul-Sep catch in the
 416 current fishing season were not used as these data would not be available by Oct of the current
 417 season (for forecast purposes).

418 As diagnostic checks, we did the same model comparison for the landings data set from
 419 1956 to 1983. The results were the same for the Jul-Sep catch (Table A5) with the model with
 420 $\ln(N_{t-1})$ included as a non-linear covariate with the lowest AIC and LOOCV. For the Oct-Mar
 421 catch (Table A6), the results were very similar but not identical. The model with $\ln(N_{t-1})$
 422 included as a non-linear covariate had the lowest LOOCV while the models with $\ln(N_{t-1})$ and
 423 $\ln(S_{t-2})$ or $\ln(S_{t-1})$ had the lowest AIC (though less than 1 from the AIC of the $\ln(N_{t-1})$
 424 model). We also did an influential years test using Leave-One-Out crossvalidation (Appendix
 425 G). This test involved leaving out one year and repeating the model selection tests. These tests
 426 also supported the selected base models. The dynamic linear models (allowing a time-varying
 427 effect of prior catch) performed poorly for the Jul-Sep catch with high AIC and LOOCV. For
 428 the Oct-Mar catch, the performance was mixed with higher AIC but lower LOOCV.

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

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

⁴³¹ Two base non-linear models were chosen for Oct-Mar (N_t) catch:

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

⁴³²

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

⁴³³ Note that although M1 was the best model for Jul-Sep catch, it was only weakly explanatory.

⁴³⁴ The maximum adjusted R^2 was less than 30% (Table A2). For the Oct-Mar catch, M2 and M3

⁴³⁵ were more explanatory with an adjusted R^2 of 45.3% for M2 and 56.6% for M3 (Table A4).

⁴³⁶ Environmental covariates as explanatory variables

⁴³⁷ There was no support for using precipitation during the summer monsoon (June-July) or pre-
⁴³⁸ monsoon period (April-May) as an explanatory variable for the quarter 3 (July-September) or
⁴³⁹ post-monsoon (October-March) catch (hypotheses S1 and S2; Tables B1 and B2). This was
⁴⁴⁰ the case whether precipitation in the current or previous season was used, if precipitation was
⁴⁴¹ included as non-linear or non-linear effect, and if either precipitation during monsoon (June-
⁴⁴² July) or pre-monsoon (April-May) were used as the covariate. Quarter 3 overlaps with the
⁴⁴³ spawning period and precipitation is often thought to trigger spawning, however we were un-
⁴⁴⁴ able to find any consistent association of catch during these spawning and early-post spawning
⁴⁴⁵ months with precipitation. Raja (1974) posited that the appropriate time period for the affect
⁴⁴⁶ of rainfall is the weeks before and after the new moon when spawning is postulated to occur
⁴⁴⁷ and not the total rainfall during the monsoon season. Thus the lack of correlation may be due
⁴⁴⁸ to using too coarse of a time average for the precipitation.

⁴⁴⁹ The sea-surface temperature before spawning (March-May) has been speculated to be cor-
⁴⁵⁰ related with successful egg development and spawning behavior (hypothesis S4 and S5) and
⁴⁵¹ extreme heat events pre-spawning have been associated with low recruitment. This suggests
⁴⁵² that March-May in the current and prior years should be associated with low catch. The sea-
⁴⁵³ surface temperature during larval and early juvenile development (October-December) may
⁴⁵⁴ affect survival and growth in multiple ways and thus could correlate with biomass in future
⁴⁵⁵ years (hypothesis L1). However we found no support for either of these SST variates as ex-
⁴⁵⁶ planatory variables for the July-September catch and only weak support (based on AIC) for
⁴⁵⁷ March-May SST in the current season for explaining variability in post-monsoon catch. The
⁴⁵⁸ fall average SST in the prior season did not explain variability in either July-September or
⁴⁵⁹ October-March catch. See Tables B3 and B4.

460 We also found no correlation between the ONI index (hypothesis A2) for either July-
461 September or post-monsoon catch (Tables B1 and B2).

462 Instead we found with the covariates indirectly and directly associated with productiv-
463 ity and food availability: upwelling intensity and surface chlorophyll. The correlation between
464 landings and upwelling was only found for upwelling in the current season. No correlation was
465 found when we used the upwelling index from the prior season. The correlation between land-
466 ings and upwelling was found for both July-September and October-March landings and with
467 either upwelling index: average nearshore SST along the Kerala coast during June-September
468 or the average SST nearshore versus offshore differential (UPW) off Kochi in June-September
469 (Table 2, Table B3 and Table B4). These two upwelling indices are correlated but not identical.
470 The model with average June-September nearshore SST was more supported than the model
471 using the SST differential off Kochi. For July-September catch, this model with a non-linear
472 response had an adjusted R^2 of 41.0 versus an adjusted R^2 of 24.4 for the model with no co-
473 variates (Table B3), and for October-March catch, the adjusted R^2 was 61.8 versus 56.6 (Table
474 B4). Note, that this covariate is June-September in the current season and overlaps with the
475 July-September catch. Thus this model cannot be used to forecast July-September catch but
476 does help us understand what factors may be influencing catch during the monsoon.

477 Chlorophyll-a density is speculated to be an important predictor of larval sardine sur-
478 vival and growth. In addition, sardines shoal in response to coastal chlorophyll blooms, which
479 brings them in contact with the coastal fisheries. Thus chlorophyll-a density is assumed to be
480 an important driver of future or current sardine catches. We had chlorophyll-a remote sensing
481 data only from 1998 onward. Our simplest covariate model required 5 degrees of freedom,
482 thus we were limited in the analyses we could conduct. In addition, the years, 1998-2014,
483 have relatively low variability in catch sizes; the logged catch sizes during this period range
484 from 10-11 during quarter 3 and 11-12 during the other three quarters. Second degree polyno-
485 mial models were fit (Appendix C) to the average log chlorophyll-a density in the current and
486 prior season from quarter 3 (July-September), 4 (October-December), and 1 (January-March).
487 Chlorophyll-a density was not a significant predictor for the July-September catch for any of
488 the tested combinations of current or prior season and quarter. The only significant effect was
489 seen for post-summer monsoon catches using chlorophyll-a density in October-December of
490 the prior season (Table C1). This is in contrast to the results with monsoon upwelling indices,
491 which found a correlation with the current season but not prior seasons.

492 The strongest correlation however was found with the multi-year average sea surface tem-
493 perature for the nearshore waters off Kerala (latitude 8 to 11). The average sea surface tem-

494 perature over multiple prior years has been found to be correlated with sardine recruitment in
495 Pacific sardines (Checkley et al., 2017; Jacobson & MacCall, 1995; Lindegren et al., 2013)
496 and southern African sardines (Boyer et al., 2001). We tested as a model covariate the average
497 SST for 2.5 years prior to the July-September catch, so January-June in the current calendar
498 year and the two prior calendar years for a 30-month average. This covariate can be used
499 for forecasting since it does not overlap with either July-September or October-March catch.
500 This variate with a non-linear response was best covariate for both the July-September and the
501 post-monsoon catch. For post-monsoon catch, the model with SST had an adjusted R^2 of 67.5
502 versus 56.6 without. For the July-September catch, the adjusted R^2 was 41.0 with SST and 24.4
503 without. The response curve was step-like with a negative effect at low temperatures and then
504 an positive flat effect at higher temperatures (Figure 5). This is similar to the step-response
505 found in studies of the correlation between average SST and recruitment in Pacific sardines
506 (Jacobson & MacCall, 1995).

507 Discussion

508 Sardines in all the world's ecosystems exhibit large fluctuations in abundance (Baumgartner et
509 al., 1992). These small forage fish are strongly influenced by natural variability in the ocean
510 environment. Upwelling, influenced by both large-scale forces such as regimes shifts and El
511 Ni\~{n}o/Southern Oscillation patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010)
512 and by seasonal wind and current patterns, brings nutrient rich and oxygen rich waters to the
513 surface. This drives the seasonal variability in phytoplankton resources and in turn sardine
514 prey (Bakun et al., 2008). Local variability in temperature, salinity, and oxygen levels have
515 both direct and indirect on sardine reproduction, recruitment and survival (Checkley et al.,
516 2017). Sardines are also influenced by competition and predation by other species and well-
517 known for their sensitivity to over-fishing which has been linked to many fishery collapses
518 (Kripa et al., 2018).

519 Many studies on Pacific sardines have looked at the correlation between ocean temperature
520 (SST) and recruitment. Temperature can have direct effect on larval survival and growth and
521 an indirect effect on food availability. Studies in the California Current System, have found
522 that SST explains year-to-year variability in Pacific sardine recruitment (Checkley et al., 2009,
523 2017; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012) and that the average nearshore
524 temperature over multiple seasons is the explanatory variable. Similar to these studies, we
525 found that the average nearshore SST over multiple seasons was the covariate that explained

526 the most variability in catch both in the monsoon and post-monsoon months. McClatchie et
527 al. (2010) found no SST relationship with SST and Pacific sardine recruitment, however their
528 analysis used a linear relationship while the other studies, and ours, that found a relationship
529 (Checkley et al., 2017; Jacobson & MacCall, 1995) allowed a non-linear relationship. Both
530 Jacobson and MacCall (1995) and Checkley et al. (2017) found a step-like response function
531 for temperature: below a threshold value the effect of temperature was linear and above the
532 threshold, the effect was flat and at lower temperatures the effect was negative and became
533 positive as temperature increased. Our analysis found a similar pattern with a negative effect
534 when the 2.5-year average temperature was below 28.35°C and positive above and with the
535 positive effect leveling off above 28.5°C (Figure 5).

536 There were four outlier years when catch were much lower than expected based on prior
537 catches: 1986, 1991, 1994 and 2013. The 2.5-year average SST predicted the collapses in
538 1986 and 1991 (Figure 6); the size of the residual with the covariate was much smaller than
539 without the covariate. The largest collapse was in 1994 and the most recent, in our dataset,
540 was 2014. The 2.5-year average SST did not predict the 1994 nor 2013 collapse. There was
541 no change in the size of the residual with and without the covariate. In fact, none of the
542 covariates we tested changed the size of the model residuals for 1994 nor 2013. The causes of
543 these unusual declines appear either unrelated to the environmental factors we studied. This
544 suggests either that other factors, biological or anthropogenic, drove these declines or that a
545 particular combination of environmental factors led to the declines. It should also be noted
546 that our upwelling indices captured on one aspect of upwelling: the nearshore intensity. Other
547 aspects of upwelling also affect oil sardines, such as the spatial extent both along the coast and
548 off the coast and the timing of the start of upwelling.

549 Seasonal productivity in the SE Arabian Sea upwelling is driven by the summer monsoon,
550 which causes strong coastal upwelling that moves from the south to the north over the summer.
551 This drives a strong seasonal pattern of zooplankton abundance (Figure 3). Despite the strong
552 connection between sardine recruitment, growth and survival with upwelling, we found no
553 correlation with upwelling in the prior season with landings. We did find a correlation between
554 upwelling in the current season with landings in the current season. The biological reasons
555 behind a positive relationship with upwelling are clear. Upwelling drives productivity and
556 higher food resources in the current season leads to higher recruitment and higher numbers
557 of 0-year fish in the landings or may bring sardines into the nearshore to feed where they are
558 exposed to the fishery. However, the explanatory power of the upwelling indices was mainly
559 due to the negative effect of extremely high upwelling (Figure 5). Extremely high upwelling

560 transports larval sardines offshore and can create regions of low oxygen which sardines avoid.

561 **Conclusions**

562 Remote sensing satellites can be used to detect changes in ocean physical, biological and chem-
563 ical properties, such as surface temperature, winds, surface height, surface waves, rainfall and
564 surface salinity, as well as the ecosystem and water quality changes. Unlike in-situ measure-
565 ments, environmental measures from remote-sensing can be acquired rapidly and over large
566 regions. However, which environmental covariates will improve forecasts is not obvious from
567 oil-sardine life-history alone. We tested using many of the covariates known or suspected to
568 have a effect on sardine spawning, growth and survival: precipitation, upwelling indices, ocean
569 temperature and chlorophyll-a in various critical months of the sardine life-cycle. We found
570 that the multi-year average nearshore ocean temperature explained the most variability in the
571 landings. This covariate is not as directly tied to stages of the oil-sardine life-cycle as the other
572 covariates we tested, though it does integrate over multiple influences (upwelling strength and
573 temperature) over multiple years.

574 The temperature of the Western Indian Ocean, of which the Southeast Arabian Sea is a
575 part, has been increasing over the last century at a rate higher than any other tropical ocean
576 (Roxy et al., 2014) and the warming has been most extreme during the summer monsoon
577 months. This ocean climate change is affecting oil sardine distributions with significant land-
578 ings now occurring north of Goa (Vivekanandan et al., 2009). Continued warming is expected
579 to affect the productivity of the region via multiple pathways, including both the direct effects
580 of temperature change on the physiology and behavior of organisms and a multiple of indirect
581 effects (Moustahfid et al., 2018). These indirect effects includes changes to salinity, oxygen
582 concentrations, currents, wind patterns, ocean stratification and upwelling spatial patterns, phe-
583 nology, and intensity. Incorporating environmental covariates into landings forecasts has the
584 potential to improve fisheries management for small pelagics such as oil sardines in the face of
585 a changing ocean environment (Haltuch et al., 2019; Tommasi et al., 2016). However, moni-
586 toring forecast performance and covariate performance in models will be crucial as a changing
587 ocean environment may also change the association between landings and average sea surface
588 temperature.

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861 **Figure Legends**

862 Figure 1. Close up of Kerala State with the latitude/longitude boxes used for the satellite data.
863 Kerala State is marked in grey and the oil sardine catch from this region is being modeled.

864 Figure 2. Quarterly catch data 1956-2014 from Kerala. The catches have a strong seasonal
865 pattern with the highest catches in quarter 4 Note that quarter 3 is July-September and that the
866 fishery is closed July 1 to August 15, thus the fishery is only open 1.5 months in quarter 3.
867 The mean catch (metric tonnes) in quarters 1 to 4 are 38, 19.2, 30.9, and 59.9 metric tonnes
868 respectively.

869 Figure 3. Key oil sardine life-history events overlaid on the monthly sea surface tempera-
870 ture in the nearshore and offshore and the nearshore chlorophyll density.

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

878 Figure 5. Effects of covariates estimated from the GAM models. Panel A) Effect of the
879 2.5 year average nearshore SST on catch during the catch during July-September (late spaw-
880 ning and early post-spawning) months. Panel B) Effect of upwelling (inshore/off-shore SST
881 differential) during June-September in the current season on July-September catch. The index
882 is the difference between offshore and inshore SST, thus a negative value indicates warmer
883 coastal surface water than off-shore. Panel C) Effect of the 2.5 year average nearshore SST on
884 catch during the catch during October-March (post-monsoon, age-0, -1, -2 year fish). Panel
885 D) Effect of upwelling (inshore/off-shore SST differential) during June-September in the cur-
886 rent season on October-March catch. Strong upwelling (positive upwelling index) in the larval
887 and juvenile high growth period (Oct-Dec) is associated with higher early survival and larger
888 cohorts of age-0 fish in the catch.

889 Figure 6. Fitted versus observed catch with models with and without environmental co-
890 variates. Panel A) Fitted versus observed log catch in the spawning months with only non-
891 spawning catch in the previous season as the covariate: $S_t = s(N_{t-1}) + \varepsilon_t$. Panel B) Fitted
892 versus observed log catch in July-September with the 2.5-year average nearshore SST added

893 as a covariate to the model in panel A. This model was: $S_t = s(N_{t-1}) + s(V_t) + \varepsilon_t$. Panel
894 C) Fitted versus observed log catch in the post-monsoon months with only post-monsoon
895 catch in the previous season and July-September catch two seasons prior as the covariates:
896 $N_t = s(N_{t-1}) + s(S_{t-2}) + \varepsilon_t$. Panel D) Fitted versus observed log catch in the post-monsoon
897 months with 2.5-year average nearshore SST (V) added as covariates. This model was $N_t =$
898 $s(N_{t-1}) + s(S_{t-2}) + s(V_t) + \varepsilon_t$.

Table 1. Hypotheses for covariates affecting landings. S_t is Jul-Sep catch in the current season, S_{t-1} is Jul-Sep catch in the previous season. N_t is the Oct-Mar catch in the current season and N_{t-1} is the Oct-Mar catch in the prior season. DD = hypotheses related to effects of past abundance (landings) on current abundance. S = hypotheses related to catch during the spawning months. L = hypotheses related to larval and juvenile growth and survival. A = hypotheses affecting all ages. See the introduction for discussion of the literature on the effects of environmental covariates on sardine landings. ns-SST = nearshore SST. r-SST = regional (nearshore and offshore) SST t , $t - 1$, and $t - 2$ indicate current, prior, and two seasons prior.

Hypothesis	Description
DD1 $S_t \sim N_{t-1}$	S_t is age 1+ age fish and reflects the 0-2yr fish in N_{t-1} which have aged 3-6 months (Nair et al. 2016).
DD2 $S_t \sim S_{t-1} + S_{t-2} N_t S_{t-1} + S_{t-2}$	S_t is age 1+ fish and is dominated by spent post-spawning fish (Nair et al. 2016). S_t should be correlated with the abundance of the spawning stock and cohort strength. If cohort strength persists over time, landings in the current season should correlate with Jul-Sep landings in the previous two seasons.
DD3 $N_t \sim N_{t-1}$	N_{t-1} includes age 0, 1, 2 and 2+ fish (Nair et al. 2016). Thus the 0, 1, and 2 yr fish will appear 1 year later in the N_t landings.
S1 $S_t \sim$ Jun-Jul precipitation in t	The magnitude of precipitation in June-July directly or indirectly signals mature fish to spawn offshore, after which the spent adults migrate inshore to the fishery (Anthony Raja 1969, 1974; Srinath 1998).
S2 $S_t \sim$ Apr-Mar precipitation in t	If there is pre-monsoon rain during Apr-May then spawning begins earlier and spent adults return to the fishery sooner and are exposed to the fishery longer.
S3 $N_t \sim$ Apr-Mar precipitation in t	Precipitation is an indicator of climatic conditions during the period of egg development. This affect the success of spawning, thus affecting the 0-year class and the Oct-Mar catch (Antony Raja 1969, 1974; Srinath 1998).
S4 $S_t \sim$ Jun-Sep UPW in t	High rates of upwelling drive mature fish further offshore and thus leads to lower exposure to the fishery. This movement may be driven by advection of high phytoplankton biomass further offshore or increased inputs of low oxygenated water to the surface (Murty and Edelman 1970, Antony Raja 1973, Pillai et al. 1991).
S5 $S_t \sim$ Mar-May r-SST in t $N_t \sim$ Mar-May r-SST in t	Extreme heating events prior to the spring monsoon drives mature fish from the spawning areas, resulting in poor recruitment and fewer age 0 year fish in the Oct-Mar catch (Antony Raja 1973, Pillai et al 1991).

Table 1. Continued.

Hypothesis	Description
L1 $S_t \sim \text{Oct-Dec ns-SST } t - 1$ $N_t \sim \text{Oct-Dec ns-SST } t - 1$	Larval and juvenile growth and survival is affected by temperature. The temperature in the critical post-monsoon window, when somatic growth of the 0-year fish is highest, should be correlated with future abundance.
L2 $S_t \sim \text{Jun-Sep UPW in } t - 1 \text{ & } t$ $N_t \sim \text{Jun-Sep UPW in } t - 1 \text{ & } t$	Higher upwelling rates leads to greater phytoplankton productivity, better larval and juvenile growth, and higher landings in the post monsoon Oct-March catch. However, extreme upwelling may decrease this catch, and future catches, due to poor oxygen conditions or advection of phytoplankton biomass.
L3 $S_t \sim \text{CHL in } t - 1 \text{ & } t$ $N_t \sim \text{CHL in } t - 1 \text{ & } t$	Surface Chl-a is a proxy for phytoplankton abundance and thus food availability, so higher bloom intensities may support greater fish abundance in the current and future years.
A1 $S_t \sim \text{2.5-yr ave. ns-SST}$ $N_t \sim \text{2.5-yr ave. ns-SST}$	Spawning, early survival, and recruitment of sardines depends on a multitude of cascading factors summarized by the multi-year average nearshore SST. The multi-year average SST has been correlated with recruitment and abundance in other sardines (Checkley et al. 2017) and is related to the optimal temperature windows for sardines (Takasuka et al. 2007).
A2 $S_t \sim \text{ONI in } t - 1$ $N_t \sim \text{ONI in } t - 1$	The El Nino/Southern Oscillation (ENSO) impacts a range of environmental parameters (e.g., precipitation, SST, frontal zones, winds, etc.) that may impact spawning and early survival of sardines (Supraba et al. 2016, Rohit et al. 2018).
A3 $S_t \sim \text{DMI in } t - 1$ $N_t \sim \text{DMI in } t - 1 \text{ & } t$	Negative Dipole Mode Index (DMI) values in Sep-Nov are associated with anoxic events on the Kerala coast while positive values are associated with a absence of such events (Vallivattathillam et al. 2017).

Table 2. Top covariates for the monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch (S_t and N_t) models. M0, M1 and M2 are the base models with only prior catch as covariates. To the base models, the listed environmental covariates are added. The full set of covariate models and the results of the tests on the nested models sets are given in Appendix B. The fitted versus observed catches from the covariate models are shown in Figure 6.

Model	Residual df	Adj. R2	RMSE	AIC	LOOCV RMSE
Jul-Sep catch models with covariates					
V_t = Jun-Sep SST current season					
W_t = Jun-Sep Bakun-UPW current season					
Z_t = 2.5-year average SST					
M0: $\ln(S_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$	28.6	24	1.184	109.52	1.299
$\ln(S_t) = M0 + s(V_t)$	25.9	41	1.007	103.43	1.192
$\ln(S_t) = M0 + \beta W_t$	27.6	28	1.133	108.66	1.404
$\Rightarrow \ln(S_t) = M1 + s(Z_t)$	26.2	41	1.011	103.26	1.338
Oct-Mar catch models with covariates					
V_t = Mar-May SST current season					
W_t = Jun-Sep SST current season					
Z_t = 2.5-year average SST					
X_t = fall DMI prior season					
M1: $\ln(N_t) = \alpha + s(\ln(N_{t-1})) + s(\ln(S_{t-2})) + \varepsilon_t$	24.8	57	0.713	79.53	1.062
$\ln(N_t) = M1 + s(V_t)$	22	63	0.628	76.01	1.002
$\ln(N_t) = M1 + \beta W_t$	23.8	63	0.648	75.57	1.042
$\Rightarrow \ln(N_t) = M1 + s(Z_t)$	22.7	67	0.597	71.88	0.827
$\ln(N_t) = M1 + s(X_t)$	21.1	68	0.58	72.69	0.89
M2: $\ln(N_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$					
$\ln(N_t) = M2 + s(V_t)$	27.6	45	0.836	84.75	0.966
$\ln(N_t) = M2 + \beta W_t$	24.8	47	0.791	85.9	0.981
$\Rightarrow \ln(N_t) = M2 + s(Z_t)$	26.6	52	0.772	81.79	0.927
$\ln(N_t) = M2 + s(X_t)$	25.3	60	0.688	76.34	0.796
	23.7	43	0.8	88.43	0.969

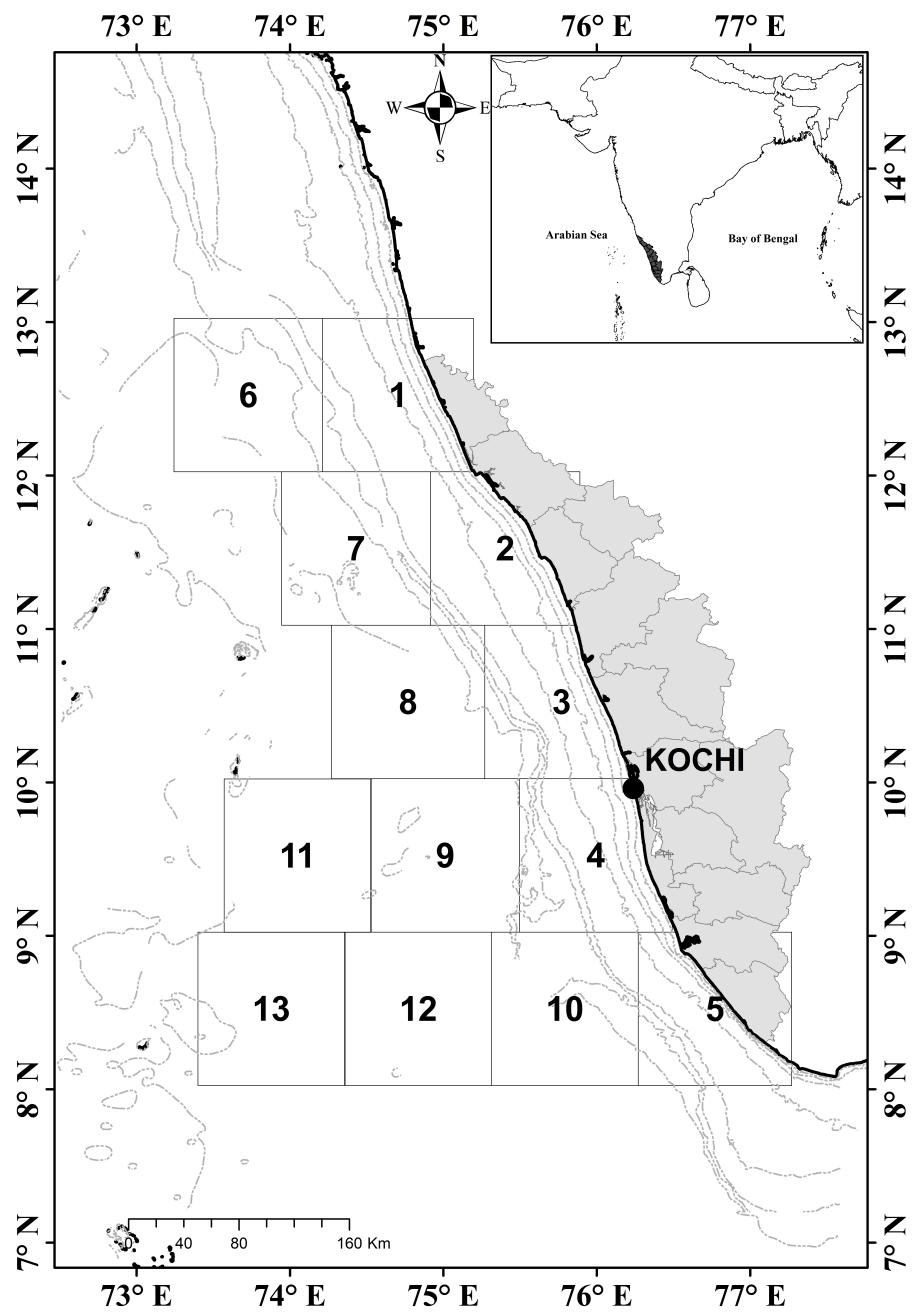


Figure 1

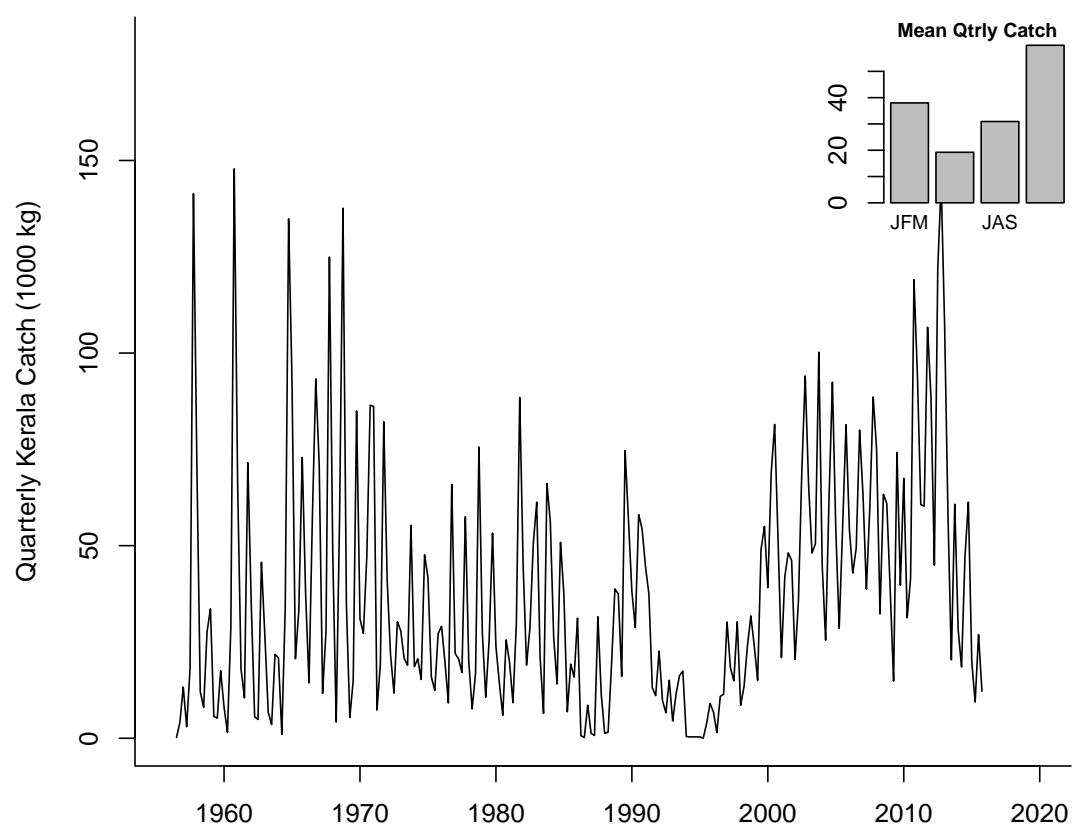


Figure 2

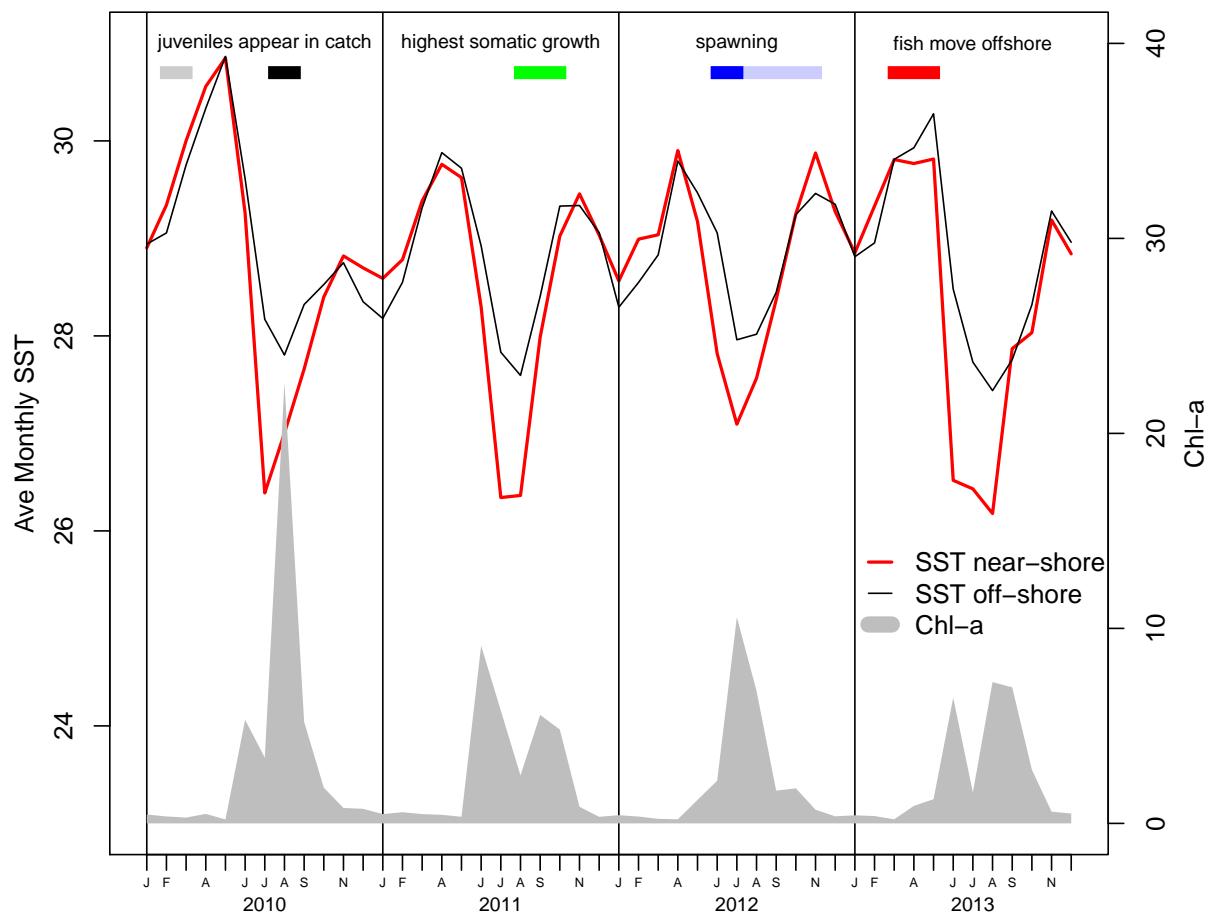


Figure 3

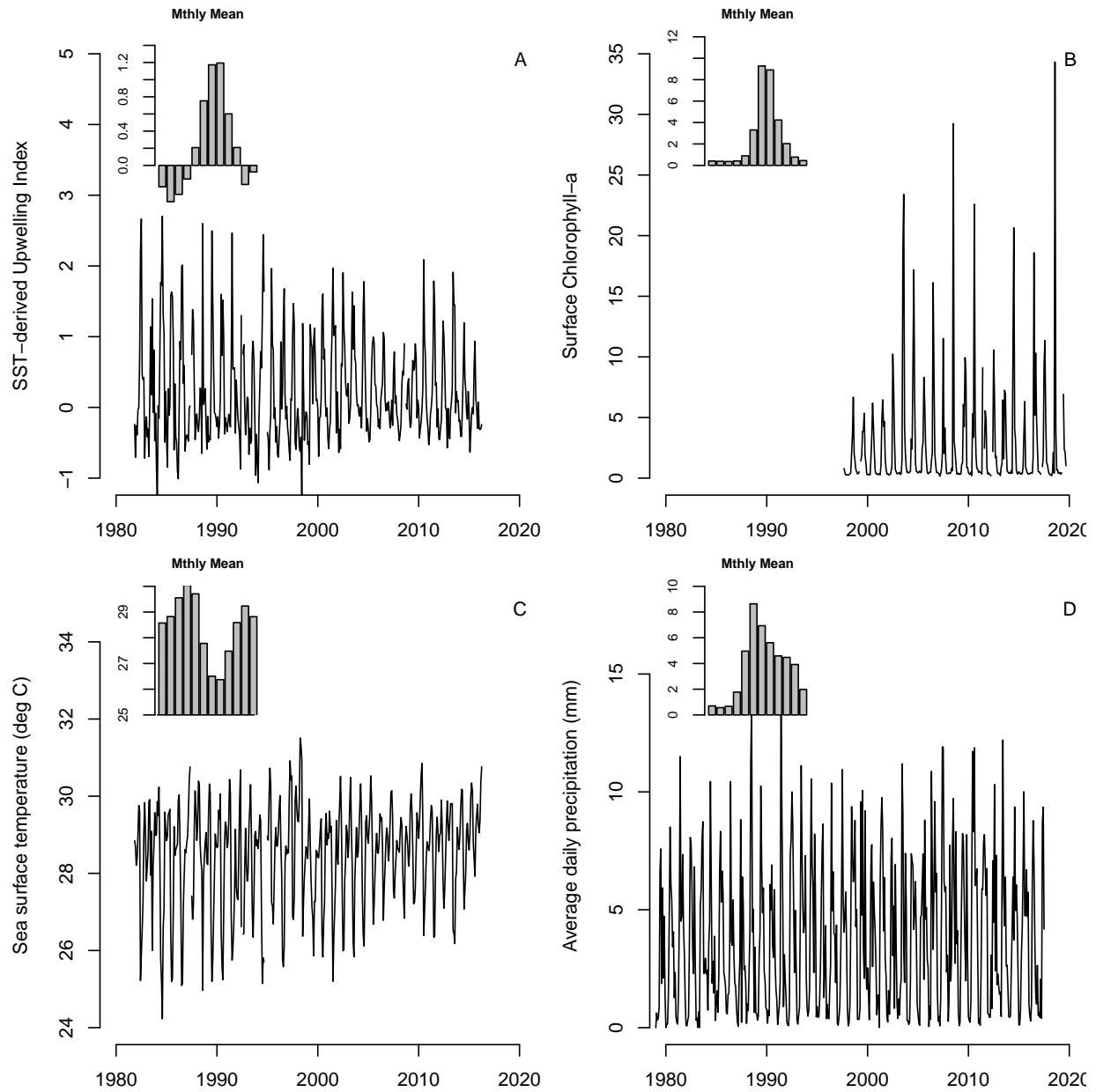


Figure 4

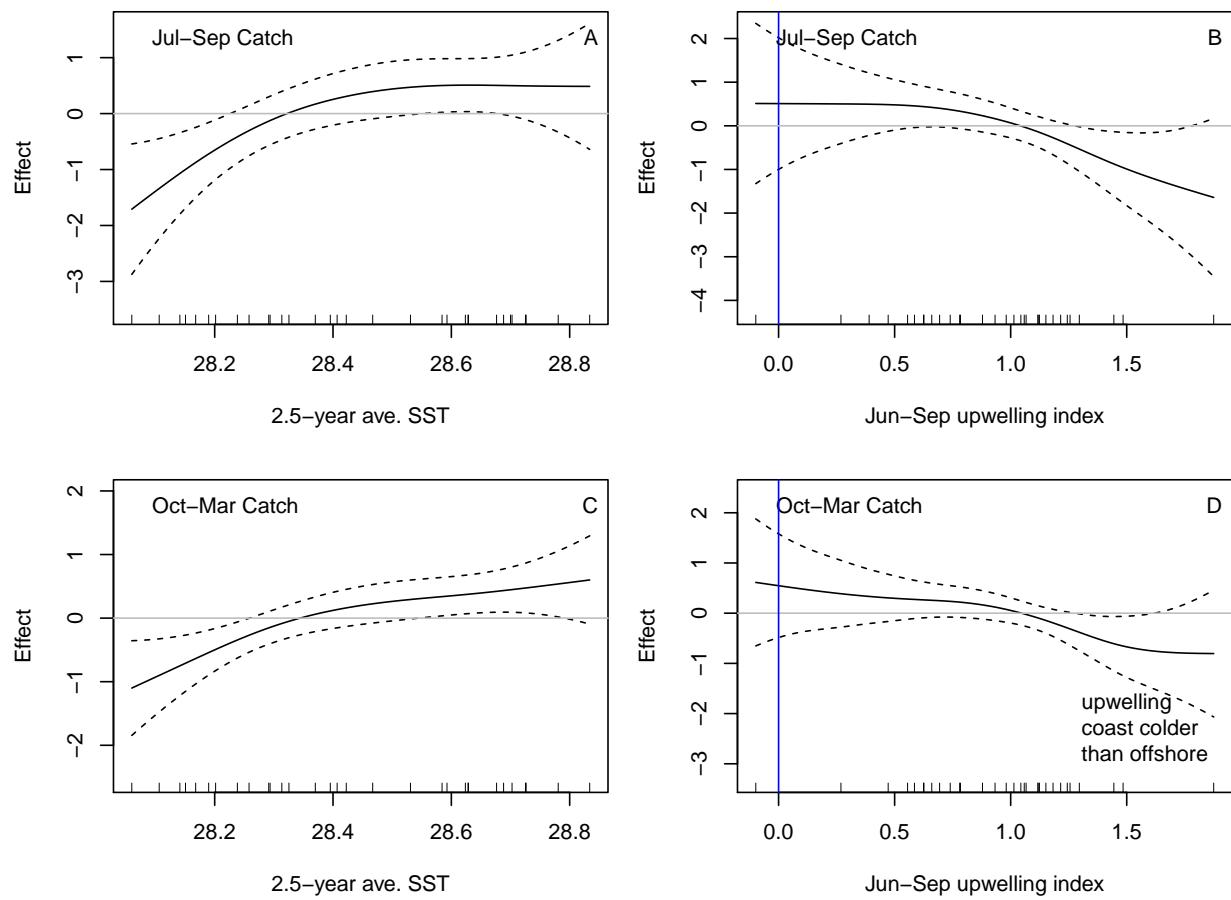


Figure 5

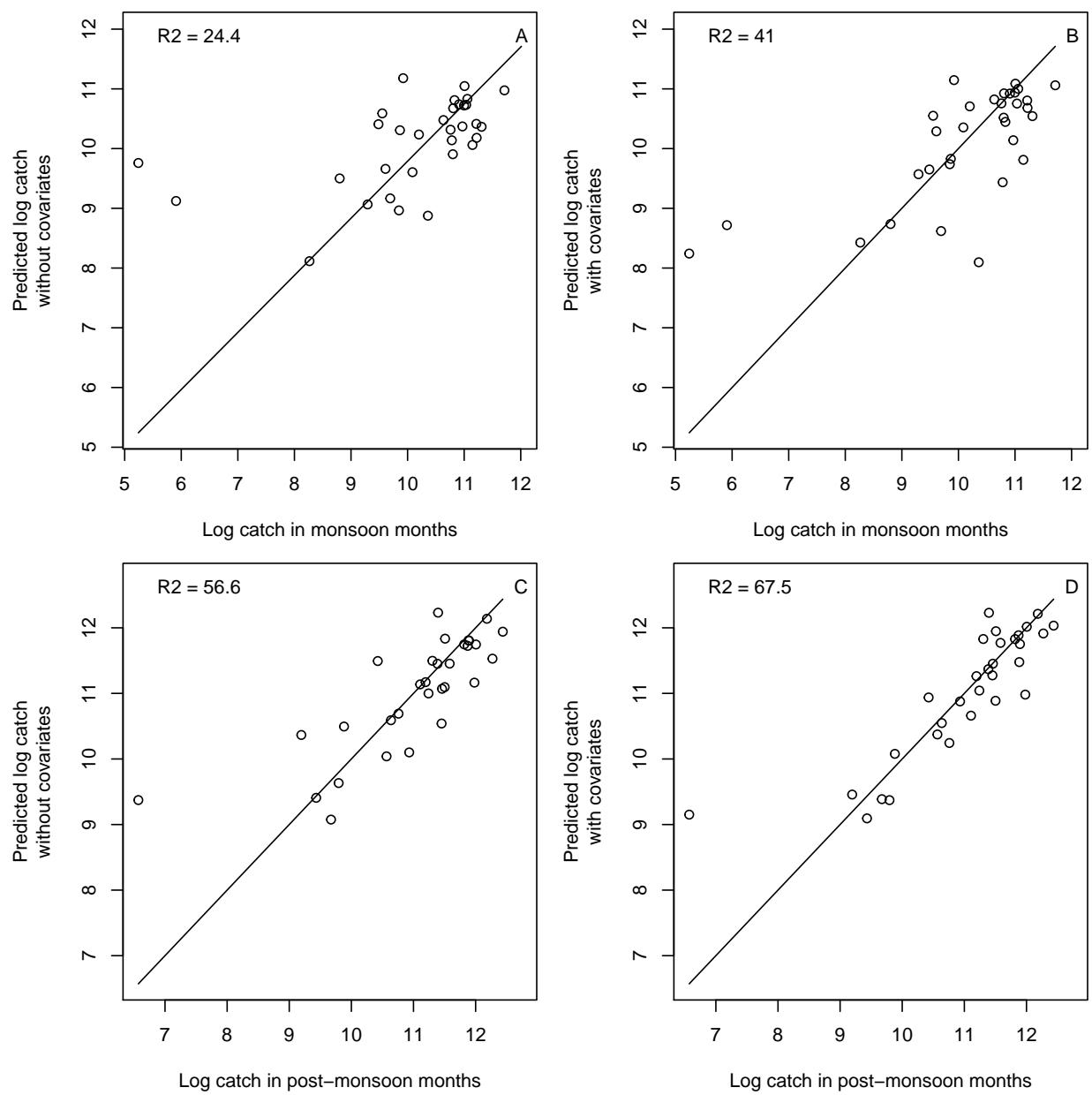


Figure 6