

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

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<sup>12</sup> **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.

<sup>148</sup> **Study Area**

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

<sup>162</sup> **Oil sardine life cycle and fishery**

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

<sup>176</sup> After eggs are spawned, they develop rapidly into larvae (Nair, 1959). The phytoplankton  
<sup>177</sup> bloom that provide sardine larvae food is dependent upon nutrient influx from coastal up-  
<sup>178</sup> welling and runoff from rivers during the summer monsoon and early fall. The blooms start in  
<sup>179</sup> 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 that overfishing and especially catch of juveniles, which are at times discarded (Das & Edwin,

<sup>212</sup> 2018) is a factor in the most recent oil sardine declines (Kripa et al., 2018).

<sup>213</sup> The relationship between the oil landings and the stock abundance is complex. It depends  
<sup>214</sup> both on the fleet size and composition, but also depends on the proximity of the stock to the  
<sup>215</sup> shore-based fishery. Although the landings are not a direct proxy for the overall abundance of  
<sup>216</sup> oil sardines, landings are often assumed to reflect the total abundance in most years for reasons  
<sup>217</sup> specific to the species and the fishery (Kripa et al., 2018): For most of the period of analysis,  
<sup>218</sup> the fishery was artisanal: small boats with small motors, no refrigeration, and limited to the  
<sup>219</sup> near shore. The ring seine was introduced but widespread mechanization of the fleet is a recent  
<sup>220</sup> development. The artisanal fisherman have limited ability to target the stock, at least not to the  
<sup>221</sup> degree that landings can remain constant as a stock declines, a pattern than can be observed in  
<sup>222</sup> a large, mobile, highly mechanized fleet. The fishery is unregulated, except for a brief closure  
<sup>223</sup> during the monsoon months. Unlike some species, oil sardine shoals do not perform long  
<sup>224</sup> distance migrations that take them out of contact with the fishery. However for the purpose  
<sup>225</sup> of our study, the assumption of a tight relationship between landings and abundance is not  
<sup>226</sup> necessary. The objective is to understand what drives landings variability, whether it be due to  
<sup>227</sup> abundance variability or due to exposure to the fishery (by being closer to shore).

## <sup>228</sup> Materials and Methods

### <sup>229</sup> Sardine landing data

<sup>230</sup> Quarterly fish landing data have been collected by the Central Marine Fisheries Research Institute  
<sup>231</sup> (CMFRI) in Kochi, India, since the early 1950s using a stratified multi-stage sample  
<sup>232</sup> design (Srinath et al., 2005). The survey visits the fish landing centers along the entire south-  
<sup>233</sup> east coast of India and samples the catch from the variety of boat types and gear types used  
<sup>234</sup> in the coastal fishery. Landings estimates are available for all the coastal states, however we  
<sup>235</sup> model the catch for the state of Kerala only, where the longest time series is available and the  
<sup>236</sup> overwhelming majority of oil sardines are landed (Figure 2). Kerala contributes a remarkable  
<sup>237</sup> 14.4% of the total marine production (CMFRI, 2017) and Major resources contributing to the  
<sup>238</sup> pelagic landings were oilsardine (57.4%). The quarterly landings (metric tons) for oil sardine  
<sup>239</sup> landed from all gears in Kerala were obtained from CMFRI reports (1956-1984) and online  
<sup>240</sup> databases (1985-2015) (CMFRI, 1969, 1995, 2016; Jacob et al., 1987; Pillai, 1982). The quar-  
<sup>241</sup> terly landing data were log-transformed to stabilize the variance. Yearly effort data for the  
<sup>242</sup> individual gears is not available for the entire catch time series and the data available on size of

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

## 246 Remote sensing data

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

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

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

269 For an index of coastal upwelling, we used the sea-surface temperature differential be-  
270 tween near shore and 3 degrees offshore as described by Naidu et al. (1999) and Smitha et  
271 al. (2008). The index was computed as the average SST in box 4 off Kochi (Figure 1) minus  
272 the average SST in box 13. For SST, we used the remote sensing sea-surface temperature data  
273 sets described above. This SST-based upwelling index has been validated as a more reliable

274 metric of upwelling off the coast of Kerala compared to wind-based upwelling indices (BR et  
275 al., 2008). The SST-based upwelling index and chlorophyll-a blooms are strongly correlated  
276 (Figure 5).

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

288 The Oceanic Niño Index (ONI) is a measure of the SST anomaly in the east-central Pacific  
289 and is a standard index of the El Niño/Southern Oscillation (ENSO) cycle. The ONI index is 3-  
290 month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region, based on centered 30-  
291 year base periods updated every 5 years. The ONI was downloaded from the NOAA National  
292 Weather Service Climate Prediction Center.

## 293 Hypotheses

294 Our statistical analyses were structured around specific hypotheses (Table 1) concerning which  
295 remote sensing covariates in which months should correlate with landings in specific quarters.  
296 These hypotheses were based on biological information concerning how environmental condi-  
297 tions affect sardine survival and recruitment and affect exposure of Indian oil sardines to the  
298 coastal fishery as reviewed in the introduction. The quarter 3 (Jul-September) catch overlaps  
299 the summer monsoon and the main spawning months. This is also the quarter where small  
300 0-year fish from early spawning (June) often appear in the catch, sometimes in large numbers.  
301 Variables that affect or are correlated with movement of sardines inshore should be correlated  
302 with quarter 3 landings. In addition, pre-spawning (March-May) environmental conditions  
303 should be correlated with the spawning strength as adult oil sardines experience an accel-  
304 eration of growth during this period along with egg development. The post-monsoon catch  
305 (October-May) is a mix of 0-year fish (less than 12 months old) and mature fish (greater than

306 12 months old). Variables that are correlated with spawning strength and larval and juvenile  
307 survival should correlate with the post-monsoon catch both in the current year and in future  
308 years, one to two years after.

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

## 318 Statistical models

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

337 We tested ARIMA models on both monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch

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

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

361 We compared the following catch models:

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

369  $\ln(C_{i,t})$  is the log catch in the current year  $t$  in season  $i$ . We modeled two different catches:  
 370 monsoon catch  $S_t$  (July-September), which is during the late part of the summer monsoon, and

371 post-monsoon catch  $N_t$  (October-June). The catches were logged to stabilize and normalize  
372 the variance.  $s()$  is a non-linear function estimated by the GAM algorithm. The model is  
373 primarily statistical, meaning it should not be thought of as being a population growth model.  
374 We tested models with prior year post-monsoon catch ( $N_{t-1}$ ) and 3rd quarter catch ( $S_{t-1}$ ) as the  
375 explanatory catch variable.  $S_t$  was not used as a predictor for  $N_t$ ;  $S_t$  is the quarter immediately  
376 prior to  $N_t$  and would not be available for a forecast model since time is required to process  
377 landings data. The catch models were fit to 1982 to 2015 catch data, corresponding to the years  
378 where the SST, upwelling and precipitation data were available. F-tests and AIC on nested sets  
379 of models (Wood et al., 2016) were used to evaluate the support for the catch models and later  
380 for the covariate models. After selection of the best model with the 1982-2015 data, the fitting  
381 was repeated with the 1956-1981 and 1956-2015 catch data to confirm the form of the catch  
382 models.

383 Once the catch models were determined, the covariates were studied individually and  
384 then jointly. As with the catch models, F-tests, AIC and LOO (leave-one-out cross-validation)  
385 on nested sets of models were used to evaluate the support for models with covariates. The  
386 smoothing term was fixed at an intermediate value ( $sp=0.6$ ) instead of treated as an estimated  
387 variable. Our models for catch with covariates typically took the form  $\ln(C_{i,t}) = M + s_1(V_{1,t}) +$   
388  $s_2(V_{2,t-1}) + \varepsilon_t$  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  
389 step 1. Thus models with covariates modeled both as a linear and non-linear effect were com-  
390 pared. The covariates tested are those discussed in the section on covariates that have been  
391 hypothesized to drive the size of the sardine biomass exposed to the fishery. We tested both  
392 models with one and two covariates, and did not use correlated covariates in the same model.

## 393 Results

### 394 Catches in prior seasons as explanatory variables

395 Using the 1984-2015 catch data, which is the time-period that overlaps our available environ-  
396 mental data, the Jul-Sep catch models were compared against a “naive” model in which the  
397 forecasted Jul-Sep catch was simply the Jul-Sep catch in the prior year. The “naive” model  
398 has no estimated parameters and is a standard null model for time series modeling. Models  
399 with  $\ln(N_{t-1})$  (Oct-Mar catch in prior year), whether linear or non-linear, as the explanatory  
400 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

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

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

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

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

$$M1 : \ln(S_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t.$$

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

$$M2 : \ln(N_t) = \alpha + s_1(\ln(N_{t-1})) + s_2(\ln(S_{t-2})) + \varepsilon_t$$

$$M3 : \ln(N_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$$

431 Note that although M1 was the best model for Jul-Sep catch, it was only weakly explanatory.  
 432 The maximum adjusted  $R^2$  was less than 30% (Table A2). For the Oct-Mar catch, M2  
 433 and M3 were more explanatory with an adjusted  $R^2$  of 45.3% for M2 and 56.6% for M3 (Table  
 434 A4).

## 435 Environmental covariates as explanatory variables

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

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

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

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

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

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

perature over multiple prior years has been found to be correlated with sardine recruitment in Pacific sardines (Checkley et al., 2017; Jacobson & MacCall, 1995; Lindegren et al., 2013) and southern African sardines (Boyer et al., 2001). We tested as a model covariate the average SST for 2.5 years prior to the July-September catch, so January-June in the current calendar year and the two prior calendar years for a 30-month average. This covariate can be used for forecasting since it does not overlap with either July-September or October-March catch. This variate with a non-linear response was best covariate for both the July-September and the post-monsoon catch. For post-monsoon catch, the model with SST had an adjusted  $R^2$  of 67.5 versus 56.6 without. For the July-September catch, the adjusted  $R^2$  was 41.0 with SST and 24.4 without. The response curve was step-like with a negative effect at low temperatures and then an positive flat effect at higher temperatures (Figure 6). This is similar to the step-response found in studies of the correlation between average SST and recruitment in Pacific sardines (Jacobson & MacCall, 1995).

## Discussion

Sardines in all the world's ecosystems exhibit large fluctuations in abundance (Baumgartner et al., 1992). 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 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 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 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 explanatory variable. Similar to these studies, we found that the average nearshore SST over multiple seasons was the covariate that explained

525 the most variability in catch both in the monsoon and post-monsoon months. McClatchie et  
526 al. (2010) found no SST relationship with SST and Pacific sardine recruitment, however their  
527 analysis used a linear relationship while the other studies, and ours, that found a relationship  
528 (Checkley et al., 2017; Jacobson & MacCall, 1995) allowed a non-linear relationship. Both  
529 Jacobson and MacCall (1995) and Checkley et al. (2017) found a step-like response function  
530 for temperature: below a threshold value the effect of temperature was linear and above the  
531 threshold, the effect was flat and at lower temperatures the effect was negative and became  
532 positive as temperature increased. Our analysis found a similar pattern with a negative effect  
533 when the 2.5-year average temperature was below 28.35°C and positive above and with the  
534 positive effect leveling off above 28.5°C (Figure 6).

535 There were four outlier years when catch were much lower than expected based on prior  
536 catches: 1986, 1991, 1994 and 2013. The 2.5-year average SST predicted the collapses in  
537 1986 and 1991 (Figure 7); the size of the residual with the covariate was much smaller than  
538 without the covariate. The largest collapse was in 1994 and the most recent, in our dataset,  
539 was 2014. The 2.5-year average SST did not predict the 1994 nor 2013 collapse. There was  
540 no change in the size of the residual with and without the covariate. In fact, none of the  
541 covariates we tested changed the size of the model residuals for 1994 nor 2013. The causes of  
542 these unusual declines appear either unrelated to the environmental factors we studied. This  
543 suggests either that other factors, biological or anthropogenic, drove these declines or that a  
544 particular combination of environmental factors led to the declines. It should also be noted  
545 that our upwelling indices captured on one aspect of upwelling: the nearshore intensity. Other  
546 aspects of upwelling also affect oil sardines, such as the spatial extent both along the coast and  
547 off the coast and the timing of the start of upwelling.

548 Seasonal productivity in the SE Arabian Sea upwelling is driven by the summer monsoon,  
549 which causes strong coastal upwelling that moves from the south to the north over the summer.  
550 This drives a strong seasonal pattern of zooplankton abundance (Figure 5). Despite the strong  
551 connection between sardine recruitment, growth and survival with upwelling, we found no  
552 correlation with upwelling in the prior season with landings. We did find a correlation between  
553 upwelling in the current season with landings in the current season. The biological reasons  
554 behind a positive relationship with upwelling are clear. Upwelling drives productivity and  
555 higher food resources in the current season leads to higher recruitment and higher numbers  
556 of 0-year fish in the landings or may bring sardines into the nearshore to feed where they are  
557 exposed to the fishery. However, the explanatory power of the upwelling indices was mainly  
558 due to the negative effect of extremely high upwelling (Figure 6). Extremely high upwelling

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

## 560 Conclusions

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

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

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860 **Figure Legends**

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

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

868 Figure 3. The sardine life-cycle in the Southeast Arabian Sea and how it interacts with the  
869 fishery.

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

877 Figure 5. Key oil sardine life-history events overlaid on the monthly sea surface tempera-  
878 ture in the nearshore and offshore and the nearshore chlorophyll density.

879 Figure 6. Effects of covariates estimated from the GAM models. Panel A) Effect of the  
880 2.5 year average nearshore SST on catch during the catch during July-September (late spaw-  
881 ning and early post-spawning) months. Panel B) Effect of upwelling (inshore/off-shore SST  
882 differential) during June-September in the current season on July-September catch. The index  
883 is the difference between offshore and inshore SST, thus a negative value indicates warmer  
884 coastal surface water than off-shore. Panel C) Effect of the 2.5 year average nearshore SST on  
885 catch during the catch during October-March (post-monsoon, age-0, -1, -2 year fish). Panel  
886 D) Effect of upwelling (inshore/off-shore SST differential) during June-September in the cur-  
887 rent season on October-March catch. Strong upwelling (positive upwelling index) in the larval  
888 and juvenile high growth period (Oct-Dec) is associated with higher early survival and larger  
889 cohorts of age-0 fish in the catch.

890 Figure 7. Fitted versus observed catch with models with and without environmental co-  
891 variates. Panel A) Fitted versus observed log catch in the spawning months with only non-

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

Table 1. Hypotheses for covariates affecting landings.  $S_t$  is quarter 3 (July-September) catch in the current season,  $S_{t-1}$  is quarter 3 catch in the previous season.  $N_t$  is the post-monsoon October-March catch in the current season and  $N_{t-1}$  is the October-March catch in the prior season. Because the fishing season is July-June,  $N_t$  spans two calendar years. 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.

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 $S_t \sim S_{t-1} + S_{t-2}$ $N_t \sim S_{t-1} + S_{t-2}$	$S_t$ 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 $S_t \sim$ June-July 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 upwelling index 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 $S_t \sim$ SST during Mar-May in $t$ $N_t \sim$ SST during Mar-May 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 $S_t \sim$ Oct-Dec nearshore SST $t - 1$ $N_t \sim$ Oct-Dec nearshore 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 $S_t \sim$ Jun-Sep UPW in $t - 1$ & $t$ $N_t \sim$ Jun-Sep UPW in $t - 1$ & $t$	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 $S_t \sim$ CHL in $t - 1$ & $t$ $N_t \sim$ CHL in $t - 1$ & $t$	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 $S_t \sim$ 2.5-yr ave. nearshore SST $N_t \sim$ 2.5-yr ave. nearshore 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 $S_t \sim$ ONI in $t - 1$ $N_t \sim$ 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 $S_t \sim$ DMI in $t - 1$ $N_t \sim$ DMI in $t - 1$ & $t$	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 7.

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

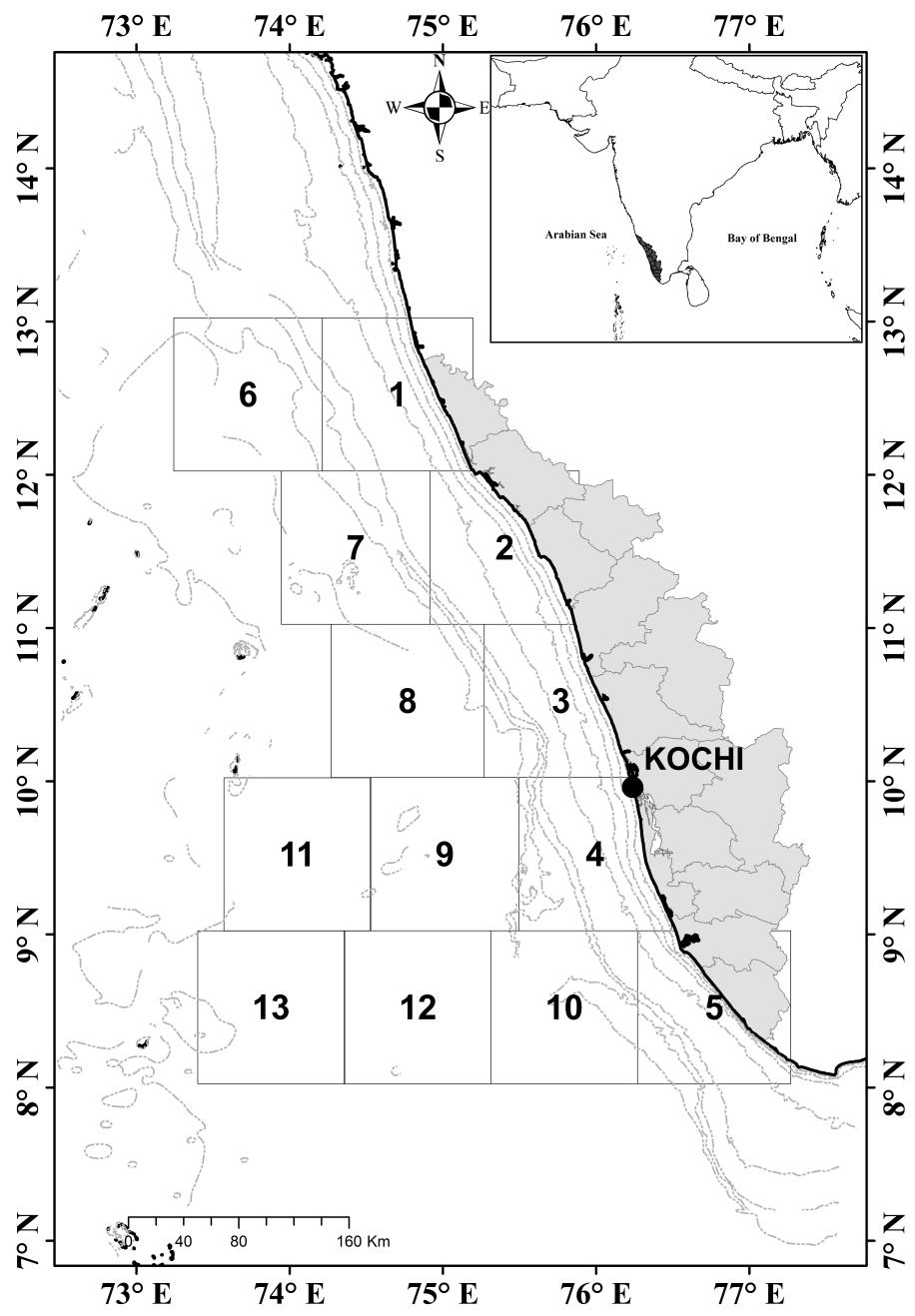


Figure 1

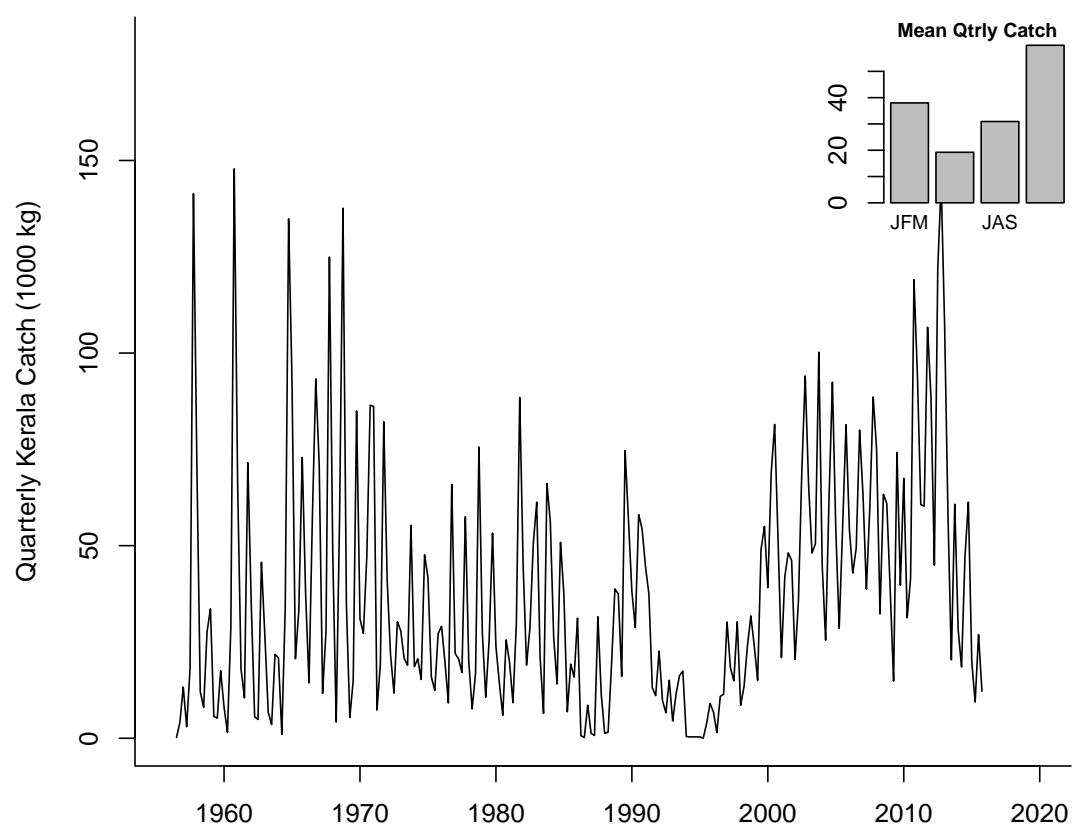


Figure 2

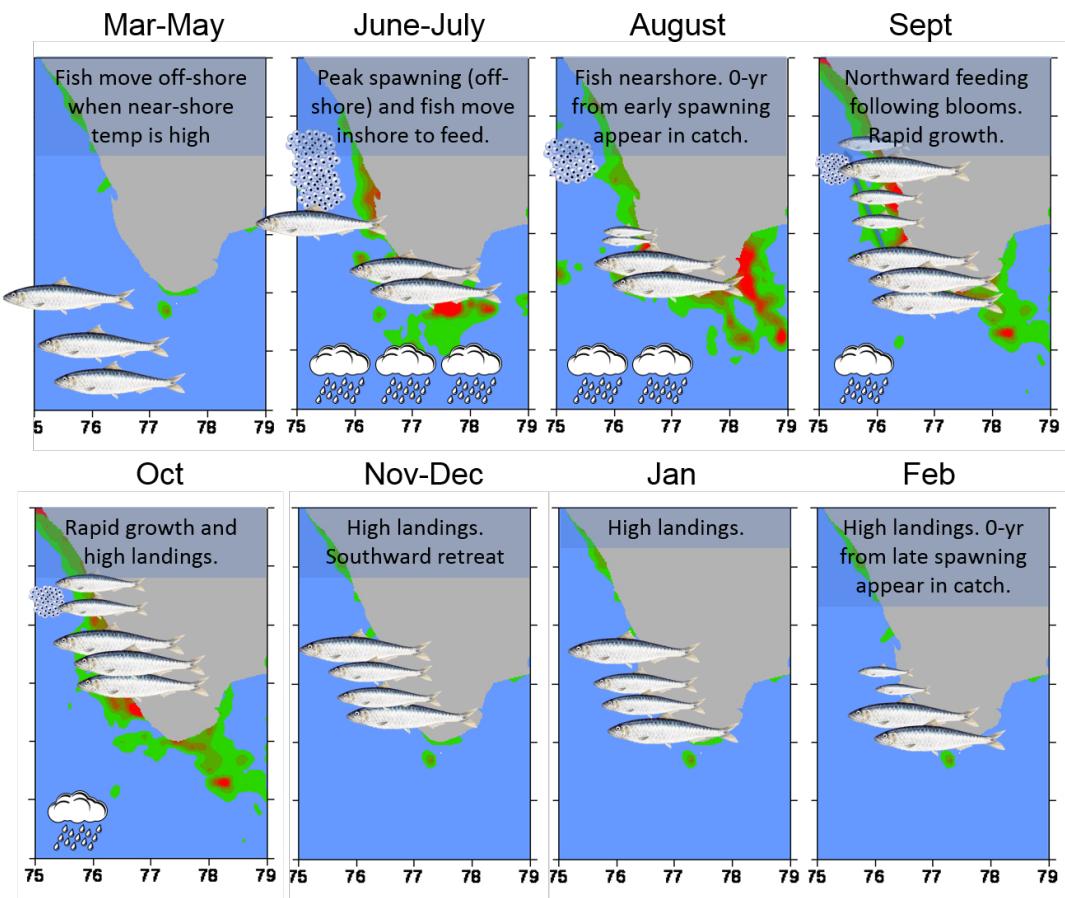


Figure 3

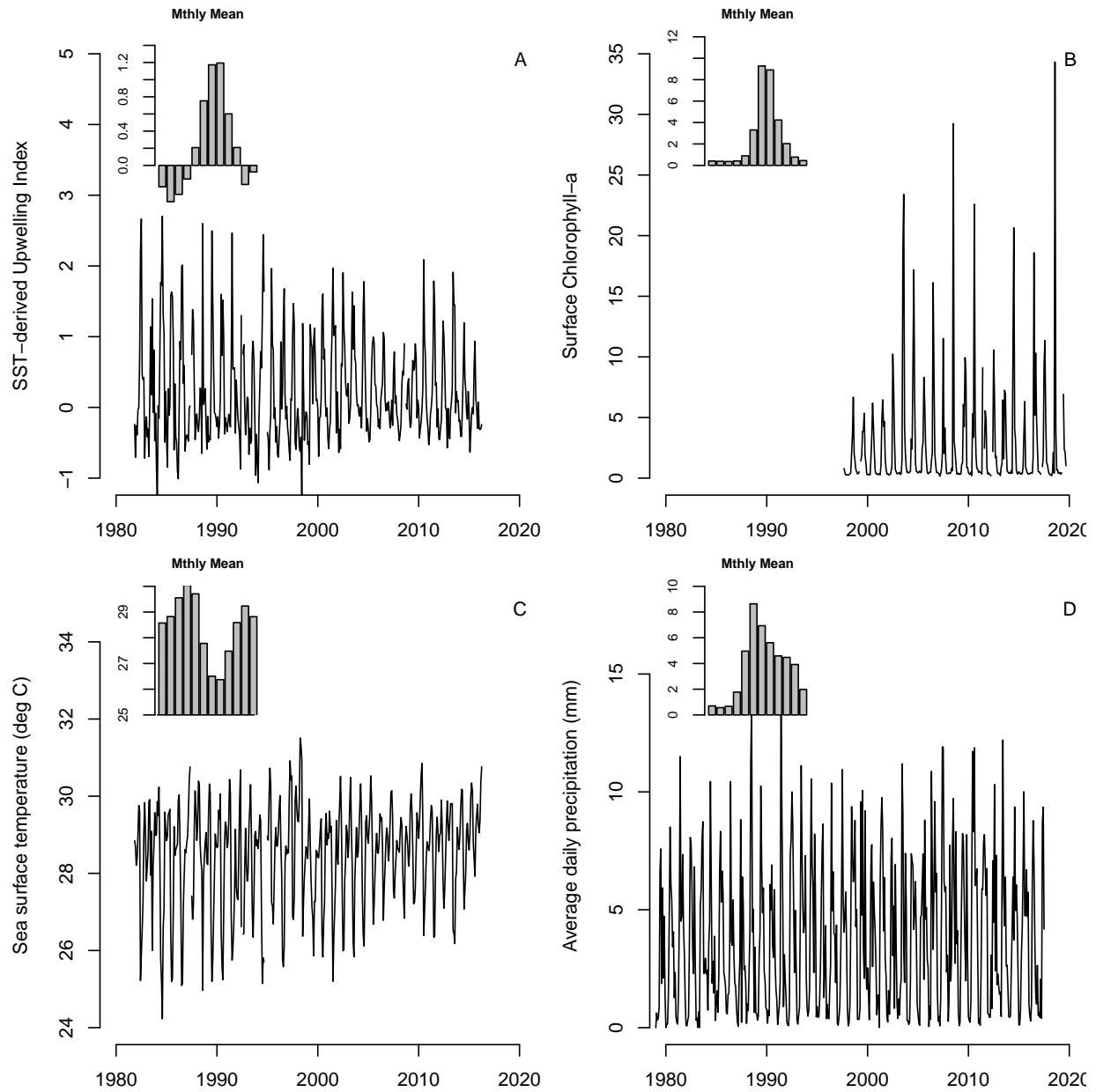


Figure 4

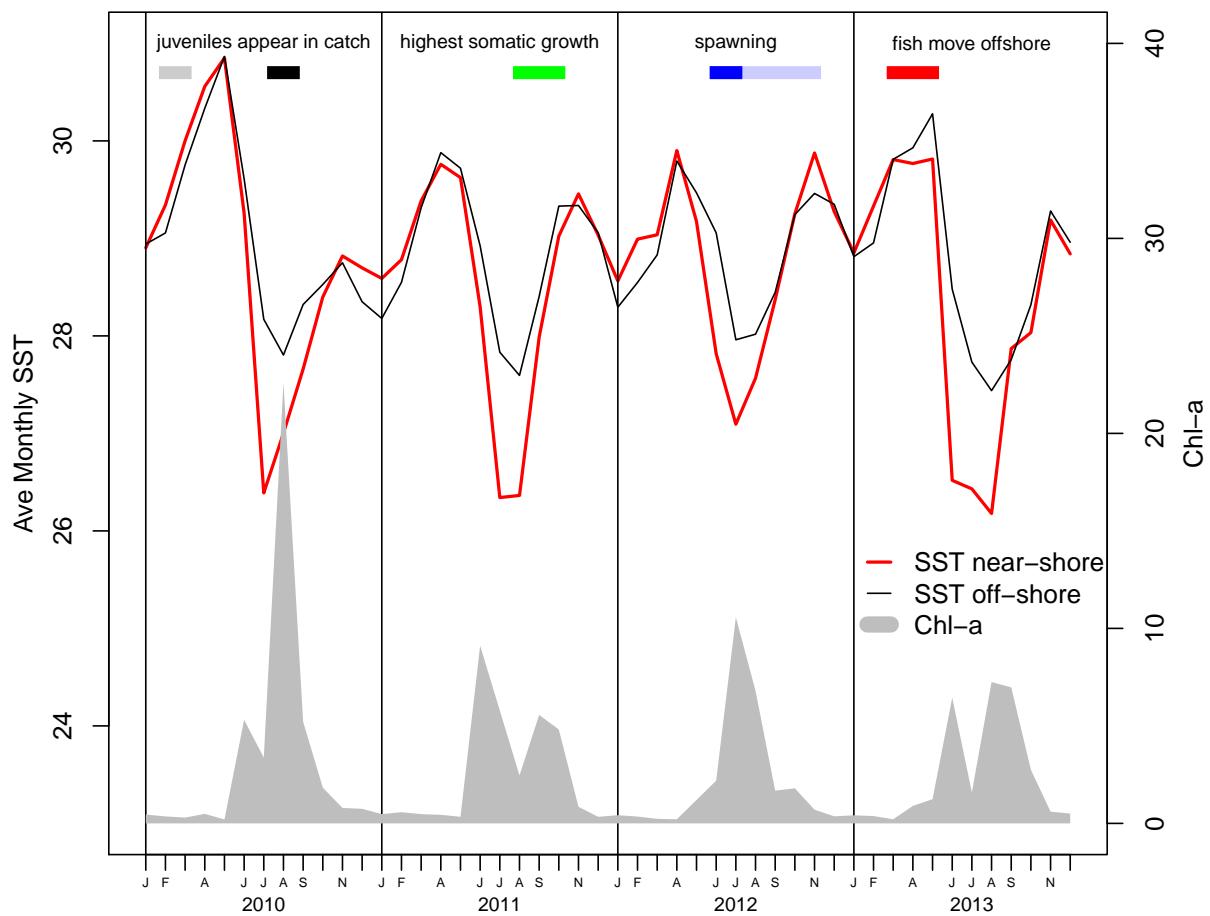


Figure 5

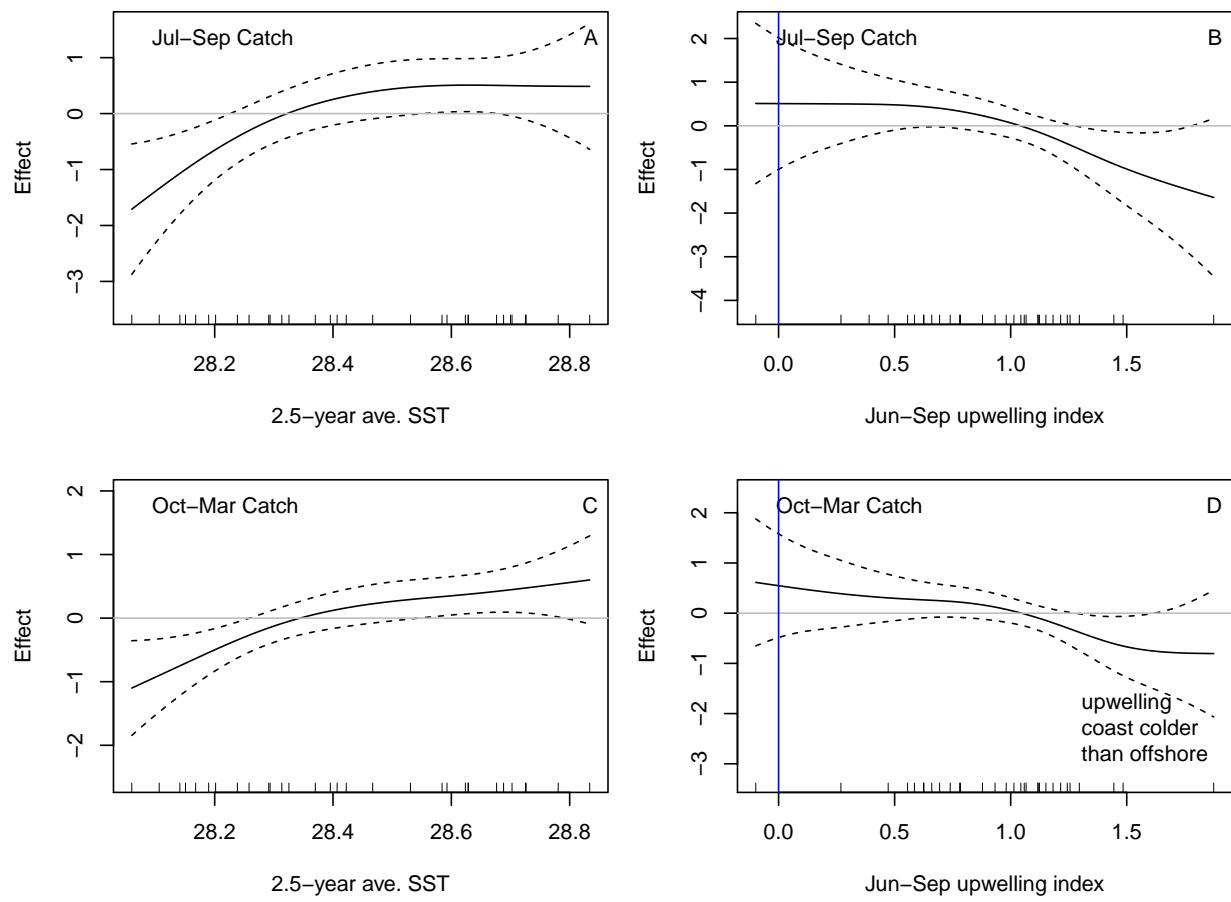


Figure 6

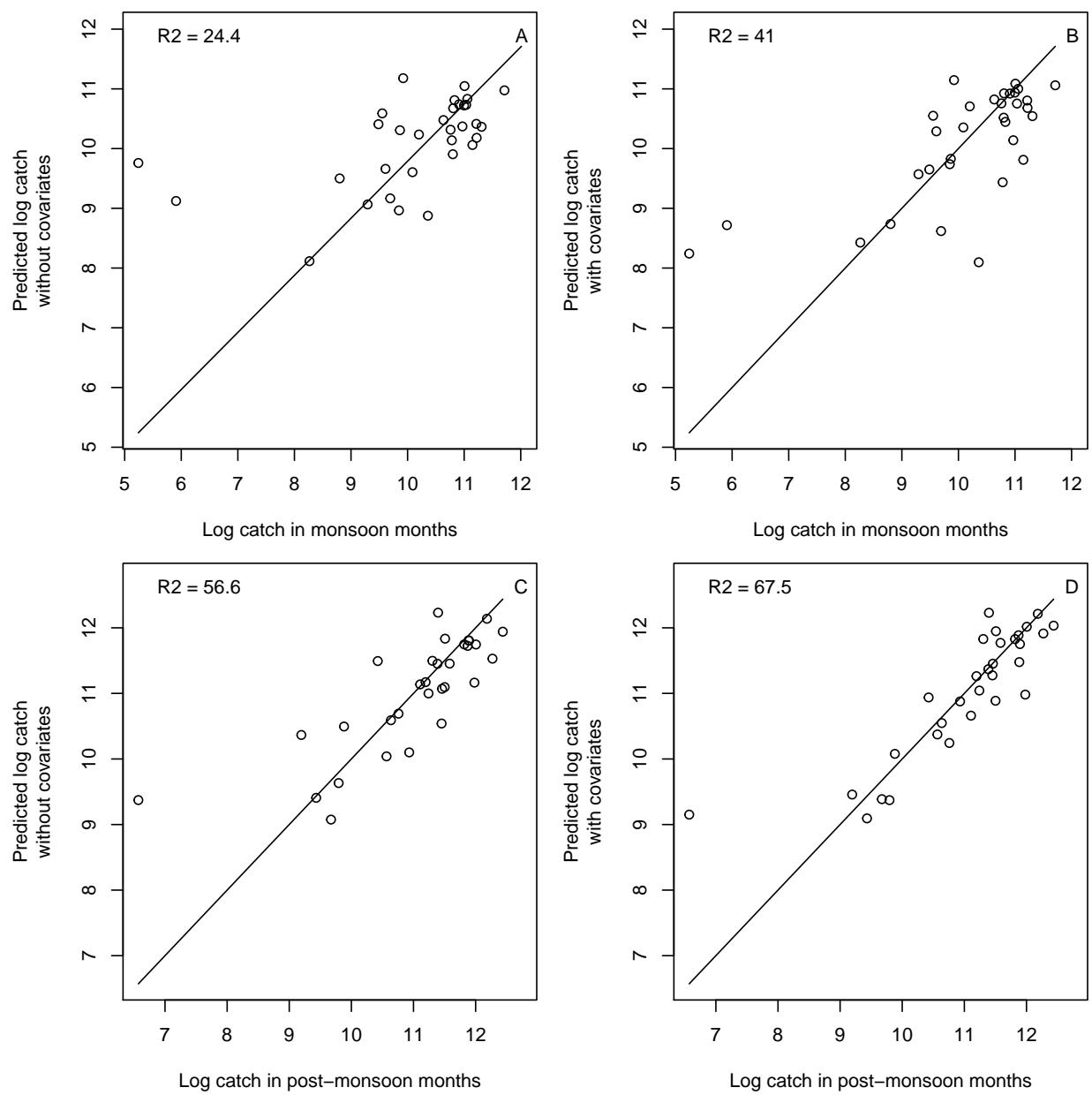


Figure 7