

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

3

4 Eli Holmes<sup>1</sup>, Smitha B.R.<sup>2</sup>, Nimit Kumar<sup>3</sup>, Sourav Maity<sup>3</sup>, David Checkley<sup>4</sup>,  
5 Mark Wells<sup>5</sup>, Vera Trainer<sup>1</sup>

6 1. Northwest Fisheries Science Center, NOAA, Seattle, WA. 2. Centre for Marine Living Resources and  
7 Ecology, MoES, Kochi, India. 3. Indian National Centre for Ocean Information Services, Hyderabad,  
8 India. 4. Scripps Institution of Oceanography, UC San Diego, San Diego, CA. 5. School of Marine  
9 Sciences, University of Maine, Orono, ME.

10

## Abstract

11 Commercial landings of sardine are known for strong year-to-year fluctuations. A key  
12 driver is thought to be environmental variability, to which small forage fish are especially  
13 sensitive. We examined the environmental drivers associated with landings fluctuations in  
14 the Indian oil sardine using a 32-year time series off Kerala state. Past research suggested  
15 a variety of influential variables: precipitation, upwelling intensity, SST, chlorophyll and  
16 ENSO. Using the life-history of the Indian oil sardine, we developed hypotheses concerning  
17 how these environmental variables might affect landings and tested them using generalized  
18 additive models which allow non-linear response curves. We found significant correlation  
19 for only two variables: upwelling intensity and the multi-year average nearshore SST. Both  
20 monsoon and post-monsoon landings were correlated with upwelling intensity in June-  
21 September. Upwelling intensity has both a positive effect (fueling higher food availability)  
22 and a negative effect at extreme intensity (bringing poorly oxygenated water to the surface).  
23 However, the most significant correlation (adjusted R<sup>2</sup> of 67.5%) was between the 2.5  
24 year average nearshore SST and post-monsoon landings. The multi-year average SST also  
25 been identified as a predictor for Pacific sardine and southern African sardine fluctuations,  
26 suggesting that the average SST over the sardine life-span successfully captures a variety of  
27 factors which predict future abundance. The temperature in the Western Indian Ocean has  
28 been increasing faster than in other tropical oceans and the warming has been most extreme  
29 during the summer monsoon. Our work highlights that these changes in summer upwelling  
30 intensity and sea temperature are likely to affect landings.

31

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

## 34 Introduction

35 Environmental variability is known to be a key driver of population variability of small forage fish  
36 such as sardines, anchovy and herring (Alheit & Hagen, 1997; A. Bakun, 1996; Checkley Jr., Asch, &  
37 Rykaczewski, 2017; Cury et al., 2000). In particular, ocean temperature and upwelling dynamics, along  
38 with density-dependent feedback, have been identified as important in affecting recruitment success and  
39 biomass of European and Pacific sardines (*Sardina pilchardus* and *Sardinops sagax*) (Alheit et al., 2012;  
40 Jacobson & MacCall, 1995; Lindegren & Checkley Jr., 2012; Lindegren, Checkley, Rouyer, MacCall,  
41 & Stenseth, 2013; Rykaczewski & Checkley, 2008). Like other sardines, the Indian oil sardines show  
42 strong interannual fluctuations and larger decadal booms and busts. The Indian oil sardine offers an  
43 instructive case study to investigate the effects of environmental variability, particularly temperature  
44 and upwelling dynamics, as they occupy an ocean system that is warmer than that occupied by other  
45 sardines and have a strong seasonal cycle driven by the Indian summer monsoon.

46 The Indian oil sardine (*Sardinella longiceps* Valenciennes, 1847) is one of the most commercially  
47 important fish resources along the southwest coast of India (Figure 1) and historically has comprised  
48 approximately 25% of the catch biomass (E. Vivekanandan, Srinath, Pillai, Immanuel, & Kurup, 2003).  
49 Landings of the Indian oil sardine are highly seasonal, peaking after the summer monsoon period in  
50 October-December and reaching a nadir in spring before the summer monsoon in April-June (Figure  
51 2). At the same time, the landings of this small pelagic finfish are highly variable from year to year.  
52 Small pelagics are well known to exhibit high variability in biomass due to the effects of environmental  
53 conditions on survival and recruitment (Alheit & Hagen, 1997; A. Bakun, 1996; Checkley Jr. et al.,  
54 2017; Cury et al., 2000). In this fishery, however, environmental conditions also affect exposure of  
55 sardines to the fishery. Until recently, the Indian oil sardine fishery was artisanal and based on small  
56 human or low powered boats with no refrigeration. The fishery was confined to nearshore waters, and  
57 thus migration of sardines in and out of the coastal zone greatly affected exposure to the fishery.

58 Researchers have examined a variety of environmental variables for their correlation with landings  
59 of the Indian oil sardine in order to understand the factors that drive landings variability. Precipitation  
60 during the southwest monsoon and the day of the monsoon arrival are thought to act as either a di-  
61 rect or indirect cue, as an index of other climatic conditions, for spawning (Antony Raja, 1969, 1974;  
62 Jayaprakash, 2002; Murty & Edelman, 1966; Srinath, 1998). Many studies have looked for correlations  
63 between precipitation, however the reported effects are positive in some studies and negative in others  
64 (Madhupratap, Shetye, Nair, & Nair, 1994). Researchers have also looked for and found correlations  
65 with various metrics of upwelling intensity, such as sea level at Cochin (Jayaprakash, 2002; Longhurst  
66 & Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara, 2011),  
67 salinity and bottom sea temperature (Krishnakumar et al., 2008), and with direct measures of productiv-  
68 ity, such as nearshore zooplankton and phytoplankton abundance (George et al., 2012; Hornell, 1910;  
69 Madhupratap et al., 1994; Menon et al., 2019; R. V. Nair, 1952; R. V. Nair & Subrahmanyam, 1955;

70 Piontkovski, Al Oufi, & Al Jufaily, 2015). Researchers have also found correlations with near-shore sea  
71 surface temperature (SST) (Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed, 1970; V. Supraba et al.,  
72 2016). SST can affect both somatic growth rates and juvenile survival but also can cause fish to move  
73 off-shore and away from the shore-based fishery. The multi-year average sea temperature is postulated  
74 to have effects on recruitment and the survival of larval and juvenile sardines, which affect the later over-  
75 all abundance (Checkley Jr. et al., 2017; Takasuka, Oozeki, & Aoki, 2007). The El Ni~{n}o/Southern  
76 Oscillation (ENSO) has a cascading effect on all the aforementioned environmental parameters (SST,  
77 precipitation, upwelling) which in turn impact oil sardines, and correlations have been found between  
78 ENSO indices and landings with a 9- to 12-month lag (Rohit et al., 2018; V. Supraba et al., 2016).

79 In this paper, we study the utility of environmental covariates from remote sensing to explain year-  
80 to-year variability in oil sardine landings using the time series of quarterly Indian oil sardine landings  
81 from the southwest coast of India. This time series is derived from a stratified sampling design that  
82 surveys landing sites along the southeast Indian coast and was first implemented in the 1950s (Srinath,  
83 Kuriakose, & Mini, 2005). This is purely a landings time series. Catch-at-length data are not available  
84 prior to 2001. Effort data are indirect (boat composition of the fishery) and appropriate effort data  
85 (estimates of number of trips or hours fishing) are only available in a few recent years. In addition,  
86 stock size estimates and fisheries independent data are unavailable. Thus traditional length- or age-  
87 structured models (e.g. virtual population analysis) which produce biomass estimates are not possible.  
88 Instead we use statistical models with covariates to model and produce a one-year ahead forecast of  
89 landings. Unlike prior work on landings models with covariates, we use non-linear time-series models  
90 to allow a flexible effect of covariates and past catch on current landings. We also specifically focus on  
91 environmental covariates measured via remote sensing. Remote sensing data provide long time series of  
92 environmental data over a wide spatial extent at a daily and monthly resolution. A better understanding  
93 of how and whether remote sensing data explains variation in seasonal catch will support future efforts  
94 to use remote sensing data to improve catch forecasts.

95 Modeling and forecasting landings data using statistical models fit to annual or seasonal catch  
96 time series has a long tradition in fisheries and has been applied to many species (Cohen & Stone, 1987;  
97 Farmer & Froeschke, 2015; Georgakarakos, Doutsouvas, & Valavanis, 2006; Hanson, Vaughan, &  
98 Narayan, 2006; Lawer, 2016; Lloret, Leonart, & Sole, 2000; Mendelssohn, 1981; Nobel & Sathianan-  
99 dan, 1991; Prista, Diawara, Costa, & Jones, 2011; Stergiou & Christou, 1996), including oil sardines  
100 (Srinath, 1998; Venugopalan & Srinath, 1998). These models can be used to identify the variables  
101 correlated with catch fluctuations and can be used to provide landings forecasts which are useful for  
102 fishery managers and the fishing industry. An example of the former is using catch forecasts to set  
103 or give warnings of seasonal fishery closures if the forecasted catch is higher than the allowed catch  
104 limits (Farmer & Froeschke, 2015). An example of the latter is the annual Gulf and Atlantic menhaden  
105 forecast produced by NOAA Fisheries; the report is titled, “Forecast for the 20XX Gulf and Atlantic  
106 purse-seine fisheries and review of the 20XX fishing season”. A multiple regression model with envi-

107 ronmental covaraites, similar to the model used in our paper, was developed by NOAA Fisheries in the  
108 1970s (Schaaf, Sykes, & Chapoton, 1975). This model has been used for the last 45 years to produce an  
109 annual forecast of menhaden landings. This forecast was requested by the menhaden fishing industry  
110 and has been used for planning purposes by the industry, not only the fishers but also fish catch sellers  
111 and buyers, businesses which provide fisheries gear, and banks which provide financing (Hanson et al.,  
112 2006).

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

## 126 Study Area

127 Our analysis focuses on the Kerala coast (Figure 1) region of India, where the majority of the Indian  
128 oil sardines are landed and where oil sardines comprise ca. 40% of the marine fish catch (Srinath,  
129 1998; E. Vivekanandan et al., 2003). This area is in the Southeast Arabian Sea (SEAS), one of world's  
130 major upwelling zones, with seasonal peaks in primary productivity driven by upwelling caused by  
131 winds during the Indian summer monsoon (Habeebrehman et al., 2008; Madhupratap, Gopalakrishnan,  
132 Haridas, & Nair, 2001) between June and September. Within the SEAS, the coastal zone off Kerala  
133 between 9°N to 13°N has especially intense upwelling due to the combined effects of wind stress and  
134 remote forcing (B. R. Smitha, 2010; B. R. Smitha, Sanjeevan, Vimalkumar, & Revichandran, 2008).  
135 The result is a strong temperature differential between the near-shore and off-shore and high primary  
136 productivity and surface chlorophyll in this region during summer and early fall (Chauhan et al., 2011;  
137 Habeebrehman et al., 2008; Jayaram, Chacko, Joseph, & Balchand, 2010; Madhupratap et al., 2001;  
138 Raghavan et al., 2010; B. R. Smitha, 2010). The primary productivity peaks subside after September  
139 while mesozooplankton abundances increase and remain high in the post-monsoon period (Madhupratap  
140 et al., 2001).

141 **Oil sardine life cycle and fishery**

142 The Indian oil sardine fishery is restricted to the narrow strip of the western India continental shelf,  
143 within 20 km from the shore (Figure 1). The yearly cycle (Figure 3) of the fishery begins at the start of  
144 spawning during June to July, corresponding with the onset of the southwest monsoon (Antony Raja,  
145 1969; Chidambaram, 1950) when the mature fish migrate from offshore to coastal spawning areas.  
146 The spawning begins during the southwest monsoon period when temperature, salinity and suitable  
147 food availability are conducive for larval survival (Chidambaram, 1950; Jayaprakash & Pillai, 2000;  
148 Krishnakumar et al., 2008; Murty & Edelman, 1966; P. G. Nair, Joseph, Kripa, Remya, & Pillai, 2016).  
149 Although peak spawning occurs in June to July, spawning continues into September (Antony Raja, 1969;  
150 Hornell, 1910; Hornell & Nayudu, 1923; Prabhu & Dhulkhed, 1970) and early- and late-spawning  
151 cohorts are evident in the length distributions of the 0-year fish. Spawning occurs in shallow waters  
152 outside of the traditional range of the fishery (Antony Raja, 1964), and after spawning the adults migrate  
153 closer to the coast and the spent fish become exposed to the fishery.

154 After eggs are spawned, they develop rapidly into larvae (R. V. Nair, 1959). The phytoplankton  
155 bloom that provide sardine larvae food is dependent upon nutrient influx from coastal upwelling and  
156 runoff from rivers during the summer monsoon and early fall. The blooms start in the south near the  
157 southern tip of India in June, increase in intensity and spread northward up the coast (B. R. Smitha,  
158 2010). Variation in the bloom initiation time and intensity leads to changes in the food supply and  
159 to corresponding changes in the growth and survival of larvae and in the later recruitment of 0-year  
160 sardines into the fishery (George et al., 2012). Oil sardines grow rapidly during their first few months,  
161 and 0-year fish (40mm to 100mm) from early spawning appear in the catch in August and September in  
162 most years (Antony Raja, 1970; P. G. Nair et al., 2016). As the phytoplankton bloom spreads northward,  
163 the oil sardines follow, and the oil sardine fishery builds from south to north during the post-monsoon  
164 period. Oil sardines remain inshore feeding throughout the winter months, until March to May when  
165 the inshore waters warm considerably and sardines move off-shore to deeper waters (Chidambaram,  
166 1950). Catches of sardines are correspondingly low during this time for all size classes. The age at first  
167 maturity occurs at approximately 150 mm size (P. G. Nair et al., 2016), which is reached within one  
168 year. When the summer monsoon returns, the oil sardine cycle begins anew.

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

<sup>177</sup> Prabhu & Dhulkhed, 1970) which is a mix of 0-year, 1-year and 2-year fish (P. G. Nair et al., 2016;  
<sup>178</sup> Rohit et al., 2018).

## <sup>179</sup> Contrast between catch modeling versus biomass modeling

<sup>180</sup> Yearly effort data for the individual gears is not available for the entire catch time series and the data  
<sup>181</sup> available on size of the fleet are a coarse metric of effort and thus are difficult to use to compute catch-  
<sup>182</sup> per-unit effort statistics. Nonetheless the number of boats and fishers involved in the fishery has been  
<sup>183</sup> increasing as the population in Kerala has increased. Oil sardines are caught primarily by ring seines,  
<sup>184</sup> which was introduced in the early 1980s. Ring seines of different sizes are used both traditional  
<sup>185</sup> small boats with a small outboard motor and large mechanized ships (Das & Edwin, 2018). Since 1985,  
<sup>186</sup> the ring seine fishery has expanded steadily in terms of horsepower, size of boats, length of nets. There  
<sup>187</sup> are concerns that overfishing and especially catch of juveniles, which are at time discarded (Das &  
<sup>188</sup> Edwin, 2018) is a factor in the most recent oil sardine declines (V. Kripa et al., 2018).

<sup>189</sup> The actual effort in the fishery is complex. It depends both on the fleet size and composition, but  
<sup>190</sup> also depends on the fishers decisions about what species to fish for, where to fish for them (which affects  
<sup>191</sup> transit time versus fishing time),

## <sup>192</sup> Materials and Methods

### <sup>193</sup> Sardine landing data

<sup>194</sup> Quarterly fish landing data have been collected by the Central Marine Fisheries Research Institute (CM-  
<sup>195</sup> FRI) in Kochi, India, since the early 1950s using a stratified multi-stage sample design (Srinath et al.,  
<sup>196</sup> 2005). The survey visits the fish landing centers along the entire southeast coast of India and samples  
<sup>197</sup> the catch from the variety of boat types and gear types used in the coastal fishery. Landings estimates  
<sup>198</sup> are available for all the coastal states, however we model the catch for the state of Kerala only, where  
<sup>199</sup> the longest time series is available and the overwhelming majority of oil sardines are landed (Figure  
<sup>200</sup> 2). Kerala contributes a remarkable 14.4% of the total marine production (CMFRI, 2017) and Major  
<sup>201</sup> resources contributing to the pelagic landings were oilsardine (57.4%). The quarterly landings (metric  
<sup>202</sup> tons) for oil sardine landed from all gears in Kerala were obtained from CMFRI reports (1956-1984)  
<sup>203</sup> and online databases (1985-2015) (CMFRI, 1969, 1995, 2016; T. Jacob, Rajendran, Pillai, Andrews, &  
<sup>204</sup> Satyavan, 1987; V. N. Pillai, 1982). The quarterly landing data were log-transformed to stabilize the  
<sup>205</sup> variance. Yearly effort data for the individual gears is not available for the entire catch time series and  
<sup>206</sup> the data available on size of the fleet are a coarse metric of effort and thus are difficult to use to compute  
<sup>207</sup> catch-per-unit effort statistics. Our analysis uses landings not catch-per-unit effort as is standard in

208 landings modeling with the goal of landings forecasting. Landings are a function of both biomass and  
209 catchability, but the goal in our study is to describe and forecast landings, not biomass.

## 210 **Remote sensing data**

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

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

221 For chlorophyll-a, we used the chlorophyll-a products developed by the Ocean Biology Processing  
222 Group in the Ocean Ecology Laboratory at the NASA Goddard Space Flight Center. For 1997 to 2002,  
223 we used the chlorophyll-a 2014.0 Reprocessing (R2014.0) product from the Sea-viewing Wide Field-  
224 of-view Sensor (SeaWiFS) on the Orbview-2 satellite. These data are on a 0.1 degree grid. For 2003 to  
225 2017, we used the MODIS-Aqua product on a 0.05 degree grid. These CHL data are taken from mea-  
226 surements by the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua Space-  
227 craft. The SST and CHL data were averaged across thirteen 1 degree by 1 degree boxes which roughly  
228 parallel the bathymetry (Figure 1). The SST and CHL satellite data were retrieved from the NOAA  
229 ERDDAP server (Simons, 2017).

230 For an index of coastal upwelling, we used the sea-surface temperature differential between near  
231 shore and 3 degrees offshore as described by Naidu et al. (1999) and Smitha et al. (2008). The index  
232 was computed as the average SST in box 4 off Kochi (Figure 1) minus the average SST in box 13.  
233 For SST, we used the remote sensing sea-surface temperature data sets described above. This SST-  
234 based upwelling index has been validated as a more reliable metric of upwelling off the coast of Kerala  
235 compared to wind-based upwelling indices (B. R. Smitha et al., 2008). The SST-based upwelling index  
236 and chlorophyll-a blooms are strongly correlated (Figure 5).

237 Precipitation data were obtained from two different sources. The first was an estimate of the  
238 monthly precipitation (in mm) over Kerala from land-based rain gauges (Kothawale & Rajeevan, 2017);  
239 these data are available from the Indian Institute of Tropical Meteorology and the data are available  
240 from the start of our landing data (1956). The second was a remote sensing precipitation product from  
241 the NOAA Global Precipitation Climatology Project (Adler et al., 2016). This provides estimate of

242 precipitation over the ocean using a global 2.5 degree grid. We used the 2.5 by 2.5 degree box defined  
243 by latitude 8.75 to 11.25 and longitude 73.25 to 75.75 for the precipitation off the coast of Kerala.  
244 These data are available from 1979 forward (NCEI, 2017). The land and nearshore ocean precipitation  
245 data are highly correlated (Appendix E), supporting the use of the land time series as a proxy for the  
246 precipitation over the ocean off the Kerala coast.

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

## 252 Hypotheses

253 Our statistical analyses were structured around specific hypotheses (Table 1) concerning which remote  
254 sensing covariates in which months should correlate with landings in specific quarters. These hypothe-  
255 ses were based on biological information concerning how environmental conditions affect sardine sur-  
256 vival and recruitment and affect exposure of Indian oil sardines to the coastal fishery as reviewed in the  
257 introduction. The quarter 3 (Jul-September) catch overlaps the summer monsoon and the main spawn-  
258 ing months. This is also the quarter where small 0-year fish from early spawning (June) often appear  
259 in the catch, sometimes in large numbers. Variables that affect or are correlated with movement of  
260 sardines inshore should be correlated with quarter 3 landings. In addition, pre-spawning (March-May)  
261 environmental conditions should be correlated with the spawning strength as adult oil sardines expe-  
262 rience an acceleration of growth during this period along with egg development. The post-monsoon  
263 catch (October-May) is a mix of 0-year fish (less than 12 months old) and mature fish (greater than  
264 12 months old). Variables that are correlated with spawning strength and larval and juvenile survival  
265 should correlate with the post-monsoon catch both in the current year and in future years, one to two  
266 years after.

267 Our hypotheses (Table 1) focus mainly on two drivers: upwelling and ocean temperature. We also  
268 test hypotheses concerning precipitation as this has historically been an environmental covariate con-  
269 sidered to influence the timing of oil sardine landings. More recently, researchers have highlighted the  
270 influence of large-scale ocean processes, specifically the El Niño/Southern Oscillation, on sardine fluc-  
271 tuations; therefore we test the Ocean Niño Index (ONI) also. Chlorophyll density is directly correlated  
272 with sardine food availability and chlorophyll fronts are known to influence sardine shoaling. However  
273 our chlorophyll time series is short (1997-2015) and the statistical power for testing correlation with  
274 landings is low. Tests of chlorophyll are shown in the appendices but are not the focus of our analyses.

275 **Statistical models**

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

292 We tested ARIMA models on both quarter 3 and post-monsoon catch time series and found little  
293 support for auto-regressive errors (ARIMA models with a MA component) based on diagnostic tests of  
294 the residuals and model selection. The best supported ARIMA models were simple AR models ( $x_t =$   
295  $b x_{t-1} + \varepsilon_t$ ). This lack of strong autocorrelation in residuals has been found in other studies that tested  
296 ARIMA models for forecasting small pelagic catch (Stergiou & Christou, 1996). We thus used AR-  
297 only models, however we tested both linear and non-linear models using generalized additive models  
298 (GAM) of the form  $x_t = s(x_{t-1}) + \varepsilon_t$ . The landings models were fit using conditional sum of squares  
299 (conditioning on the first 2 landings values in the time series). We investigated correlations between  
300 environmental variables and sardine catch using generalized additive models (GAMs, Wood, 2017) to  
301 allow one to model the effect of a covariate as a flexible non-linear function. It was known that the  
302 effects of the environmental covariates were likely to be non-linear, albeit in an unknown way. Our  
303 approach is analogous to that taken by Jacobson and MacCall (1995) in a study of the effects of SST on  
304 Pacific sardine recruitment.

305 The first step in our analysis was to determine the catch model: the model for current catch as  
306 a function of the past catch. One feature of GAMs is that they allow the smoothing parameter of the  
307 response curve to be estimated. However we fixed the smoothing parameter at an intermediate value  
308 so that reasonably smooth responses were achieved and to limit the flexibility of the models being fit.  
309 Multi-modal or overly flexible response curves would not be realistic for our application. We used  
310 GAMs with smooth terms represented by penalized regression splines (Wood, 2011, using the mgcv

311 package in R) and fixed the smoothing term at an intermediate value (sp=0.6).

312 Our catch models took the following forms

- 313 • random walk:  $\ln(C_{i,t}) = \alpha + \ln(C_{j,t-1}) + \varepsilon_t$   
314 • AR-1:  $\ln(C_{i,t}) = \alpha + \phi_1 \ln(C_{j,t-1}) + \varepsilon_t$   
315 • AR-2:  $\ln(C_{i,t}) = \alpha + \phi_1 \ln(C_{j,t-1}) + \phi_2 \ln(C_{k,t-2}) + \varepsilon_t$   
316 • non-linear:  $\ln(C_{i,t}) = \alpha + s_1(\ln(C_{j,t-1})) + s_2(\ln(C_{k,t-2})) + \varepsilon_t$

317 where  $\ln(C_{i,t})$  is the log catch in the current year  $t$  in season  $i$ . We modeled two different catches:  
318 3rd quarter catch  $S_t$  (July-September), which is during the late part of the summer monsoon, and post-  
319 monsoon catch  $N_t$  (October-June). The catches were logged to stabilize and normalize the variance.  $s()$   
320 is a non-linear function estimated by the GAM algorithm. The model is primarily statistical, meaning  
321 it should not be thought of as being a population growth model. We tested models with prior year post-  
322 monsoon catch ( $N_{t-1}$ ) and 3rd quarter catch ( $S_{t-1}$ ) as the explanatory catch variable.  $S_t$  was not used  
323 as a predictor for  $N_t$ ;  $S_t$  is the quarter immediately prior to  $N_t$  and would not be available for a forecast  
324 model since time is required to process landings data. The catch models were fit to 1982 to 2015 catch  
325 data, corresponding to the years where the SST, upwelling and precipitation data were available. F-tests  
326 and AIC on nested sets of models (Wood, Pya, & Safken, 2016) were used to evaluate the support for the  
327 catch models and later for the covariate models. After selection of the best model with the 1982-2015  
328 data, the fitting was repeated with the 1956-1981 and 1956-2015 catch data to confirm the form of the  
329 catch models.

330 Once the catch models were determined, the covariates were studied individually and then jointly.  
331 As with the catch models, F-tests and AIC on nested sets of GAM models were used to evaluate the  
332 support for models with covariates. The smoothing term was fixed at an intermediate value (sp=0.6)  
333 instead of treated as an estimated variable. Our models for catch with covariates typically took the form  
334  $\ln(C_{i,t}) = M + s_1(V_{1,t}) + s_2(V_{2,t-1}) + \varepsilon_t$  or  $\ln(C_{i,t}) = M + \beta_1 V_{1,t} + \beta_2 V_{2,t-1} + \varepsilon_t$  where  $M$  was the best  
335 catch model from step 1. Thus models with covariates modeled both as a linear and non-linear effect  
336 were compared. The covariates tested are those discussed in the section on covariates that have been  
337 hypothesized to drive the size of the sardine biomass exposed to the fishery. We tested both models with  
338 one and two covariates, and did not use correlated covariates in the same model.

## 339 Results

### 340 Catches in prior seasons as explanatory variables

341 The monsoon catch models were compared against a “naive” model which was the “last year’s catch”  
342 model (Table 2). The “naive” model has no estimated parameters and is a standard null model for

343 time series modeling. Models with  $\ln(N_{t-1})$  (post-monsoon catch in prior year), whether linear or non-  
344 linear, as explanatory covariate were strongly supported over the naive model and over models with  
345  $\ln(S_{t-1})$  (monsoon catch in prior year) as the explanatory variable. Addition of the catch two years  
346 prior,  $\ln(N_{t-2})$  or  $\ln(S_{t-2})$ , did not reduce AIC and for  $\ln(N_{t-2})$  led to either no decrease in the residual  
347 error (MASE) or an increased the residual error for the model with linearity (Table 2, Linearity test).  
348 Addition of  $\ln(S_{t-2})$  did decrease the residual errors, but the was not warranted given the increased  
349 number of estimated parameters based on AIC. We also tested the support for non-linearity in the effect  
350 of the prior year catch on the monsoon catch. This was done by comparing models with  $\ln(N_{t-1})$  or  
351  $\ln(S_{t-1})$  included as a linear term or as a non-linear function  $s()$  (Table 2, Linearity test). The residual  
352 error decreased using a non-linear response at the cost increased degrees of freedom. The result was  
353 only weak (non-significant) support for allowing a non-linear response based on AIC and the F-test. The  
354 full set of models tested, including tests using catch during the spawning months in previous seasons as  
355 a covariate are shown in Tables A1 and A2. The results were the same if we used the full landings data  
356 set from 1956 to 2015 (Table A3). Overall, the landings in prior seasons was only weakly explanatory  
357 for the monsoon catch, and the maximum adjusted  $R^2$  for these models was less than 30% (Table 2).

358 The results on model structure were similar for models of the post-monsoon landings ( $N_t$ ) during  
359 the post-summer monsoon months (Table 3), but the models explained much more of the variance  
360 (adjusted  $R^2 = 57.0$ ). The most supported model for  $N_t$  (Table 3) used a non-linear response to landings  
361 during the post-monsoon months of the previous season  $\ln(N_{t-1})$  with a non-linear response to quarter  
362 3 landings two years prior  $\ln(S_{t-2})$ . There was low support for including landings earlier than two  
363 seasons prior or for using the quarter 3 landings during in the immediately prior season (Tables A4, A5,  
364 and A6). We did not test models for the October-June catch using the quarter 3 (July-September) catch  
365 in the current fishing season, so immediately prior. These data would not be available in a forecasting  
366 setting as the data require time to process.

## 367 Environmental covariates as explanatory variables

368 There was no support for using precipitation during the summer monsoon (June-July) or pre-monsoon  
369 period (April-May) as an explanatory variable for the quarter 3 (July-September) or post-monsoon  
370 (October-March) catch (hypotheses S1 and S2; Tables B1 and B2). This was the case whether pre-  
371 precipitation in the current or previous season was used, if precipitation was included as non-linear or  
372 non-linear effect, and if either precipitation during monsoon (June-July) or pre-monsoon (April-May)  
373 were used as the covariate. Quarter 3 overlaps with the spawning period and precipitation is often  
374 thought to trigger spawning, however we were unable to find any consistent association of catch during  
375 these spawning and early-post spawning months with precipitation. Raja (1974) posited that the appro-  
376 priate time period for the affect of rainfall is the weeks before and after the new moon when spawning  
377 is postulated to occur and not the total rainfall during the monsoon season. Thus the lack of correlation

378 may be due to using too coarse of a time average for the precipitation.

379       The sea-surface temperature before spawning (March-May) has been speculated to be correlated  
380 with successful egg development and spawning behavior (hypothesis S4 and S5) and extreme heat events  
381 pre-spawning have been associated with low recruitment. This suggests that March-May in the current  
382 and prior years should be associated with low catch. The sea-surface temperature during larval and early  
383 juvenile development (October-December) may affect survival and growth in multiple ways and thus  
384 could correlate with biomass in future years (hypothesis L1). However we found no support for either  
385 of these SST variates as explanatory variables for the July-September catch and only weak support  
386 (based on AIC) for March-May SST in the current season for explaining variability in post-monsoon  
387 catch. The fall average SST in the prior season did not explain variability in either July-September or  
388 October-March catch. See Tables B3 and B4.

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

391       Instead we found with the covariates indirectly and directly associated with productivity and food  
392 availability: upwelling intensity and surface chlorophyll. The correlation between landings and up-  
393 welling was only found for upwelling in the current season. No correlation was found when we used the  
394 upwelling index from the prior season. The correlation between landings and upwelling was found for  
395 both July-September and October-March landings and with either upwelling index: average nearshore  
396 SST along the Kerala coast during June-September or the average SST nearshore versus offshore dif-  
397 ferential (UPW) off Kochi in June-September (Table 4, Table B3 and Table B4). These two upwelling  
398 indices are correlated but not identical. The model with average June-September nearshore SST was  
399 more supported than the model using the SST differential off Kochi. For July-September catch, this  
400 model with a non-linear response had an adjusted  $R^2$  of 41.0 versus an adjusted  $R^2$  of 24.4 for the  
401 model with no covariates (Table B3), and for October-March catch, the adjusted  $R^2$  was 61.8 versus  
402 56.6 (Table B4). Note, that this covariate is June-September in the current season and overlaps with the  
403 July-September catch. Thus this model cannot be used to forecast July-September catch but does help  
404 us understand what factors may be influencing catch during the monsoon.

405       Chlorophyll-a density is speculated to be an important predictor of larval sardine survival and  
406 growth. In addition, sardines shoal in response to coastal chlorophyll blooms, which brings them in  
407 contact with the coastal fisheries. Thus chlorophyll-a density is assumed to be an important driver of  
408 future or current sardine catches. We had chlorophyll-a remote sensing data only from 1998 onward.  
409 Our simplest covariate model required 5 degrees of freedom, thus we were limited in the analyses we  
410 could conduct. In addition, the years, 1998-2014, have relatively low variability in catch sizes; the  
411 logged catch sizes during this period range from 10-11 during quarter 3 and 11-12 during the other  
412 three quarters. Second degree polynomial models were fit (Appendix C) to the average log chlorophyll-  
413 a density in the current and prior season from quarter 3 (July-September), 4 (October-December), and  
414 1 (January-March). Chlorophyll-a density was not a significant predictor for the July-September catch

415 for any of the tested combinations of current or prior season and quarter. The only significant effect was  
416 seen for post-summer monsoon catches using chlorophyll-a density in October-December of the prior  
417 season (Table C1). This is in contrast to the results with monsoon upwelling indices, which found a  
418 correlation with the current season but not prior seasons.

419 The strongest correlation however was found with the multi-year average sea surface temperature  
420 for the nearshore waters off Kerala (latitude 8 to 11). The average sea surface temperature over multiple  
421 prior years has been found to be correlated with sardine recruitment in Pacific sardines (Checkley Jr.  
422 et al., 2017; Jacobson & MacCall, 1995; Lindegren et al., 2013) and southern African sardines (D.  
423 C. Boyer, Boyer, Fossen, & Kreiner, 2001). We tested as a model covariate the average SST for 2.5  
424 years prior to the July-September catch, so January-June in the current calendar year and the two prior  
425 calendar years for a 30-month average. This covariate can be used for forecasting since it does not  
426 overlap with either July-September or October-March catch. This variate with a non-linear response  
427 was best covariate for both the July-September and the post-monsoon catch. For post-monsoon catch,  
428 the model with SST had an adjusted  $R^2$  of 67.5 versus 56.6 without. For the July-September catch, the  
429 adjusted  $R^2$  was 41.0 with SST and 24.4 without. The response curve was step-like with a negative  
430 effect at low temperatures and then an positive flat effect at higher temperatures (Figure 6). This is  
431 similar to the step-response found in studies of the correlation between average SST and recruitment in  
432 Pacific sardines (Jacobson & MacCall, 1995).

## 433 Discussion

434 Sardines in all the world's ecosystems exhibit large fluctuations in abundance (Baumgartner, Soutar,  
435 & Ferreira-Bartrina, 1992). These small forage fish are strongly influenced by natural variability in  
436 the ocean environment. Upwelling, influenced by both large-scale forces such as regimes shifts and  
437 El Ni~{n}o/Southern Oscillation patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010) and by  
438 seasonal wind and current patterns, brings nutrient rich and oxygen rich waters to the surface. This  
439 drives the seasonal variability in phytoplankton resources and in turn sardine prey (A. Bakun, Roy, &  
440 Lluch-Cota, 2008). Local variability in temperature, salinity, and oxygen levels have both direct and  
441 indirect on sardine reproduction, recruitment and survival (Checkley Jr. et al., 2017). Sardines are  
442 also influenced by competition and predation by other species and well-known for their sensitivity to  
443 over-fishing which has been linked to many fishery collapses (V. Kripa et al., 2018).

444 Many studies on Pacific sardines have looked at the correlation between ocean temperature (SST)  
445 and recruitment. Temperature can have direct effect on larval survival and growth and an indirect effect  
446 on food availability. Studies in the California Current System, have found that SST explains year-to-year  
447 variability in Pacific sardine recruitment (Checkley Jr., Alheit, Oozeki, & Roy, 2009; Checkley Jr. et  
448 al., 2017; Jacobson & MacCall, 1995; Lindegren & Checkley Jr., 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 the most variability in catch both in the monsoon and post-monsoon months. McClatchie et al. (2010) found no SST relationship with SST and Pacific sardine recruitment, however their analysis used a linear relationship while the other studies, and ours, that found a relationship (Checkley Jr. et al., 2017; Jacobson & MacCall, 1995) allowed a non-linear relationship. Both Jacobson and MacCall (1995) and Checkley et al. (2017) found a step-like response function for temperature: below a threshold value the effect of temperature was linear and above the threshold, the effect was flat and at lower temperatures the effect was negative and became positive as temperature increased. Our analysis found a similar pattern with a negative effect when the 2.5-year average temperature was below 28.35°C and positive above and with the positive effect leveling off above 28.5°C (Figure 6).

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

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

483 **Conclusions**

484 Remote sensing satellites can be used to detect changes in ocean physical, biological and chemical  
485 properties, such as surface temperature, winds, surface height, surface waves, rainfall and surface salin-  
486 ity, as well as the ecosystem and water quality changes. Unlike in-situ measurements, environmental  
487 measures from remote-sensing can be acquired rapidly and over large regions. However, which envi-  
488 ronmental covariates will improve forecasts is not obvious from oil-sardine life-history alone. We tested  
489 using many of the covariates known or suspected to have a effect on sardine spawning, growth and sur-  
490 vival: precipitation, upwelling indices, ocean temperature and chlorophyll-a in various critical months  
491 of the sardine life-cycle. We found that the multi-year average nearshore ocean temperature explained  
492 the most variability in the landings. This covariate is not as directly tied to stages of the oil-sardine  
493 life-cycle as the other covariates we tested, though it does integrate over multiple influences (upwelling  
494 strength and temperature) over multiple years.

495 The temperature of the Western Indian Ocean, of which the Southeast Arabian Sea is a part, has  
496 been increasing over the last century at a rate higher than any other tropical ocean (Roxy, Ritika, Ter-  
497 ray, & Masson, 2014) and the warming has been most extreme during the summer monsoon months.  
498 This ocean climate change is affecting oil sardine distributions with significant landings now occurring  
499 north of Goa (E. Vivekanandan, Rajagopalan, & Pillai, 2009). Continued warming is expected to affect  
500 the productivity of the region via multiple pathways, including both the direct effects of temperature  
501 change on the physiology and behavior of organisms and a multiple of indirect effects (Moustahfid,  
502 Marsac, & Grangopadhyay, 2018). These indirect effects includes changes to salinity, oxygen con-  
503 centrations, currents, wind patterns, ocean stratification and upwelling spatial patterns, phenology, and  
504 intensity. Incorporating environmental covariates into landings forecasts has the potential to improve  
505 fisheries management for small pelagics such as oil sardines in the face of a changing ocean environment  
506 (Haltuch et al., 2019; Tommasi et al., 2016). However, monitoring forecast performance and covariate  
507 performance in models will be crucial as a changing ocean environment may also change the association  
508 between landings and average sea surface temperature.

509 **References**

- 510 Adler, R., Wang, J.-J., Sapiano, M., Huffman, G., Chiu, L., Xie, P. P., ... Program, N. C. (2016).  
511 *Global Precipitation Climatology Project (GPCP) Climate Data Record (CDR), version 2.3 (monthly)*  
512 [Report]. <https://doi.org/10.7289/V56971M6>
- 513 Alheit, J., & Hagen, E. (1997). Long-term climate forcing of European herring and sardine popu-  
514 lations [Journal Article]. *Fisheries Oceanography*, 6, 130–139. <https://doi.org/10.1046/>

- 515 j.1365-2419.1997.00035.x
- 516 Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., ... Wagner, C. (2012).  
517 Climate variability drives anchovies and sardines into the North and Baltic Seas [Journal Article].  
518 *Progress in Oceanography*, 96, 128–139. [https://doi.org/https://doi.org/10.1016/j.pocean.2011.11.015](https://doi.org/10.1016/j.pocean.2011.11.015)
- 519 Annigeri, G. G. (1969). Fishery and biology of the oil sardine at Karwar [Journal Article]. *Indian*  
520 *Journal of Fisheries*, 16(1/2), 35–50.
- 521 Antony Raja, B. T. (1964). Some aspects of spawning biology of Indian oil sardine Sardinella  
522 longiceps Valenciennes [Journal Article]. *Indian Journal of Fisheries*, 11(1), 45–120.
- 523 Antony Raja, B. T. (1969). Indian oil sardine [Journal Article]. *CMFRI Bulletin*, 16, 1–142.
- 524 Antony Raja, B. T. (1970). Estimation of age and growth of the Indian oil sardine, Sardinella  
525 longiceps Val [Journal Article]. *Indian Journal of Fisheries*, 17(1&2), 26–42.
- 526 Antony Raja, B. T. (1974). Possible explanation for the fluctuation in abundance of the Indian oil  
527 sardine, Sardinella longiceps Valenciennes [Journal Article]. *Proceedings of the Indo-Pacific Fisheries*  
528 *Council*, 15(3), 241–252.
- 529 Bakun, A. (1996). *Patterns in the ocean: Ocean processes and marine population dynamics*  
530 [Book]. La Paz, Mexico: California Sea Grant, in cooperation with Centro de Investigaciones Biologi-  
531 cas del Noroeste.
- 532 Bakun, A., Roy, C., & Lluch-Cota, S. (2008). Coastal upwelling and other processes regulating  
533 ecosystem productivity and fish production in the western Indian Ocean [Book Section]. In K. Sherman,  
534 E. N. Okemwa, & M. J. Ntiba (Eds.), *Large marine ecosystems of the indian ocean : Assessment,*  
535 *sustainability and management* (pp. 103–141). Londres: Blackwell.
- 536 Baumgartner, T. R., Soutar, A., & Ferreira-Bartrina, V. (1992). Reconstruction of the history of  
537 the Pacific sardine and northern anchovy populations over the past two millennia from sediments of the  
538 Santa Barbara basin, California [Journal Article]. *CalCOFI Report*, 33, 24–40.
- 539 Bensam, P. (1964). Growth variations in the Indian oil sardine, Sardinella longiceps Valenciennes  
540 [Journal Article]. *Indian Journal of Fisheries*, 11 A(2), 699–708.
- 541 Boyer, D. C., Boyer, H. J., Fossen, I., & Kreiner, A. (2001). Changes in abundance of the northern  
542 Benguela sardine stock during the decade 1990 to 2000 with comments on the relative importance of  
543 fishing and the environment [Journal Article]. *South African Journal of Marine Science*, 23, 67–84.  
544 <https://doi.org/https://doi.org/10.2989/025776101784528854>
- 545 Chauhan, O. S., Raghavan, B. R., Singh, K., Rajawat, A. S., Kader, U., & Nayak, S. (2011).  
546 Influence of orographically enhanced SW monsoon flux on coastal processes along the SE Arabian Sea  
547 [Journal Article]. *Journal of Geophysical Research. Oceans*, 116(12), C12037. <https://doi.org/https://doi.org/10.1029/2010JC006854>

- 548 //doi.org/10.1029/2011JC007454
- 549 Checkley Jr., D. M., Alheit, J., Oozeki, Y., & Roy, C. (2009). *Climate change and small pelagic*  
550 *fish* [Edited Book]. [https://doi.org/https://doi.org/10.1017/CBO9780511596681](https://doi.org/10.1017/CBO9780511596681)
- 551 Checkley Jr., D. M., Asch, R. G., & Rykaczewski, R. R. (2017). Climate, anchovy, and sardine  
552 [Journal Article]. *Annual Review of Marine Science*, 9, 469–493. <https://doi.org/https://doi.org/10.1146/annurev-marine-122414-033819>
- 553 Chidambaram, K. (1950). Studies on the length frequency of oil sardine, *Sardinella longiceps* Cuv.  
554 & Val. and on certain factors influencing their appearance on the Calicut coast of the Madras Presidency  
555 [Journal Article]. *Proceedings of Indian Academy of Sciences*, 31, 352–286.
- 556 CMFRI. (1969). Marine fish production in India 1950-1968 [Journal Article]. *Bulletin of the*  
557 *Central Marine Fisheries Research Institute*, 13, 1–171.
- 558 CMFRI. (1995). Marine fish landings in India during 1985-93 [Journal Article]. *Marine Fisheries*  
559 *Information Service, Technical and Extension Series*, 136, 1–33.
- 560 CMFRI. (2016). *Marine fishery landings 1985-2015* [Report]. Central Marine Fisheries Research  
561 Institute.
- 562 Cohen, Y., & Stone, N. (1987). Multivariate time series analysis of the Canadian fisheries system  
563 in Lake Superior [Journal Article]. *Canadian Journal of Fisheries and Aquatic Sciences*, 44, 171–181.  
564 <https://doi.org/https://doi.org/10.1139/f87-321>
- 565 Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., & Verheyen,  
566 H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in  
567 “wasp-waist” ecosystems [Journal Article]. *ICES Journal of Marine Science*, 57(3), 603–618. <https://doi.org/https://doi.org/10.1006/jmsc.2000.0712>
- 568 Das, P. H. D., & Edwin, L. (2018). Temporal changes in the ring seine fishery of Kerala, India  
569 [Journal Article]. *Indian Journal of Fisheries*, 65(1), 47–54. <https://doi.org/https://doi.org/10.21077/ijf.2018.65.1.69105-08>
- 570 Farmer, N. A., & Froeschke, J. T. (2015). Forecasting for recreational fisheries management:  
571 What’s the catch? [Journal Article]. *North American Journal of Fisheries Management*, 35, 720–735.  
572 <https://doi.org/https://doi.org/10.1080/02755947.2015.1044628>
- 573 Georgakarakos, S., Doutsoubas, D., & Valavanis, V. (2006). Time series analysis and forecasting  
574 techniques applied on loliginid and ommastrephid landings in Greek waters [Journal Article]. *Fisheries*  
575 *Research*, 78, 55–71. <https://doi.org/https://doi.org/10.1016/j.fishres.2005.12.003>
- 576 George, G., Meenakumari, B., Raman, M., Kumar, S., Vethamony, P., Babu, M. T., & Verlecar,  
577 X. (2012). Remotely sensed chlorophyll: A putative trophic link for explaining variability in Indian oil

- 581 sardine stocks [Journal Article]. *Journal of Coastal Research*, 28(1A), 105–113. <https://doi.org/https://doi.org/10.2112/JCOASTRES-D-10-00070.1>
- 583 Habeebrehman, H., Prabhakaran, M. P., Jacob, J., Sabu, P., Jayalakshmi, K. J., Achuthankutty, C.  
584 T., & Revichandran, C. (2008). Variability in biological responses influenced by upwelling events in the  
585 eastern Arabian Sea [Journal Article]. *Journal of Marine Systems*, 74, 545–560. <https://doi.org/https://doi.org/10.1016/j.jmarsys.2008.04.002>
- 587 Haltuch, M. A., Brooks, E. N., Brodziak, J., Devine, J. A., Johnson, K. F., Klibansky, N., . . . Wells,  
588 B. K. (2019). Unraveling the recruitment problem: A review of environmentally-informed forecasting  
589 and management strategy evaluation [Journal Article]. *Fisheries Research*, 217, 198–216. <https://doi.org/https://doi.org/10.1016/j.fishres.2018.12.016>
- 591 Hanson, P. J., Vaughan, D. S., & Narayan, S. (2006). Forecasting annual harvests of Atlantic and  
592 Gulf menhaden [Journal Article]. *North American Journal of Fisheries Management*, 26.3, 753–764.  
593 <https://doi.org/https://doi.org/10.1577/M04-096.1>
- 594 Hornell, J. (1910). Report on the results of a fishery cruise along the Malabar coast and to the  
595 Laccadive Islands in 1908 [Journal Article]. *Madras Fishery Bulletin*, 4(4), 76–126.
- 596 Hornell, J., & Nayudu, M. R. (1923). A contribution to the life history of the Indian sardine with  
597 note, on the plankton of the Malabar coast [Journal Article]. *Madras Fishery Bulletin*, 17, 129.
- 598 Jacob, T., Rajendran, V., Pillai, P. K. M., Andrews, J., & Satyavan, U. K. (1987). *An appraisal of  
599 the marine fisheries in Kerala* [Report]. Central Marine Fisheries Research Institute.
- 600 Jacobson, L. D., & MacCall, A. D. (1995). Stock-recruitment models for Pacific sardine  
601 (*Sardinops sagax*) [Journal Article]. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 566–577.  
602 <https://doi.org/https://doi.org/10.1139/f95-057>
- 603 Jayaprakash, A. A. (2002). Long term trends in rainfall, sea level and solar periodicity: A case  
604 study for forecast of Malabar sole and oil sardine fishery [Journal Article]. *Journal of the Marine  
605 Biological Association of India*, 44(1 & 2), 163–175.
- 606 Jayaprakash, A. A., & Pillai, N. G. K. (2000). The Indian oil sardine [Book Section]. In V. N.  
607 Pillai & N. G. Menon (Eds.), *Marine fisheries research and management* (pp. 259–281). Kerala, India:  
608 Central Marine Fisheries Research Institute.
- 609 Jayaram, C., Chacko, N., Joseph, K. A., & Balchand, A. N. (2010). Interannual variability of  
610 upwelling indices in the southeastern Arabian Sea: A satellite based study [Journal Article]. *Ocean  
611 Science Journal*, 45(1), 27–40. <https://doi.org/https://doi.org/10.1007/s12601-010-0003-6>
- 612 Kothawale, D. R., & Rajeevan, M. (2017). *Monthly, seasonal and annual rainfall time series for  
613 all-India, homogeneous regions and meteorological subdivisions: 1871-2016* [Report]. Indian Institute

- 614 of Tropical Meteorology.
- 615 Kripa, V., Mohamed, K. S., Koya, K. P. S., Jeyabaskaran, R., Prema, D., Padua, S., ... Vishnu, P.  
616 G. (2018). Overfishing and climate drives changes in biology and recruitment of the Indian oil sardine  
617 *Sardinella longiceps* in southeastern Arabian sea [Journal Article]. *Frontiers in Marine Science*, 5,  
618 Article 443. [https://doi.org/https://doi.org/10.3389/fmars.2018.00443](https://doi.org/10.3389/fmars.2018.00443)
- 619 Krishnakumar, P. K., Mohamed, K. S., Asokan, P. K., Sathianandan, T. V., Zacharia, P. U., Ab-  
620 durahiman, K. P., ... Durgekar, N. R. (2008). How environmental parameters influenced fluctuations  
621 in oil sardine and mackerel fishery during 1926-2005 along the south-west coast of India? [Journal  
622 Article]. *Marine Fisheries Information Service, Technical and Extension Series*, 198, 1–5.
- 623 Lawer, E. A. (2016). Empirical modeling of annual fishery landings [Journal Article]. *Natural  
624 Resources*, 7, 193–204. [https://doi.org/https://doi.org/10.4236/nr.2016.74018](https://doi.org/10.4236/nr.2016.74018)
- 625 Lindegren, M., & Checkley Jr., D. M. (2012). Temperature dependence of Pacific sardine  
626 (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised [Journal  
627 Article]. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(2), 245–252. <https://doi.org/https://doi.org/10.1139/cjfas-2012-0211>
- 629 Lindegren, M., Checkley, D. M., Rouyer, T., MacCall, A. D., & Stenseth, N. C. (2013). Climate,  
630 fishing, and fluctuations of sardine and anchovy in the California Current [Journal Article]. *Proceedings  
631 of the National Academy of Sciences*, 110(33), 13672–13677. <https://doi.org/https://doi.org/10.1073/pnas.1305733110>
- 633 Lloret, J., Lleonart, J., & Sole, I. (2000). Time series modelling of landings in Northwest Mediter-  
634 ranean Sea [Journal Article]. *ICES Journal of Marine Science*, 57, 171–184. <https://doi.org/https://doi.org/10.1006/jmsc.2000.0570>
- 636 Longhurst, A. R., & Wooster, W. S. (1990). Abundance of oil sardine (*Sardinella longiceps*) and  
637 upwelling on the southwest coast of India [Journal Article]. *Canadian Journal of Fisheries and Aquatic  
638 Sciences*, 47(12), 2407–2419. <https://doi.org/https://doi.org/10.1139/f90-268>
- 639 Madhupratap, M., Gopalakrishnan, T. C., Haridas, P., & Nair, K. K. C. (2001). Mesozooplankton  
640 biomass, composition and distribution in the Arabian Sea during the fall intermonsoon: Implications  
641 of oxygen gradients [Journal Article]. *Deep Sea Research Part II: Topical Studies in Oceanography*,  
642 48(6), 1345–1368. [https://doi.org/https://doi.org/10.1016/S0967-0645\(00\)00142-9](https://doi.org/https://doi.org/10.1016/S0967-0645(00)00142-9)
- 643 Madhupratap, M., Shetye, S. R., Nair, K. N. V., & Nair, S. R. S. (1994). Oil sardine and Indian  
644 mackerel: Their fishery, problems and coastal oceanography [Journal Article]. *Current Science*, 66(5),  
645 340–348. <https://doi.org/https://doi.org/10.1029/2004GL019652>
- 646 McClatchie, S., Goericke, R., Auad, G., & Hill, K. (2010). Re-assessment of the stock-recruit  
647 and temperature-recruit relationships for Pacific sardine (*Sardinops sagax*) [Journal Article]. *Canadian*

- 648     *Journal of Fisheries and Aquatic Sciences*, 67(11), 1782–1790. <https://doi.org/https://doi.org/10.1139/F10-101>
- 650     Mendelssohn, R. (1981). Using Box-Jenkins models to forecast fishery dynamics: Identification,  
651     estimation and checking [Journal Article]. *Fishery Bulletin*, 78, 887–896.
- 652     Menon, N. N., Sankar, S., Smitha, A., George, G., Shalin, S., Sathyendranath, S., & Platt, T.  
653     (2019). Satellite chlorophyll concentration as an aid to understanding the dynamics of Indian oil sardine  
654     in the southeastern Arabian Sea [Journal Article]. *Marine Ecology Progress Series*, 617-618, 137–147.  
655     <https://doi.org/https://doi.org/10.3354/meps12806>
- 656     Moustahfid, H., Marsac, F., & Grangopadhyay, A. (2018). Climate change impacts, vulnerabilities  
657     and adaptations: Western Indian ocean marine fisheries [Book Section]. In M. Barange, T. Bahri, M.  
658     C. M. Beveridge, K. L. Cochrane, S. Funge-Smith, & F. Poulain (Eds.), *Impacts of climate change  
659     on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options* (pp.  
660     251–280). Rome: FAO Fisheries; Aquaculture Technical Paper No. 627.
- 661     Murty, A. V. S., & Edelman, M. S. (1966). On the relation between the intensity of the south-west  
662     monsoon and the oil-sardine fishery of India [Journal Article]. *Indian Journal of Fisheries*, 13(1 & 2),  
663     142–149.
- 664     Naidu, P. D., Kumar, M. R. R., & Babu, V. R. (1999). Time and space variations of monsoonal  
665     upwelling along the west and east coasts of India [Journal Article]. *Continental Shelf Research*, 19(4),  
666     559–572. [https://doi.org/https://doi.org/10.1016/S0278-4343\(98\)00104-6](https://doi.org/https://doi.org/10.1016/S0278-4343(98)00104-6)
- 667     Nair, P. G., Joseph, S., Kripa, V., Remya, R., & Pillai, V. N. (2016). Growth and maturity of  
668     Indian oil sardine *Sardinella longiceps* (Valenciennes, 1847) along southwest coast of India [Journal  
669     Article]. *Journal of Marine Biological Association of India*, 58(1), 64–68. <https://doi.org/https://doi.org/10.6024/jmbai.2016.58.1.1899-07>
- 671     Nair, R. V. (1952). Studies on the revival of the Indian oil sardine fishery [Journal Article]. *Proceedings of Indo-Pacific Fisheries Council*, 2, 1–15.
- 673     Nair, R. V. (1959). Notes on the spawning habits and early life-history of the oil sardine, *Sardinella  
674     longiceps* Cuv. & Val [Journal Article]. *Indian Journal of Fisheries*, 6(2), 342–359.
- 675     Nair, R. V., & Subrahmanyam, R. (1955). The diatom, *Fragilaria oceanica* Cleve, an indicator of  
676     abundance of the Indian oil sardine, *Sardinella longiceps* Cuv. and Val. [Journal Article]. *Current  
677     Science*, 24(2), 41–42.
- 678     NCEI. (2017). *Global Precipitation Climatology Project Monthly Product Version 2.3* [Report].  
679     Retrieved from National Centers for Environmental Information website: <https://www.ncei.noaa.gov/data/global-precipitation-climatology-project-gpcp-monthly/access/>
- 681     Nobel, A., & Sathianandan, T. V. (1991). Trend analysis in all-India mackerel catches using

- 682 ARIMA models [Journal Article]. *Indian Journal of Fisheries*, 38(2), 119–122.
- 683 Pillai, V. N. (1982). *Physical characteristics of the coastal waters off the south-west coast of India with an attempt to study the possible relationship with sardine, mackerel and anchovy fisheries* (Thesis).
- 685 Pillai, V. N. (1991). Salinity and thermal characteristics of the coastal waters off southwest coast of  
686 India and their relation to major pelagic fisheries of the region [Journal Article]. *Journal of the Marine  
687 Biological Association of India*, 33(1&2), 115–133.
- 688 Piontkovski, S., Al Oufi, H., & Al Jufaily, S. (2015). Seasonal and interannual changes of Indian  
689 oil sardine, *Sardinella longiceps*, landings in the governorate of Muscat (the Sea of Oman) [Journal  
690 Article]. *Marine Fisheries Review*, 76, 48–58. <https://doi.org/https://doi.org/10.7755/MFR.76.3.3>
- 691 Prabhu, M. S., & Dhulkhed, M. H. (1967). On the occurrence of small-sized oil sardine *Sardinella*  
692 *longiceps* Val. [Journal Article]. *Current Science*, 35(15), 410–411.
- 693 Prabhu, M. S., & Dhulkhed, M. H. (1970). The oil sardine fishery in the Mangalore zone during  
694 the seasons 1963-64 and 1967-68 [Journal Article]. *Indian Journal of Fisheries*, 17, 57–75.
- 695 Prista, N., Diawara, N., Costa, M. J., & Jones, C. (2011). Use of SARIMA models to assess data-  
696 poor fisheries: A case study with a sciaenid fishery off Portugal [Journal Article]. *Fisheries Bulletin*,  
697 109, 170–185.
- 698 Raghavan, B. R., Deepthi, T., Ashwini, S., Shylini, S. K., Kumarswami, M., Kumar, S., & Lotlike,  
699 A. A. (2010). Spring inter monsoon algal blooms in the Eastern Arabian Sea: Shallow marine encounter  
700 off Karwar and Kumbla coast using a hyperspectral radiometer [Journal Article]. *International Journal  
701 of Earth Sciences and Engineering*, 3(6), 827–832.
- 702 Rohit, P., Sivadas, M., Abdussamad, E. M., Margaret Muthu Rathinam, A., Koya, K. P. S., Ganga,  
703 U., ... Supraba, V. (2018). *Enigmatic Indian oil sardine: An insight* [Report]. ICAR-Central Marine  
704 Fisheries Research Institute.
- 705 Roxy, M. K., Ritika, K., Terray, P., & Masson, S. (2014). The curious case of Indian Ocean  
706 warming [Journal Article]. *Journal of Climate*, 27(22), 8501–8509. <https://doi.org/https://doi.org/10.1175/JCLI-D-14-00471.1>
- 708 Rykaczewski, R. R., & Checkley, D. M. (2008). Influence of ocean winds of the pelagic ecosystem  
709 in upwelling regions [Journal Article]. *Proceedings of the National Academy of Science*, 105(6), 1965–  
710 1970. <https://doi.org/https://doi.org/10.1073/pnas.0711777105>
- 711 Schaaf, W. E., Sykes, J. E., & Chapoton, R. B. (1975). Forecasts of Atlantic and Gulf menhaden  
712 catches based on the historical relation of catch and fishing effort [Journal Article]. *Marine Fisheries  
713 Review*, 37, 5–9.
- 714 Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., ...  
715 Zuzunaga, J. Z. (2010). Worldwide large-scale fluctuations of sardine and anchovy populations [Journal

- 716 Article]. *South African Journal of Marine Science*, 21(1), 289–347. <https://doi.org/https://doi.org/10.2989/025776199784125962>
- 718 Simons, R. A. (2017). *ERDDAP*. <https://coastwatch.pfeg.noaa.gov/erddap> [Report]. Monterey,  
719 CA: NOAA/NMFS/SWFSC/ERD.
- 720 Smitha, B. R. (2010). *Coastal upwelling of the south eastern Arabian Sea — an integrated ap-*  
721 *proach* (Thesis).
- 722 Smitha, B. R., Sanjeevan, V. N., Vimalkumar, K. G., & Revichandran, C. (2008). On the upwelling  
723 of the southern tip and along the west coast of India [Journal Article]. *Journal of Coastal Research*,  
724 24(4C), 95–102. <https://doi.org/https://doi.org/10.2112/06-0779.1>
- 725 Srinath, M. (1998). Exploratory analysis on the predictability of oil sardine landings in Kerala  
726 [Journal Article]. *Indian Journal of Fisheries*, 45(4), 363–374.
- 727 Srinath, M., Kuriakose, S., & Mini, K. G. (2005). Methodology for estimation of marine fish  
728 landings in India [Book Section]. In *CMFRI special publications* (Vol. 86, p. 57). Central Marine  
729 Fisheries Research Institute.
- 730 Stergiou, K. I., & Christou, E. D. (1996). Modeling and forecasting annual fisheries catches:  
731 Comparison of regression, univariate and multivariate time series methods [Journal Article]. *Fisheries*  
732 *Research*, 25(2), 105–138. [https://doi.org/https://doi.org/10.1016/0165-7836\(95\)00389-4](https://doi.org/https://doi.org/10.1016/0165-7836(95)00389-4)
- 733 Supraba, V., Dineshbabu, A. P., Thomas, S., Rohit, P., Rajesh, K. M., & Zacharia, P. U. (2016).  
734 Climate influence on oil sardine and Indian mackerel in southeastern Arabian sea [Journal Article].  
735 *International Journal of Development Research*, 6(8), 9152–9159.
- 736 Takasuka, A., Oozeki, Y., & Aoki, I. (2007). Optimal growth temperature hypothesis: Why do  
737 anchovy flourish and sardine collapse or vice versa under the same ocean regime? [Journal Article].  
738 *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 768–776. <https://doi.org/https://doi.org/10.1139/f07-052>
- 740 Thara, K. J. (2011). *Response of eastern Arabian Sea to extreme climatic events with special*  
741 *reference to selected pelagic fishes* (Thesis).
- 742 Tommasi, D., Stock, C. A., Pegion, K., Vecchi, G. A., Methot, R. D., Alexander, M. A., & Jr., D. M.  
743 C. (2016). Improved management of small pelagic fisheries through seasonal climate prediction [Journal  
744 Article]. *Ecological Applications*, 27(2), 378–388. <https://doi.org/https://doi.org/10.1002/eap.1458>
- 745 Venugopalan, R., & Srinath, M. (1998). Modelling and forecasting fish catches: Comparison of re-  
746 gression, univariate and multivariate time series methods [Journal Article]. *Indian Journal of Fisheries*,  
747 45(3), 227–237.
- 748 Vivekanandan, E., Rajagopalan, M., & Pillai, N. G. K. (2009). Recent trends in sea surface tem-  
749 perature and its impact on oil sardine [Book Section]. In *Global climate change and indian agriculture*

- 750 (pp. 89–92).
- 751 Vivekanandan, E., Srinath, M., Pillai, V. N., Immanuel, S., & Kurup, K. N. (2003). Marine fisheries  
752 along the southwest coast of India [Book Section]. In G. Silvestre, L. Garces, I. Stobutzki, C. Luna, M.  
753 Ahmad, R. A. Valmonte-Santos, ... D. Pauly (Eds.), *Assessment, management, and future directions*  
754 *for coastal fisheries in Asian countries* (pp. 759–792). WorldFish Center, Penang.: WorldFish Center  
755 Conference Proceedings 67.
- 756 Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation  
757 of semiparametric generalized linear models. [Journal Article]. *Journal of the Royal Statistical Society*  
758 *B*, 73(1), 3–36. [https://doi.org/https://doi.org/10.1111/j.1467-9868.2010.00749.x](https://doi.org/10.1111/j.1467-9868.2010.00749.x)
- 759 Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.) [Book].  
760 Chapman; Hall/CRC.
- 761 Wood, S. N., Pya, N., & Safken, B. (2016). Smoothing parameter and model selection for general  
762 smooth models (with discussion) [Journal Article]. *Journal of the American Statistical Association*,  
763 111, 1548–1575. [https://doi.org/https://doi.org/10.1080/01621459.2016.1180986](https://doi.org/10.1080/01621459.2016.1180986)

764 **Figure Legends**

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

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

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

772 Figure 4. Remote sensing covariates used in the analysis. All data are monthly averages over Box  
773 4 in Figure 1 on the Kerala coast off of Kochi. Panel A) Upwelling Index. The upwelling index is  
774 the difference between the near-shore sea surface temperature (SST) and the off-shore SST defined as  
775 3 degrees longitude offshore. Panel B) Surface chlorophyll-a (CHL). The CHL data are only available  
776 from 1997 onward. Panel C) Sea surface temperature constructed from Advanced Very High Resolution  
777 Radiometer (AVHRR). Panel D) Average daily rainfall (mm/day) off the Kerala coast.

778 Figure 5. Key oil sardine life-history events overlaid on the monthly sea surface temperature in the  
779 nearshore and offshore and the nearshore chlorophyll density.

780 Figure 6. Effects of covariates estimated from the GAM models. Panel A) Effect of the 2.5  
781 year average nearshore SST on catch during the catch during July-September (late spawning and early  
782 post-spawning) months. Panel B) Effect of upwelling (inshore/off-shore SST differential) during June-  
783 September in the current season on July-September catch. The index is the difference between offshore  
784 and inshore SST, thus a negative value indicates warmer coastal surface water than off-shore. Panel C)  
785 Effect of the 2.5 year average nearshore SST on catch during the catch during October-March (post-  
786 monsoon, age-0, -1, -2 year fish). Panel D) Effect of upwelling (inshore/off-shore SST differential)  
787 during June-September in the current season on October-March catch. Strong upwelling (positive up-  
788 welling index) in the larval and juvenile high growth period (Oct-Dec) is associated with higher early  
789 survival and larger cohorts of age-0 fish in the catch.

790 Figure 7. Fitted versus observed catch with models with and without environmental covariates.  
791 Panel A) Fitted versus observed log catch in the spawning months with only non-spawning catch in the  
792 previous season as the covariate:  $S_t = s(N_{t-1}) + \varepsilon_t$ . Panel B) Fitted versus observed log catch in July-  
793 September with the 2.5-year average nearshore SST added as a covariate to the model in panel A. This  
794 model was:  $S_t = s(N_{t-1}) + s(V_t) + \varepsilon_t$ . Panel C) Fitted versus observed log catch in the post-monsoon  
795 months with only post-monsoon catch in the previous season and July-September catch two seasons  
796 prior as the covariates:  $N_t = s(N_{t-1}) + s(S_{t-2}) + \varepsilon_t$ . Panel D) Fitted versus observed log catch in the  
797 post-monsoon months with 2.5-year average nearshore SST ( $V$ ) added as covariates. This model was  
798  $N_t = s(N_{t-1}) + s(S_{t-2}) + s(V_t) + \varepsilon_t$ .

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-year ave. nearshore SST $N_t \sim$ 2.5-year 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).



Table 2. Model selection tests of time-dependency and linearity for the monsoon (Jul-Sep) catch model using F-tests and AIC of nested models fit to log of landings data.  $S_t$  is the catch during the monsoon (Jul-Sep) of season  $t$ .  $N_{t-1}$  is the post-monsoon (Oct-Mar) catch in the prior sardine season.  $N_{t-2}$  is the same for two seasons prior.  $s()$  is a non-linear function of the response variable. MASE is mean absolute squared error of the residuals. The tests are nested and the numbers before the models indicates the nest level. In the list with numbers 1, 2, 3a, 3b, two nested tests were done; one on 1, 2, 3a and one on 1, 2, 3b. A simple base model may be indicated as M0 or M1, and the nested model as M0 (or M1) + an extra component. See tables in Appendix A for the full set of time-dependency and linearity tests. This table only shows the nested model sets that were most supported. The top model based on smallest AIC is marked with an arrow.

Model	Residual df	MASE	Adj. R2	F	p value	AIC
Naive Model 1984-2015 data						
$\ln(S_t) = \ln(S_{t-1}) + \varepsilon_t$	32		1			122.85
AR-1 Model						
$\ln(S_t) = \alpha + \beta \ln(S_{t-1}) + \varepsilon_t$	30	0.814				114.14
Time dependency test						
1. $\ln(S_t) = \alpha + \ln(N_{t-1}) + \varepsilon_t$	31	0.856	14.2			111.78
2. M0 $\ln(S_t) = \alpha + \beta \ln(N_{t-1}) + \varepsilon_t$	30	0.794	22.2	4.06	0.053	109.59
3a. $\ln(S_t) = M0 + \beta_2 \ln(N_{t-2})$	29	0.797	19.6	0.01	0.919	111.57
3b. $\ln(S_t) = M0 + \beta_2 \ln(S_{t-2})$	29	0.778	20.8	0.45	0.508	111.09
Linearity and time-dependency test						
1. $\ln(S_t) = \alpha + \beta \ln(N_{t-1}) + \varepsilon_t$	30	0.794	22.2			109.59
$\Rightarrow$ 2. M1 $\ln(S_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$	28.6	0.761	24.4	1.26	0.287	109.52
3a. $\ln(S_t) = M1 + s(\ln(N_{t-2}))$	26.4	0.761	21.2	0.28	0.785	112.42
3b. $\ln(S_t) = M1 + s(\ln(S_{t-2}))$	25.9	0.724	26.3	1.09	0.367	110.63

Table 3. Model selection tests for the post-monsoon (Oct-Mar) catch model ( $N_t$ ) using F-tests and AIC.  $S_t$  is the catch during the monsoon (Jul-Sep).  $N_t$  is the catch during the post-monsoon period (Oct-Mar) of season  $t$ ; note the fishing season is defined as Jul-Jun not calendar year.  $S_{t-1}$  and  $N_{t-1}$  are the catch during the prior sardine season during and after the monsoon respectively.  $S_{t-2}$  and  $N_{t-2}$  are the same for two seasons prior. See Table 2 for more details.

Model	Residual df	MASE	Adj. R2	F	p value	AIC
Naive Model 1984-2014 data						
$\ln(N_t) = \ln(N_{t-1}) + \varepsilon_t$	31		1			90.87
Time dependency test						
1. $\ln(N_t) = \alpha + \beta \ln(S_{t-1}) + \varepsilon_t$	30	1.018	26.2			93.17
2. $\ln(N_t) = \alpha + \beta \ln(N_{t-1}) + \varepsilon_t$	28.6	0.978	37			88.28
Linearity and time-dependency test						
1. $\ln(N_t) = \alpha + \beta \ln(N_{t-1}) + \varepsilon_t$	29	0.978	37			88.28
2. M1 $\ln(N_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$	27.6	0.874	45	4.87	0.026	84.75
3a. $\ln(N_t) = M1 + s_2(\ln(N_{t-2}))$	25.4	0.805	46	1.09	0.357	86.11
$\Rightarrow$ 3b. $\ln(N_t) = M1 + s_2(\ln(S_{t-2}))$	24.8	0.743	57	11.05	0.007	79.53

Table 4. Top covariates for the monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch ( $S_t$  and  $N_t$ ) models. The models are nested; the number indicates the level of nestedness. Models at levels 2 and higher are shown with the component that is added to the base level model (M0 or M1) at top. The full set of covariate models tested are given in Appendix B. The fitted versus observed catches from the covariate models are shown in Figure 7.

Model	Residual df	MASE	Adj. R2	F	p value	AIC
Jul-Sep catch models with covariates						
$V_t$ = Jun-Sep SST current season						
$W_t$ = Jun-Sep UPW current season						
$Z_t$ = 2.5-year average SST						
1. M0 $\ln(S_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$	28.6	0.761	24			109.52
2a. $\ln(S_t) = M0 + s(V_t)$	25.9	0.683	41	3.84	0.025	103.43
2b. $\ln(S_t) = M0 + \beta W_t$	27.6	0.706	33	4.96	0.034	106.32
$\Rightarrow$ 2c. $\ln(S_t) = M1 + s(Z_t)$	23.7	0.641	47	5.43	0.01	101.65
Oct-Mar catch models with covariates						
$V_t$ = Mar-May SST current season						
$W_t$ = Jun-Sep upwelling current season						
$Z_t$ = 2.5-year average SST						
1. M1 $\ln(N_t) = \alpha + s(\ln(N_{t-1})) + s(\ln(S_{t-2})) + \varepsilon_t$	24.8	0.45	57			79.53
2a. $\ln(N_t) = M1 + s(V_t)$	22	0.413	63	2.53	0.089	76.01
2b. $\ln(N_t) = M1 + \beta W_t$	23.8	0.46	62	4.91	0.037	76
$\Rightarrow$ 2c. $\ln(N_t) = M1 + s(Z_t)$	22.7	0.36	67	4.98	0.016	71.88

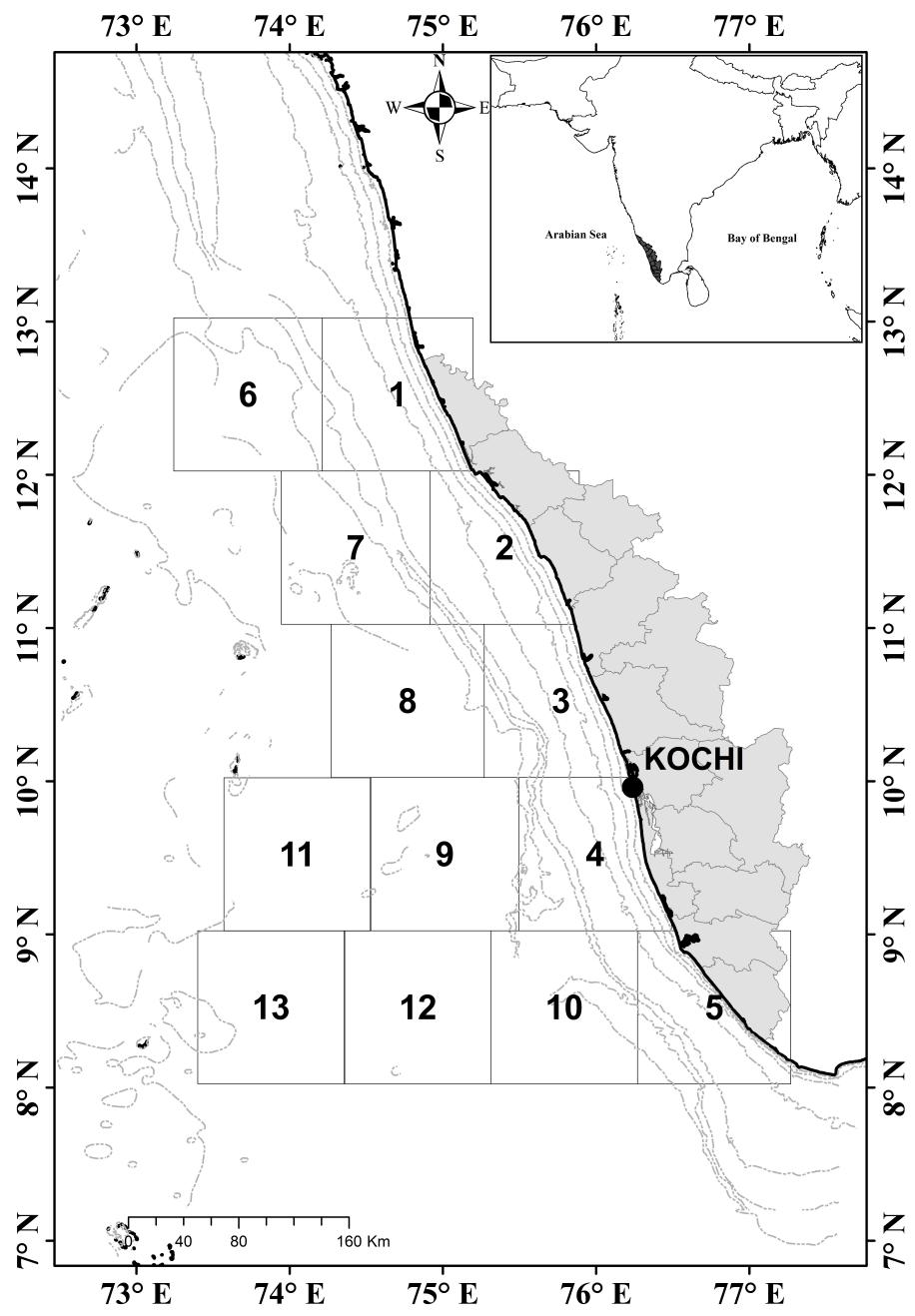


Figure 1

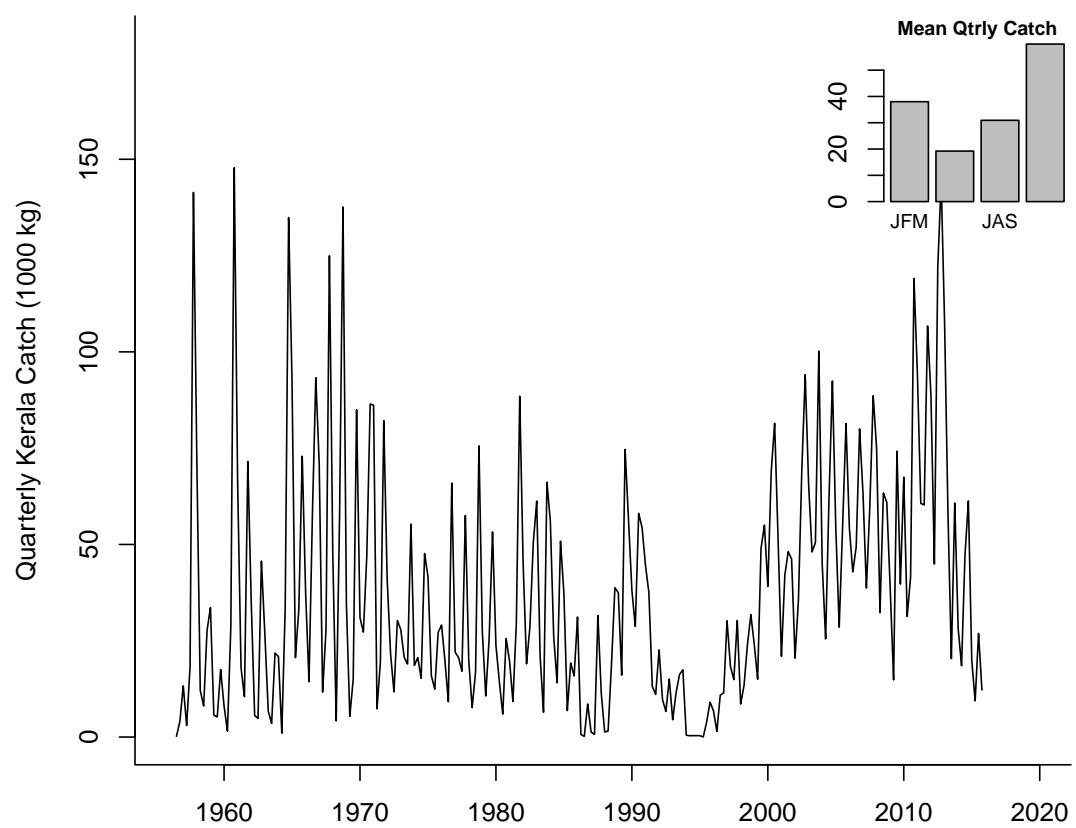


Figure 2

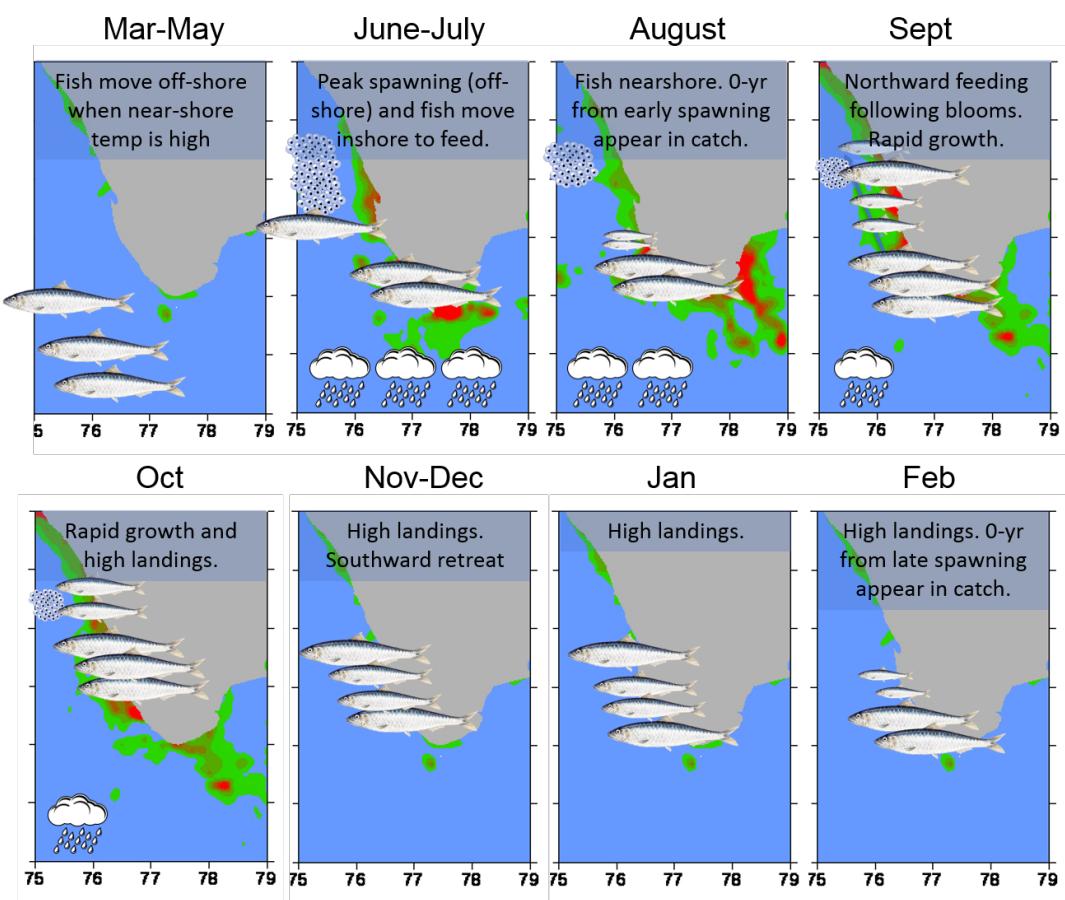


Figure 3

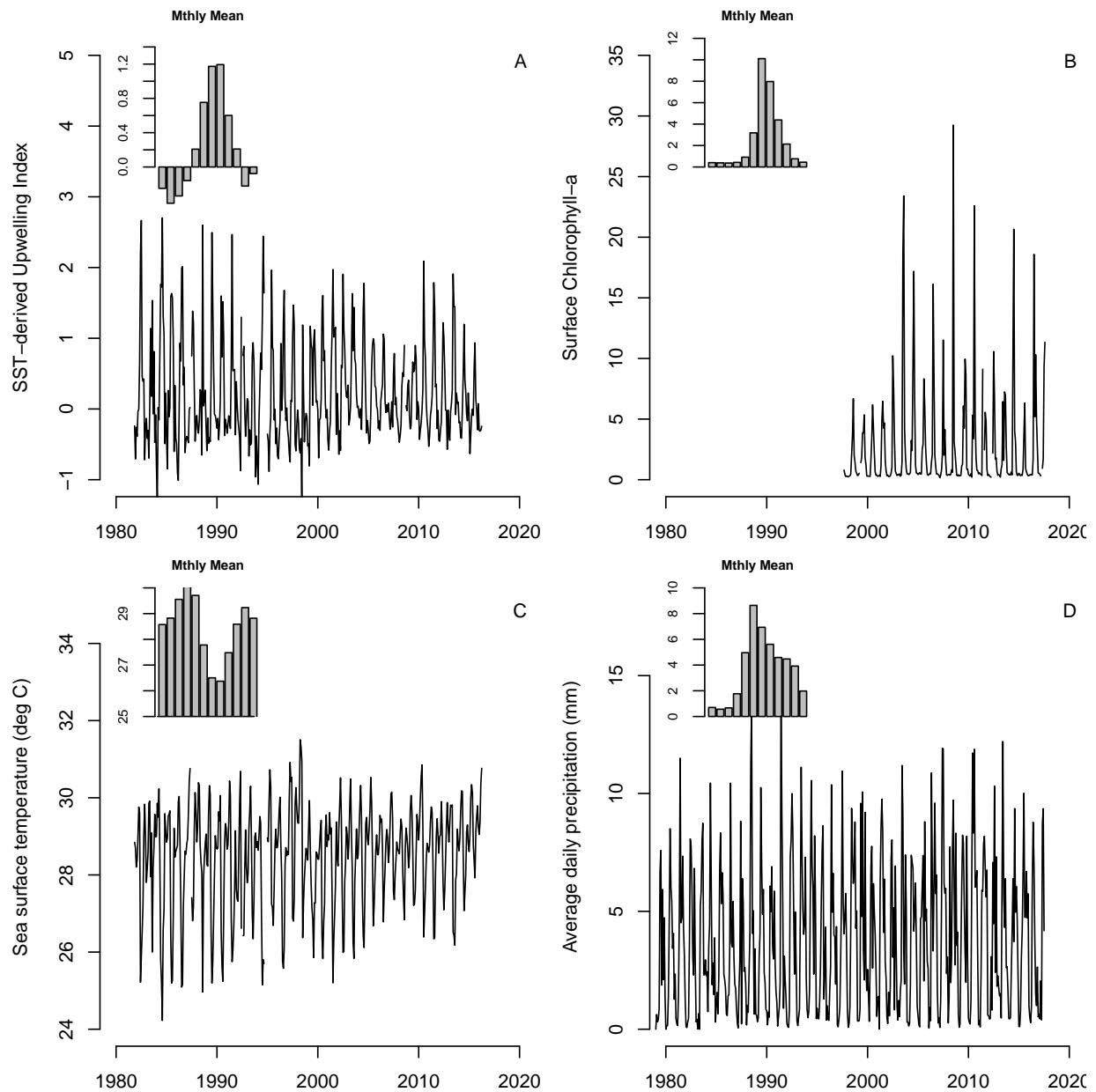
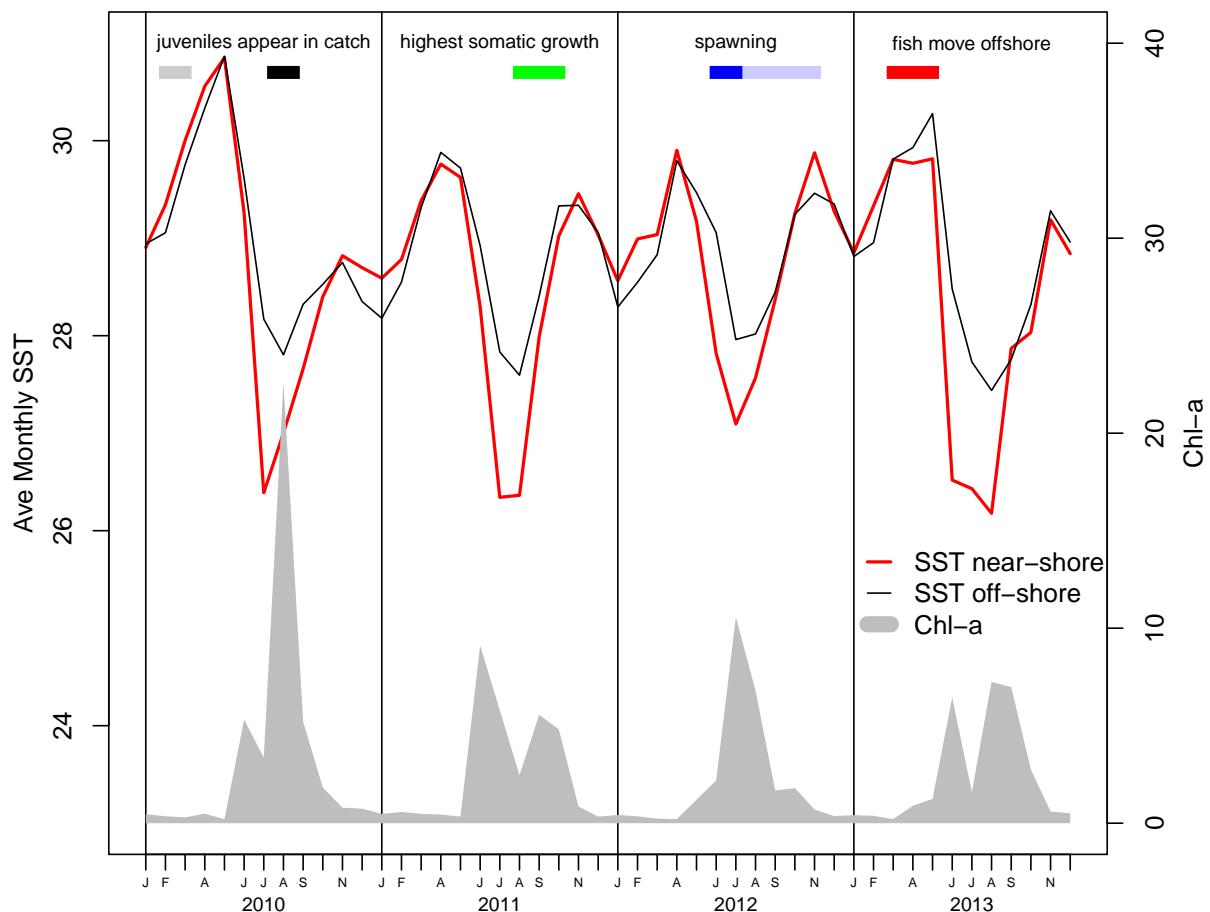


Figure 4



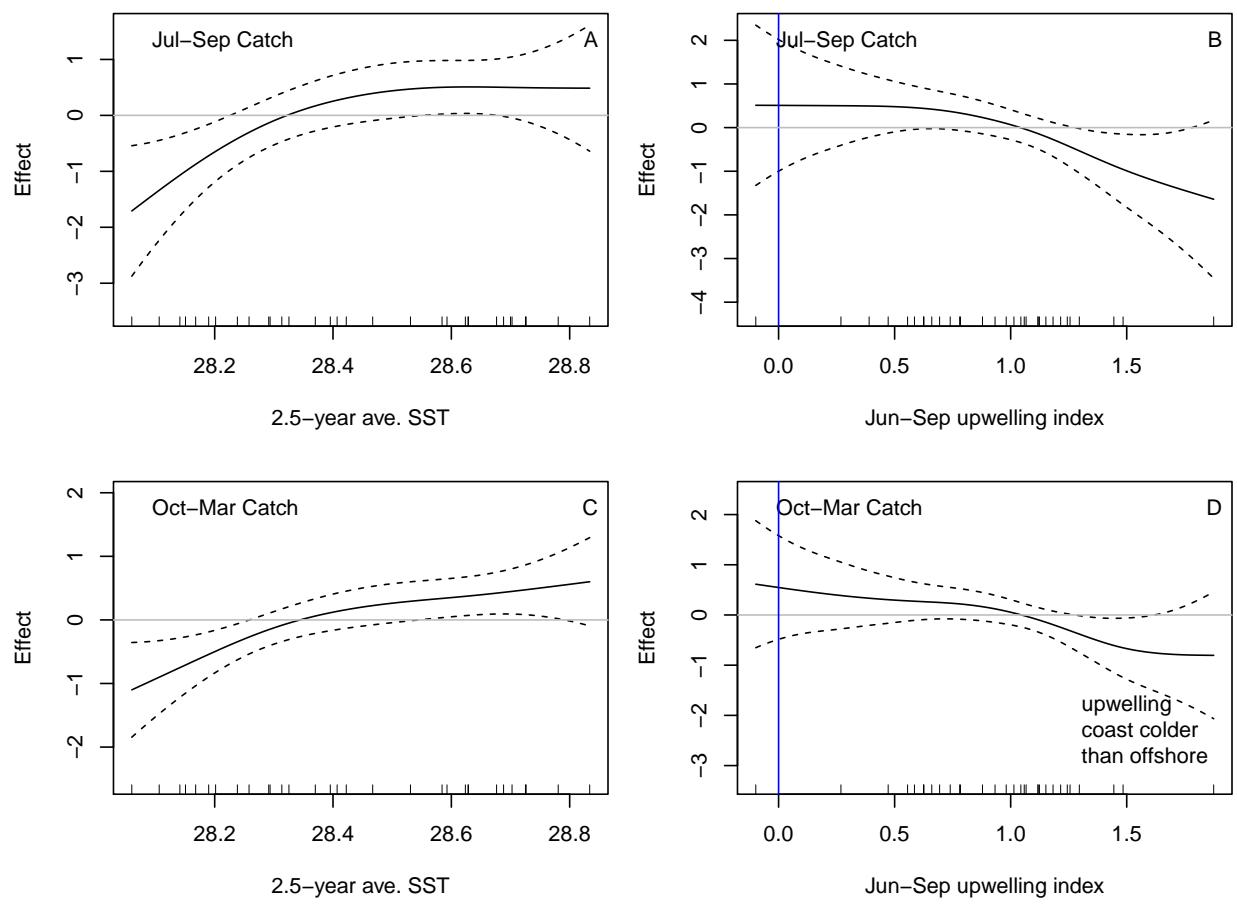


Figure 6

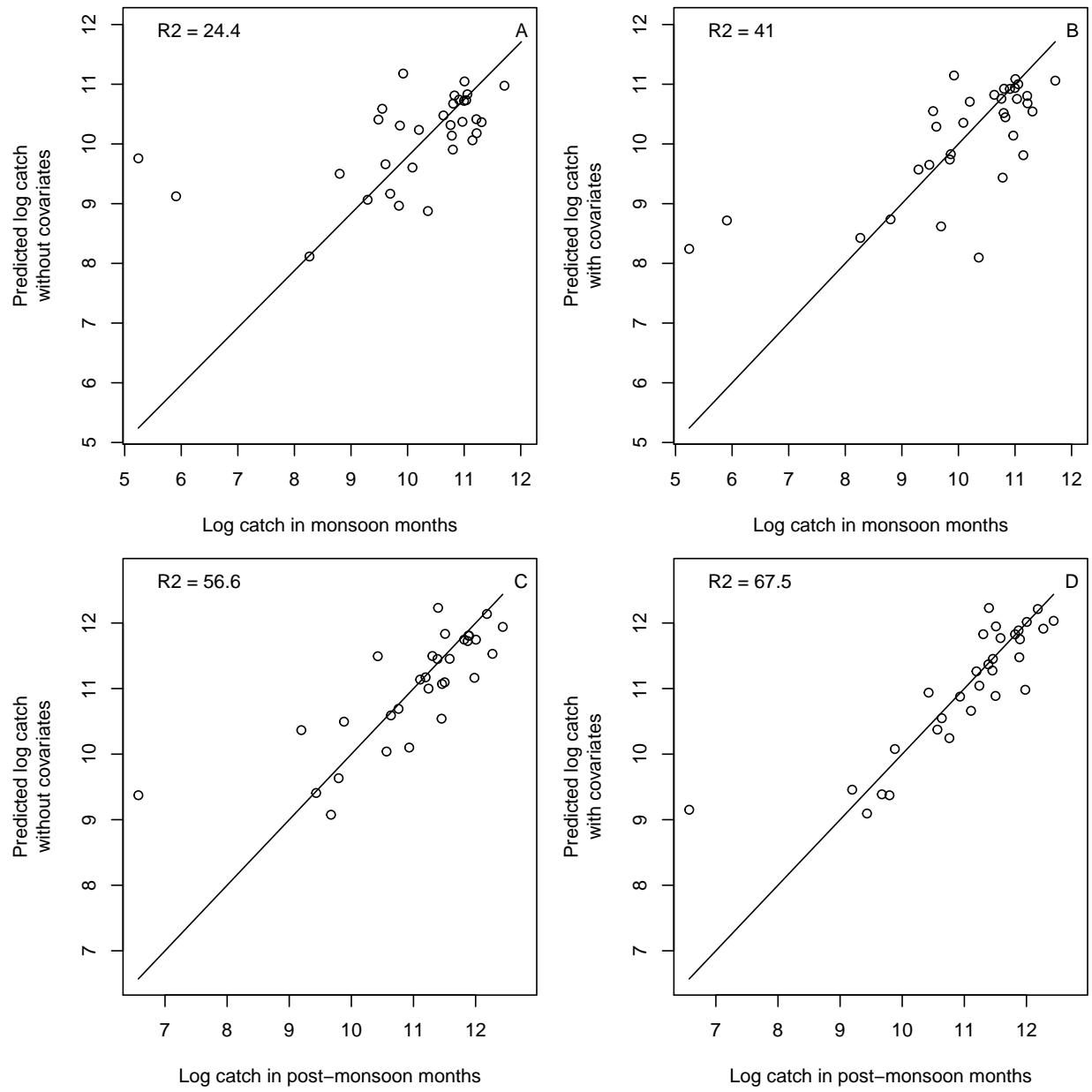


Figure 7