

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

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

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## Abstract

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

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

53 **Introduction**

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

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

81 The fishery was confined to nearshore waters, and thus migration of sardines  
82 in and out of the coastal zone greatly affected exposure to the fishery.

83 Researchers have examined a variety of environmental variables for their  
84 correlation with landings of the Indian oil sardine. Precipitation during the  
85 monsoon and the day of the monsoon arrival are thought to act as either a  
86 direct or indirect cue for spawning (Antony Raja, 1969, 1974; Jayaprakash,  
87 2002; Murty & Edelman, 1966; Pitchaikani & Lipton, 2012; Srinath, 1998; Xu  
88 & Boyce, 2009). Although many studies have looked for and some have found  
89 correlations between precipitation and landings, the reported relationships are  
90 positive in some studies and negative in others (Madhupratap et al., 1994).  
91 Researchers have also looked for and found correlations with various metrics  
92 of upwelling intensity (Jayaprakash, 2002; Longhurst & Wooster, 1990; Mad-  
93 hupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara, 2011),  
94 with direct measures of productivity such as nearshore zooplankton and phy-  
95 toplankton abundance (George et al., 2012; Hornell, 1910; Madhupratap et  
96 al., 1994; Menon et al., 2019; Nair, 1952; Nair & Subrahmanyam, 1955; Pi-  
97 ontkovski et al., 2015; Pitchaikani & Lipton, 2012), and with near-shore sea  
98 surface temperature (SST) (Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed,  
99 1970; Supraba et al., 2016). SST can affect both somatic growth rates and ju-  
100 venile survival but also can cause fish to move off-shore and away from the  
101 shore-based fishery. The multi-year average sea temperature is postulated to  
102 have effects on recruitment and the survival of larval and juvenile sardines,  
103 which affect the later overall abundance (Checkley et al., 2017; Takasuka et  
104 al., 2007). The El Niño/Southern Oscillation (ENSO) has a cascading effect  
105 on all the aforementioned environmental parameters (SST, precipitation, up-  
106 welling) which in turn impact oil sardines, and correlations have been found  
107 between ENSO indices and landings (Rohit et al., 2018; Supraba et al., 2016)  
108 and coastal anoxia events (Vallivattathillam et al., 2017).

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

Modeling and forecasting landings data using statistical models fit to annual or seasonal catch time series has a long tradition in fisheries and has been applied to many species (Cohen & Stone, 1987; Farmer & Froeschke, 2015; Georgakarakos et al., 2006; Hanson et al., 2006; Lawer, 2016; Lloret et al., 2000; Mendelssohn, 1981; Nobel & Sathianandan, 1991; Prista et al., 2011; Stergiou & Christou, 1996), including oil sardines (Srinath, 1998; Venugopalan & Srinath, 1998). These models can be used to 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 covaraites, 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 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.

<sup>167</sup> The project objective is to develop a operational forecast of sardine landings,  
<sup>168</sup> to be used by the Indian fishery industry for planning.

<sup>169</sup> **Study Area**

<sup>170</sup> Our analysis focuses on the Kerala coast (Figure 1) region of India, where  
<sup>171</sup> the majority of the Indian oil sardines are landed and where oil sardines com-  
<sup>172</sup> prise ca. 40% of the marine fish catch (Srinath, 1998; Vivekanandan et al.,  
<sup>173</sup> 2003). This area is in the Southeast Arabian Sea (SEAS), one of world's major  
<sup>174</sup> upwelling zones, with seasonal peaks in primary productivity driven by up-  
<sup>175</sup> welling caused by winds during the Indian summer monsoon (Habeebrehman  
<sup>176</sup> et al., 2008; Madhupratap et al., 2001) between June and September. Within  
<sup>177</sup> the SEAS, the coastal zone off Kerala between 9°N to 13°N has especially in-  
<sup>178</sup> tense upwelling due to the combined effects of wind stress and remote forcing  
<sup>179</sup> (BR, 2010; BR et al., 2008). The result is a strong temperature differential be-  
<sup>180</sup> tween the near-shore and off-shore and high primary productivity and surface  
<sup>181</sup> chlorophyll in this region during summer and early fall (BR, 2010; Chauhan  
<sup>182</sup> et al., 2011; Habeebrehman et al., 2008; Jayaram et al., 2010; Madhupratap  
<sup>183</sup> et al., 2001; Raghavan et al., 2010). The primary productivity peaks subside  
<sup>184</sup> after September while mesozooplankton abundances increase and remain high  
<sup>185</sup> in the post-monsoon period (Madhupratap et al., 2001).

<sup>186</sup> **Oil sardine life cycle and fishery**

<sup>187</sup> The Indian oil sardine fishery is restricted to the narrow strip of the western  
<sup>188</sup> India continental shelf, within 20 km from the shore (Figure 1). The yearly cy-  
<sup>189</sup> cle (Figure 3) of the fishery begins at the start of spawning during June to July,  
<sup>190</sup> corresponding with the onset of the southwest monsoon (Antony Raja, 1969;  
<sup>191</sup> Chidambaran, 1950) when the mature fish migrate from offshore to coastal

192 spawning areas. The spawning begins during the southwest monsoon period  
193 when temperature, salinity and suitable food availability are conducive for lar-  
194 val survival (Chidambaram, 1950; Jayaprakash & Pillai, 2000; Krishnakumar  
195 et al., 2008; Murty & Edelman, 1966; Nair et al., 2016). Although peak spawn-  
196 ing occurs in June to July, spawning continues into September (Antony Raja,  
197 1969; Hornell, 1910; Hornell & Nayudu, 1923; Prabhu & Dhulkhed, 1970)  
198 and early- and late-spawning cohorts are evident in the length distributions of  
199 the 0-year fish. Spawning occurs in shallow waters outside of the traditional  
200 range of the fishery (Antony Raja, 1964), and after spawning the adults migrate  
201 closer to the coast and the spent fish become exposed to the fishery.

202 After eggs are spawned, they develop rapidly into larvae (Nair, 1959). The  
203 phytoplankton bloom that provide sardine larvae food is dependent upon nu-  
204 trient influx from coastal upwelling and runoff from rivers during the summer  
205 monsoon and early fall. The blooms start in the south near the southern tip  
206 of India in June, increase in intensity and spread northward up the coast (BR,  
207 2010). Variation in the bloom initiation time and intensity leads to changes in  
208 the food supply and to corresponding changes in the growth and survival of  
209 larvae and in the later recruitment of 0-year sardines into the fishery (George  
210 et al., 2012). Oil sardines grow rapidly during their first few months, and 0-  
211 year fish (40mm to 100mm) from early spawning appear in the catch in August  
212 and September in most years (Antony Raja, 1970; Nair et al., 2016). As the  
213 phytoplankton bloom spreads northward, the oil sardines follow, and the oil  
214 sardine fishery builds from south to north during the post-monsoon period. Oil  
215 sardines remain inshore feeding throughout the winter months, until March to  
216 May when the inshore waters warm considerably and sardines move off-shore  
217 to deeper waters (Chidambaram, 1950). Catches of sardines are correspond-  
218 ingly low during this time for all size classes. The age at first maturity occurs  
219 at approximately 150 mm size (Nair et al., 2016), which is reached within one  
220 year. When the summer monsoon returns, the oil sardine cycle begins anew.

221 Catches along the Kerala coast are high throughout the year except during  
222 quarter 2, April-June (Figure 2). The age-distribution caught by the fishery  
223 varies through the year. The fishery is closed during June to mid-July during  
224 the monsoon and peak spawning, and when it resumes in mid-July, it is first  
225 dominated by 1-2.5 year old mature fish (Antony Raja, 1969; Bensam, 1964;  
226 Nair et al., 2016). In August or September a spike of 0-year (40mm) juveniles  
227 from the June spawning typically appears in the catch (Antony Raja, 1969; Nair  
228 et al., 2016) and another spike of 0-year fish is sometimes seen in February  
229 from the late fall spawning (Prabhu & Dhulkhed, 1967, 1970). From October  
230 through June, the catch is dominated by fish from 120mm-180mm (Antony  
231 Raja, 1970; Nair et al., 2016; Prabhu & Dhulkhed, 1970) which is a mix of  
232 0-year, 1-year and 2-year fish (Nair et al., 2016; Rohit et al., 2018).

233 **Contrast between catch modeling versus biomass modeling**

234 Detailed yearly effort data for the individual gears is not available for the entire  
235 catch time series and the data available on size of the fleet are a coarse metric  
236 of effort and thus are difficult to use to compute catch-per-unit effort statistics.  
237 Nonetheless the number of boats and fishers involved in the fishery has been  
238 increasing as the population in Kerala has increased. Oil sardines are caught  
239 primarily by ring seines, which were introduced in the early 1980s. Ring seines  
240 of different sizes are used both by traditional small boats with a small out-  
241 board motor and large mechanized ships (Das & Edwin, 2018). Since 1985,  
242 the ring seine fishery has expanded steadily in terms of horsepower, size of  
243 boats, length of nets. There are concerns that overfishing and especially catch  
244 of juveniles, which are at times discarded (Das & Edwin, 2018) is a factor in  
245 the most recent oil sardine declines (Kripa et al., 2018).

246 The relationship between the oil landings and the stock abundance is com-  
247 plex. It depends both on the fleet size and composition, but also depends on

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

## Materials and Methods

### Sardine landing data

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

<sup>274</sup> tributes a remarkable 14.4% of the total marine production (CMFRI, 2017) and  
<sup>275</sup> Major resources contributing to the pelagic landings were oilsardine (57.4%).  
<sup>276</sup> The quarterly landings (metric tons) for oil sardine landed from all gears in  
<sup>277</sup> Kerala were obtained from CMFRI reports (1956-1984) and online databases  
<sup>278</sup> (1985-2015) (CMFRI, 1969, 1995, 2016; Jacob et al., 1987; Pillai, 1982). The  
<sup>279</sup> quarterly landing data were log-transformed to stabilize the variance. Yearly  
<sup>280</sup> effort data for the individual gears is not available for the entire catch time se-  
<sup>281</sup> ries and the data available on size of the fleet are a coarse metric of effort and  
<sup>282</sup> thus are difficult to use to compute catch-per-unit effort stastistics. However  
<sup>283</sup> the goal in this study is to describe and forecast landings, not biomass, and our  
<sup>284</sup> analysis uses landings data as is standard in landings modeling.

## <sup>285</sup> **Remote sensing data**

<sup>286</sup> We analysed monthly composites of the following environmental data derived  
<sup>287</sup> from satellite data: sea surface temperature (SST), chlorophyll-a (CHL), up-  
<sup>288</sup> welling (UPW), the Oceanic Niño Index (ONI) and precipitation. The monthly  
<sup>289</sup> means of the covariate time series are shown in Figure 4.

<sup>290</sup> For sea surface temperature, we used Advanced Very-High Resolution  
<sup>291</sup> Radiometer (AVHRR) data, which provides accurate nearshore SST values.  
<sup>292</sup> Although the ICOADS product provides SST values for earlier years, ICOADS  
<sup>293</sup> does not provide accurate nearshore temperatures. For 1981 to 2003, we used  
<sup>294</sup> the Pathfinder Version 5.2 product on a 0.0417 degree grid. These data  
<sup>295</sup> were developed by the Group for High Resolution Sea Surface Temperature  
<sup>296</sup> (GHRSST) and served by the US National Oceanographic Data Center. For  
<sup>297</sup> 2004 to 2016, we used the NOAA CoastWatch SST products derived from  
<sup>298</sup> NOAA's Polar Operational Environmental Satellites (POES).

<sup>299</sup> For chlorophyll-a, we used the chlorophyll-a products developed by  
<sup>300</sup> the Ocean Biology Processing Group in the Ocean Ecology Laboratory at

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

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

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

329 data are available from 1979 forward (NCEI, 2017). The land and nearshore  
330 ocean precipitation data are highly correlated (Appendix E), supporting the use  
331 of the land time series as a proxy for the precipitation over the ocean off the  
332 Kerala coast.

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

## 339 **Hypotheses**

340 Our statistical analyses were structured around specific hypotheses (Table 1)  
341 concerning which remote sensing covariates in which months should correlate  
342 with landings in specific quarters. These hypotheses were based on biologi-  
343 cal information concerning how environmental conditions affect sardine sur-  
344 vival and recruitment and affect exposure of Indian oil sardines to the coastal  
345 fishery as reviewed in the introduction. The quarter 3 (Jul-September) catch  
346 overlaps the summer monsoon and the main spawning months. This is also  
347 the quarter where small 0-year fish from early spawning (June) often appear  
348 in the catch, sometimes in large numbers. Variables that affect or are corre-  
349 lated with movement of sardines inshore should be correlated with quarter 3  
350 landings. In addition, pre-spawning (March-May) environmental conditions  
351 should be correlated with the spawning strength as adult oil sardines experi-  
352 ence an acceleration of growth during this period along with egg development.  
353 The post-monsoon catch (October-May) is a mix of 0-year fish (less than 12  
354 months old) and mature fish (greater than 12 months old). Variables that are  
355 correlated with spawning strength and larval and juvenile survival should cor-

<sup>356</sup> relate with the post-monsoon catch both in the current year and in future years,  
<sup>357</sup> one to two years after.

<sup>358</sup> Our hypotheses (Table 1) focus mainly on two drivers: upwelling and  
<sup>359</sup> ocean temperature. We also test hypotheses concerning precipitation as this  
<sup>360</sup> has historically been an environmental covariate considered to influence the  
<sup>361</sup> timing of oil sardine landings. More recently, researchers have highlighted the  
<sup>362</sup> influence of large-scale ocean processes, specifically the El Niño/Southern Os-  
<sup>363</sup> cillation, on sardine fluctuations; therefore we test the Ocean Niño Index (ONI)  
<sup>364</sup> also. Chlorophyll density is directly correlated with sardine food availability  
<sup>365</sup> and chlorophyll fronts are known to influence sardine shoaling. However our  
<sup>366</sup> chlorophyll time series is short (1997-2015) and the statistical power for test-  
<sup>367</sup> ing correlation with landings is low. Tests of chlorophyll are shown in the  
<sup>368</sup> appendices but are not the focus of our analyses.

## <sup>369</sup> Statistical models

<sup>370</sup> We modeled the catches during the late-monsoon season (quarter 3, July-  
<sup>371</sup> September) separately from the post-monsoon season (October-March). Thus  
<sup>372</sup> there is no seasonality in our catch time series, as we analyzed a yearly time se-  
<sup>373</sup> ries of quarter 3 catches separately from a yearly time series of post-monsoon  
<sup>374</sup> catches. We divided the catch in this way for biological and statistical reasons.  
<sup>375</sup> Catch in quarter 3 (July-September) captures a mix of spawning age fish as it  
<sup>376</sup> overlaps with the tail end of the spawning season, is affected by a fishery clo-  
<sup>377</sup> sure from July to mid-August during the summer monsoon, and is periodically  
<sup>378</sup> inflated by the appearance of small 0-year fish from early summer spawning.  
<sup>379</sup> In addition, the covariates that affect the timing of spawning, movement of  
<sup>380</sup> post-spawning mature fish inshore, and early egg and larval survival may be  
<sup>381</sup> different than those that affect later growth, survival and shoaling that exposes  
<sup>382</sup> fish to the inshore fishery. Analyzing catch and covariate time series without

383 seasonality also had an important statistical benefit—we removed the problem  
384 of seasonality in the catch and all the covariates. The oil sardine life-cycle  
385 is seasonal and driven by the strong seasonality in this monsoon influenced  
386 system. A simple statistical model with quarters will explain much of the  
387 quarterly catch data since most of the yearly variability is due to seasonality  
388 and any environmental covariate with a similar seasonality will also show  
389 high correlation with the landings. Our goal was to explain year-to-year  
390 variability thus eliminating the confounding effect of seasonality in the data  
391 was important.

392 We tested ARIMA models on both monsoon (Jul-Sep) and post-monsoon  
393 (Oct-Mar) catch time series and found little support for auto-regressive errors  
394 (ARIMA models with a MA component) based on diagnostic tests of the resid-  
395 uals and model selection. The best supported ARIMA models were simple AR  
396 models ( $x_t = bx_{t-1} + \varepsilon_t$ ). This lack of strong autocorrelation in residuals has  
397 been found in other studies that tested ARIMA models for forecasting small  
398 pelagic catch (Stergiou & Christou, 1996). We thus used AR-only models,  
399 however we tested both linear and non-linear models using generalized addi-  
400 tive models (GAMs, Wood, 2017) of the form  $x_t = s(x_{t-1}) + \varepsilon_t$  and tested time-  
401 varying linear models with dynamic linear models (DLM). GAMs allow one  
402 to model the effect of a covariate as a flexible non-linear function while DLMs  
403 allow one to allow the effect of the covariate to vary over time. It was known  
404 that the effects of the environmental covariates were likely to be non-linear,  
405 albeit in an unknown way. Our GAM approach is analogous to that taken by  
406 Jacobson and MacCall (1995) in a study of the effects of SST on Pacific sardine  
407 recruitment.

408 The first step in our analysis was to determine the catch model: the model  
409 for current catch as a function of the past catch. We explored four classes of  
410 models: null models with a simple function of prior catch, linear regressive

411 models with one to two years of prior catch, dynamic linear models (DLM)  
 412 which allow the regression parameters to vary (Holmes et al., 2012, using the  
 413 MARSS package in R), and GAMs to allow the effect of prior catch to be  
 414 non-linear. One feature of GAMs is that they allow the smoothing parameter  
 415 of the response curve to be estimated. We fixed the smoothing parameter at  
 416 an intermediate value so that smooth responses were achieved. Multi-modal  
 417 or overly flexible response curves would not be realistic for our application.  
 418 We fit GAMs with smooth terms represented by penalized regression splines  
 419 (Wood, 2011, using the mgcv package in R) and fixed the smoothing term at  
 420 an intermediate value (sp=0.6).

421 We compared the following catch models:

- 422 • null:  $\ln(C_{i,t}) = \ln(C_{j,t-1})$
- 423 • random walk:  $\ln(C_{i,t}) = \alpha + \ln(C_{j,t-1}) + \varepsilon_t$
- 424 • linear AR-1:  $\ln(C_{i,t}) = \alpha + \phi \ln(C_{j,t-1}) + \varepsilon_t$
- 425 • linear AR-2:  $\ln(C_{i,t}) = \alpha + \phi_1 \ln(C_{j,t-1}) + \phi_2 \ln(C_{k,t-2}) + \varepsilon_t$
- 426 • DLM AR-1:  $\ln(C_{i,t}) = \alpha_t + \phi_t \ln(C_{j,t-1}) + \varepsilon_t$
- 427 • GAM AR-1:  $\ln(C_{i,t}) = \alpha + s(\ln(C_{j,t-1})) + \varepsilon_t$
- 428 • GAM AR-2:  $\ln(C_{i,t}) = \alpha + s_1(\ln(C_{j,t-1})) + s_2(\ln(C_{k,t-2})) + \varepsilon_t$

429  $\ln(C_{i,t})$  is the log catch in the current year  $t$  in season  $i$ . We modeled two  
 430 different catches: monsoon catch  $S_t$  (July-September), which is during the late  
 431 part of the summer monsoon, and post-monsoon catch  $N_t$  (October-June). The  
 432 catches were logged to stabilize and normalize the variance.  $s()$  is a non-linear  
 433 function estimated by the GAM algorithm. The model is primarily statistical,  
 434 meaning it should not be thought of as being a population growth model. We  
 435 tested models with prior year post-monsoon catch ( $N_{t-1}$ ) and 3rd quarter catch  
 436 ( $S_{t-1}$ ) as the explanatory catch variable.  $S_t$  was not used as a predictor for  
 437  $N_t$ ;  $S_t$  is the quarter immediately prior to  $N_t$  and would not be available for

438 a forecast model since time is required to process landings data. The catch  
439 models were fit to 1982 to 2015 catch data, corresponding to the years where  
440 the SST, upwelling and precipitation data were available. F-tests and AIC on  
441 nested sets of models (Wood et al., 2016) were used to evaluate the support for  
442 the catch models and later for the covariate models. After selection of the best  
443 model with the 1982-2015 data, the fitting was repeated with the 1956-1981  
444 and 1956-2015 catch data to confirm the form of the catch models.

445 Once the catch models were determined, the covariates were studied in-  
446 dividually and then jointly. As with the catch models, F-tests, AIC and LOO  
447 (leave-one-out cross-validation) on nested sets of models were used to eval-  
448 uate the support for models with covariates. The smoothing term was fixed  
449 at an intermediate value ( $sp=0.6$ ) instead of treated as an estimated variable.  
450 Our models for catch with covariates typically took the form  $\ln(C_{i,t}) = M +$   
451  $s_1(V_{1,t}) + s_2(V_{2,t-1}) + \varepsilon_t$  or  $\ln(C_{i,t}) = M + \beta_1 V_{1,t} + \beta_2 V_{2,t-1} + \varepsilon_t$  where  $M$  was  
452 the best catch model from step 1. Thus models with covariates modeled both as  
453 a linear and non-linear effect were compared. The covariates tested are those  
454 discussed in the section on covariates that have been hypothesized to drive the  
455 size of the sardine biomass exposed to the fishery. We tested both models with  
456 one and two covariates, and did not use correlated covariates in the same model.

## 457 Results

### 458 Catches in prior seasons as explanatory variables

459 The monsoon catch models were compared against a “naive” model which was  
460 the “last year’s catch” model (Table 2). The “naive” model has no estimated  
461 parameters and is a standard null model for time series modeling. Models  
462 with  $\ln(N_{t-1})$  (post-monsoon catch in prior year), whether linear or non-linear,  
463 as explanatory covariate were strongly supported over the naive model and

over models with  $\ln(S_{t-1})$  (monsoon catch in prior year) as the explanatory variable. Addition of the catch two years 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 error (MASE) or an increased the residual error for the model with linearity (Table 2, Linearity test). Addition of  $\ln(S_{t-2})$  did decrease the residual errors, but the was not warranted given the increased number of estimated parameters based on AIC. We also tested the support for non-linearity in the effect of the prior year catch on the monsoon catch. This was done by comparing models with  $\ln(N_{t-1})$  or  $\ln(S_{t-1})$  included as a linear term or as a non-linear function  $s()$  (Table 2, Linearity test). The residual error decreased using a non-linear response at the cost increased degrees of freedom. The result was only weak (non-significant) support for allowing a non-linear response based on AIC and the F-test. The full set of models tested, including tests using catch during the spawning months in previous seasons as a covariate are shown in Tables A1 and A2. The results were the same if we used the full landings data set from 1956 to 2015 (Table A3). Overall, the landings in prior seasons was only weakly explanatory for the monsoon catch, and the maximum adjusted  $R^2$  for these models was less than 30% (Table 2).

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

493 require time to process.

494 **Environmental covariates as explanatory variables**

495 There was no support for using precipitation during the summer monsoon  
496 (June-July) or pre-monsoon period (April-May) as an explanatory variable for  
497 the quarter 3 (July-September) or post-monsoon (October-March) catch (hy-  
498 potheses S1 and S2; Tables B1 and B2). This was the case whether precipita-  
499 tion in the current or previous season was used, if precipitation was included  
500 as non-linear or non-linear effect, and if either precipitation during monsoon  
501 (June-July) or pre-monsoon (April-May) were used as the covariate. Quar-  
502 ter 3 overlaps with the spawning period and precipitation is often thought to  
503 trigger spawning, however we were unable to find any consistent association  
504 of catch during these spawning and early-post spawning months with precip-  
505 itation. Raja (1974) posited that the appropriate time period for the affect of  
506 rainfall is the weeks before and after the new moon when spawning is postu-  
507 lated to occur and not the total rainfall during the monsoon season. Thus the  
508 lack of correlation may be due to using too coarse of a time average for the  
509 precipitation.

510 The sea-surface temperature before spawning (March-May) has been spec-  
511 ulated to be correlated with successful egg development and spawning behavior  
512 (hypothesis S4 and S5) and extreme heat events pre-spawning have been asso-  
513 ciated with low recruitment. This suggests that March-May in the current and  
514 prior years should be associated with low catch. The sea-surface temperature  
515 during larval and early juvenile development (October-December) may affect  
516 survival and growth in multiple ways and thus could correlate with biomass in  
517 future years (hypothesis L1). However we found no support for either of these  
518 SST variates as explanatory variables for the July-September catch and only  
519 weak support (based on AIC) for March-May SST in the current season for

520 explaining variability in post-monsoon catch. The fall average SST in the prior  
521 season did not explain variability in either July-September or October-March  
522 catch. See Tables B3 and B4.

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

525 Instead we found with the covariates indirectly and directly associated with  
526 productivity and food availability: upwelling intensity and surface chlorophyll.  
527 The correlation between landings and upwelling was only found for upwelling  
528 in the current season. No correlation was found when we used the upwelling in-  
529 dex from the prior season. The correlation between landings and upwelling was  
530 found for both July-September and October-March landings and with either  
531 upwelling index: average nearshore SST along the Kerala coast during June-  
532 September or the average SST nearshore versus offshore differential (UPW)  
533 off Kochi in June-September (Table 4, Table B3 and Table B4). These two  
534 upwelling indices are correlated but not identical. The model with average  
535 June-September nearshore SST was more supported than the model using the  
536 SST differential off Kochi. For July-September catch, this model with a non-  
537 linear response had an adjusted  $R^2$  of 41.0 versus an adjusted  $R^2$  of 24.4 for  
538 the model with no covariates (Table B3), and for October-March catch, the  
539 adjusted  $R^2$  was 61.8 versus 56.6 (Table B4). Note, that this covariate is June-  
540 September in the current season and overlaps with the July-September catch.  
541 Thus this model cannot be used to forecast July-September catch but does help  
542 us understand what factors may be influencing catch during the monsoon.

543 Chlorophyll-a density is speculated to be an important predictor of larval  
544 sardine survival and growth. In addition, sardines shoal in response to coastal  
545 chlorophyll blooms, which brings them in contact with the coastal fisheries.  
546 Thus chlorophyll-a density is assumed to be an important driver of future or  
547 current sardine catches. We had chlorophyll-a remote sensing data only from

548 1998 onward. Our simplest covariate model required 5 degrees of freedom,  
549 thus we were limited in the analyses we could conduct. In addition, the years,  
550 1998-2014, have relatively low variability in catch sizes; the logged catch sizes  
551 during this period range from 10-11 during quarter 3 and 11-12 during the  
552 other three quarters. Second degree polynomial models were fit (Appendix C)  
553 to the average log chlorophyll-a density in the current and prior season from  
554 quarter 3 (July-September), 4 (October-December), and 1 (January-March).  
555 Chlorophyll-a density was not a significant predictor for the July-September  
556 catch for any of the tested combinations of current or prior season and quar-  
557 ter. The only significant effect was seen for post-summer monsoon catches  
558 using chlorophyll-a density in October-December of the prior season (Table  
559 C1). This is in contrast to the results with monsoon upwelling indices, which  
560 found a correlation with the current season but not prior seasons.

561 The strongest correlation however was found with the multi-year average  
562 sea surface temperature for the nearshore waters off Kerala (latitude 8 to 11).  
563 The average sea surface temperature over multiple prior years has been found  
564 to be correlated with sardine recruitment in Pacific sardines (Checkley et al.,  
565 2017; Jacobson & MacCall, 1995; Lindegren et al., 2013) and southern African  
566 sardines (Boyer et al., 2001). We tested as a model covariate the average SST  
567 for 2.5 years prior to the July-September catch, so January-June in the current  
568 calendar year and the two prior calendar years for a 30-month average. This  
569 covariate can be used for forecasting since it does not overlap with either July-  
570 September or October-March catch. This variate with a non-linear response  
571 was best covariate for both the July-September and the post-monsoon catch.  
572 For post-monsoon catch, the model with SST had an adjusted  $R^2$  of 67.5 versus  
573 56.6 without. For the July-September catch, the adjusted  $R^2$  was 41.0 with SST  
574 and 24.4 without. The response curve was step-like with a negative effect at low  
575 temperatures and then an positive flat effect at higher temperatures (Figure 6).  
576 This is similar to the step-response found in studies of the correlation between

577 average SST and recruitment in Pacific sardines (Jacobson & MacCall, 1995).

## 578 Discussion

579 Sardines in all the world's ecosystems exhibit large fluctuations in abundance  
580 (Baumgartner et al., 1992). These small forage fish are strongly influenced by  
581 natural variability in the ocean environment. Upwelling, influenced by both  
582 large-scale forces such as regimes shifts and El Ni\~{n}o/Southern Oscillation  
583 patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010) and by seasonal  
584 wind and current patterns, brings nutrient rich and oxygen rich waters to the  
585 surface. This drives the seasonal variability in phytoplankton resources and in  
586 turn sardine prey (Bakun et al., 2008). Local variability in temperature, salin-  
587 ity, and oxygen levels have both direct and indirect on sardine reproduction,  
588 recruitment and survival (Checkley et al., 2017). Sardines are also influenced  
589 by competition and predation by other species and well-known for their sensi-  
590 tivity to over-fishing which has been linked to many fishery collapses (Kripa et  
591 al., 2018).

592 Many studies on Pacific sardines have looked at the correlation between  
593 ocean temperature (SST) and recruitment. Temperature can have direct effect  
594 on larval survival and growth and an indirect effect on food availability. Stud-  
595 ies in the California Current System, have found that SST explains year-to-year  
596 variability in Pacific sardine recruitment (Checkley et al., 2009, 2017; Jacobson  
597 & MacCall, 1995; Lindegren & Checkley, 2012) and that the average nearshore  
598 temperature over multiple seasons is the explanatory variable. Similar to these  
599 studies, we found that the average nearshore SST over multiple seasons was  
600 the covariate that explained the most variability in catch both in the monsoon  
601 and post-monsoon months. McClatchie et al. (2010) found no SST relation-  
602 ship with SST and Pacific sardine recruitment, however their analysis used a

linear relationship while the other studies, and ours, that found a relationship (Checkley 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 sar-

631 dine recruitment, growth and survival with upwelling, we found no correlation  
632 upwelling in the prior season with landings. We did find a correlation  
633 between upwelling in the current season with landings in the current season.  
634 The biological reasons behind a positive relationship with upwelling are clear.  
635 Upwelling drives productivity and higher food resources in the current season  
636 leads to higher recruitment and higher numbers of 0-year fish in the landings  
637 or may bring sardines into the nearshore to feed where they are exposed to the  
638 fishery. However, the explanatory power of the upwelling indices was mainly  
639 due to the negative effect of extremely high upwelling (Figure 6). Extremely  
640 high upwelling transports larval sardines offshore and can create regions of low  
641 oxygen which sardines avoid.

## 642 **Conclusions**

643 Remote sensing satellites can be used to detect changes in ocean physical, bi-  
644 ological and chemical properties, such as surface temperature, winds, surface  
645 height, surface waves, rainfall and surface salinity, as well as the ecosystem and  
646 water quality changes. Unlike in-situ measurements, environmental measures  
647 from remote-sensing can be acquired rapidly and over large regions. However,  
648 which environmental covariates will improve forecasts is not obvious from oil-  
649 sardine life-history alone. We tested using many of the covariates known or  
650 suspected to have a effect on sardine spawning, growth and survival: precipi-  
651 tation, upwelling indices, ocean temperature and chlorophyll-a in various crit-  
652 ical months of the sardine life-cycle. We found that the multi-year average  
653 nearshore ocean temperature explained the most variability in the landings.  
654 This covariate is not as directly tied to stages of the oil-sardine life-cycle as  
655 the other covariates we tested, though it does integrate over multiple influences  
656 (upwelling strength and temperature) over multiple years.

657 The temperature of the Western Indian Ocean, of which the Southeast Ara-  
658 bian Sea is a part, has been increasing over the last century at a rate higher than  
659 any other tropical ocean (Roxy et al., 2014) and the warming has been most  
660 extreme during the summer monsoon months. This ocean climate change is af-  
661 fecting oil sardine distributions with significant landings now occurring north  
662 of Goa (Vivekanandan et al., 2009). Continued warming is expected to affect  
663 the productivity of the region via multiple pathways, including both the direct  
664 effects of temperature change on the physiology and behavior of organisms and  
665 a multiple of indirect effects (Moustahfid et al., 2018). These indirect effects  
666 includes changes to salinity, oxygen concentrations, currents, wind patterns,  
667 ocean stratification and upwelling spatial patterns, phenology, and intensity.  
668 Incorporating environmental covariates into landings forecasts has the poten-  
669 tial to improve fisheries management for small pelagics such as oil sardines in  
670 the face of a changing ocean environment (Haltuch et al., 2019; Tommasi et al.,  
671 2016). However, monitoring forecast performance and covariate performance  
672 in models will be crucial as a changing ocean environment may also change  
673 the association between landings and average sea surface temperature.

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988 **Figure Legends**

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

992 Figure 2. Quarterly catch data 1956-2014 from Kerala. The catches have a  
993 strong seasonal pattern with the highest catches in quarter 4 Note that quarter  
994 3 is July-September and that the fishery is closed July 1 to August 15, thus the  
995 fishery is only open 1.5 months in quarter 3. The mean catch (metric tonnes)  
996 in quarters 1 to 4 are 38, 19.2, 30.9, and 59.9 metric tonnes respectively.

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

999 Figure 4. Remote sensing covariates used in the analysis. All data are  
1000 monthly averages over Box 4 in Figure 1 on the Kerala coast off of Kochi.  
1001 Panel A) Upwelling Index. The upwelling index is the difference between  
1002 the near-shore sea surface temperature (SST) and the off-shore SST defined  
1003 as 3 degrees longitude offshore. Panel B) Surface chlorophyll-a (CHL). The  
1004 CHL data are only available from 1997 onward. Panel C) Sea surface tempera-  
1005 ture constructed from Advanced Very High Resolution Radiometer (AVHRR).  
1006 Panel D) Average daily rainfall (mm/day) off the Kerala coast.

1007 Figure 5. Key oil sardine life-history events overlaid on the monthly sea  
1008 surface temperature in the nearshore and offshore and the nearshore chloro-  
1009 phyll density.

1010 Figure 6. Effects of covariates estimated from the GAM models. Panel A)  
1011 Effect of the 2.5 year average nearshore SST on catch during the catch during  
1012 July-September (late spawning and early post-spawning) months. Panel B) Ef-  
1013 fect of upwelling (inshore/off-shore SST differential) during June-September  
1014 in the current season on July-September catch. The index is the difference be-

1015 tween offshore and inshore SST, thus a negative value indicates warmer coastal  
1016 surface water than off-shore. Panel C) Effect of the 2.5 year average nearshore  
1017 SST on catch during the catch during October-March (post-monsoon, age-0, -1,  
1018 -2 year fish). Panel D) Effect of upwelling (inshore/off-shore SST differential)  
1019 during June-September in the current season on October-March catch. Strong  
1020 upwelling (positive upwelling index) in the larval and juvenile high growth pe-  
1021 riod (Oct-Dec) is associated with higher early survival and larger cohorts of  
1022 age-0 fish in the catch.

1023 Figure 7. Fitted versus observed catch with models with and without envi-  
1024 ronmental covariates. Panel A) Fitted versus observed log catch in the spawn-  
1025 ing months with only non-spawning catch in the previous season as the co-  
1026 variate:  $S_t = s(N_{t-1}) + \varepsilon_t$ . Panel B) Fitted versus observed log catch in July-  
1027 September with the 2.5-year average nearshore SST added as a covariate to the  
1028 model in panel A. This model was:  $S_t = s(N_{t-1}) + s(V_t) + \varepsilon_t$ . Panel C) Fitted  
1029 versus observed log catch in the post-monsoon months with only post-monsoon  
1030 catch in the previous season and July-September catch two seasons prior as the  
1031 covariates:  $N_t = s(N_{t-1}) + s(S_{t-2}) + \varepsilon_t$ . Panel D) Fitted versus observed log  
1032 catch in the post-monsoon months with 2.5-year average nearshore SST ( $V$ )  
1033 added as covariates. This model was  $N_t = s(N_{t-1}) + s(S_{t-2}) + s(V_t) + \varepsilon_t$ .

1034

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. 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. 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	LOO 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	1.29
$\ln(S_t) = M0 + s(V_t)$						
		25.9	41	1.007	103.43	1.19
$\ln(S_t) = M0 + \beta W_t$						
		27.6	28	1.133	108.66	1.40
$\Rightarrow \ln(S_t) = M1 + s(Z_t)$						
		26.2	41	1.011	103.26	1.33
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	1.00
$\ln(N_t) = M1 + s(V_t)$						
		22	63	0.628	76.01	1.00
$\ln(N_t) = M1 + \beta W_t$						
		23.8	63	0.648	75.57	1.04
$\Rightarrow \ln(N_t) = M1 + s(Z_t)$						
		22.7	67	0.597	71.88	0.82
$\ln(N_t) = M1 + s(X_t)$						
		21.1	68	0.58	72.69	0.82
M2: $\ln(N_t) = \alpha + s(\ln(N_{t-1})) + \varepsilon_t$						
		27.6	45	0.836	84.75	0.96
$\ln(N_t) = M2 + s(V_t)$						
		24.8	47	0.791	85.9	0.98
$\ln(N_t) = M2 + \beta W_t$						
		26.6	52	0.772	81.79	0.92

Model	Residual df	Adj. R2	RMSE	AIC	LOO RMSE
$\Rightarrow \ln(N_t) = M2 + s(Z_t)$	25.3	60	0.688	76.34	0.79
$\ln(N_t) = M2 + s(X_t)$	23.7	43	0.8	88.43	0.90

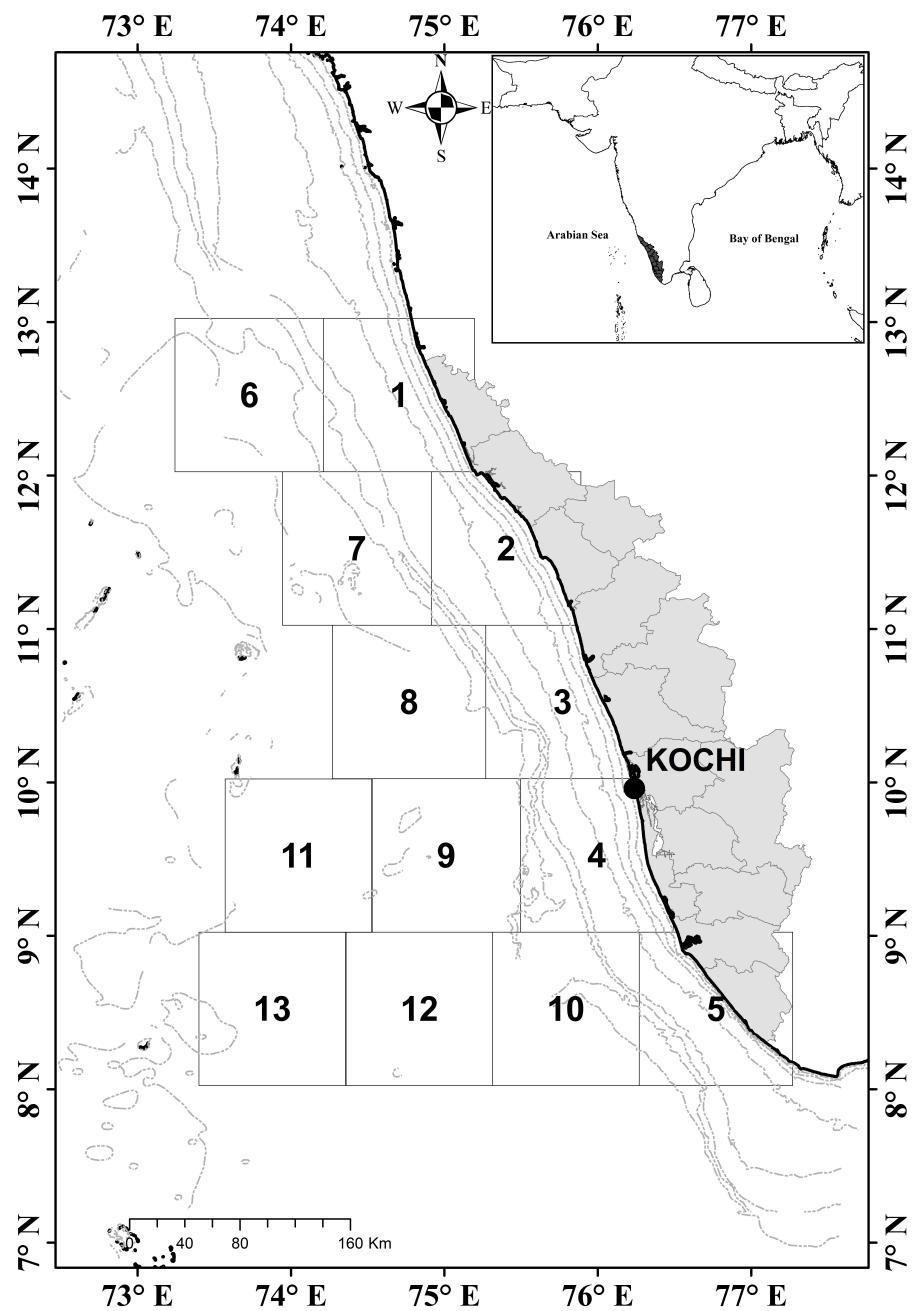


Figure 1

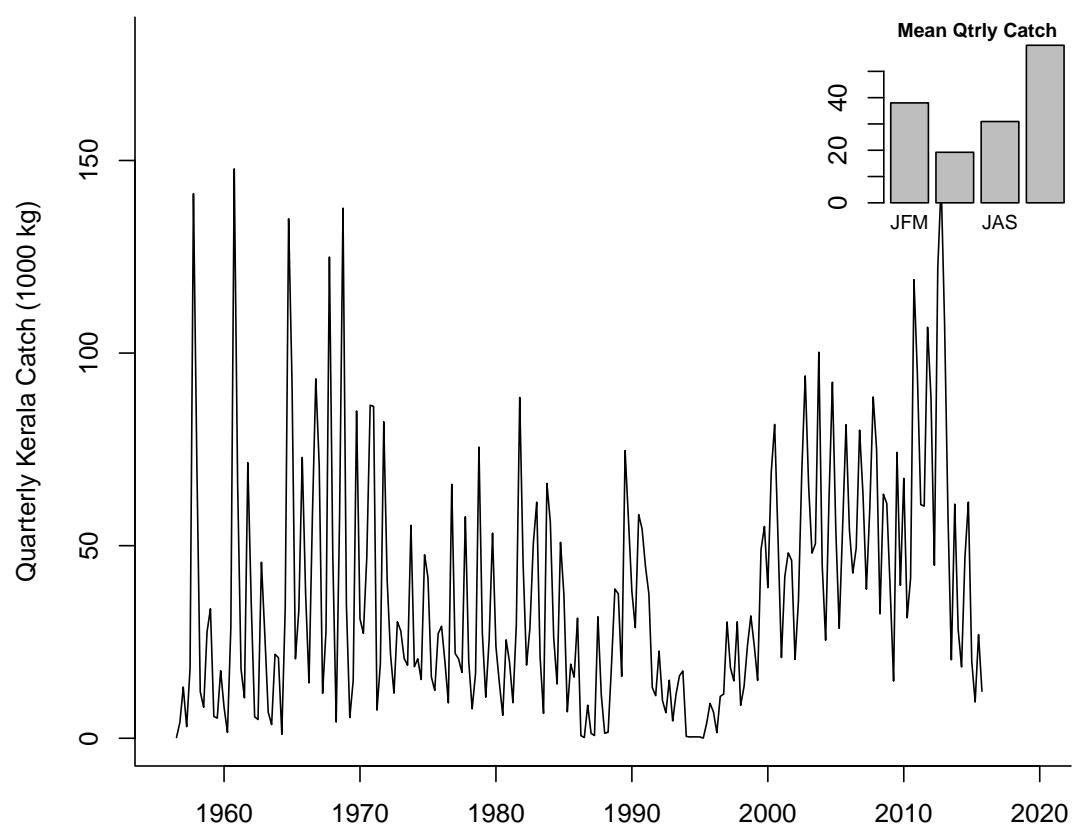


Figure 2

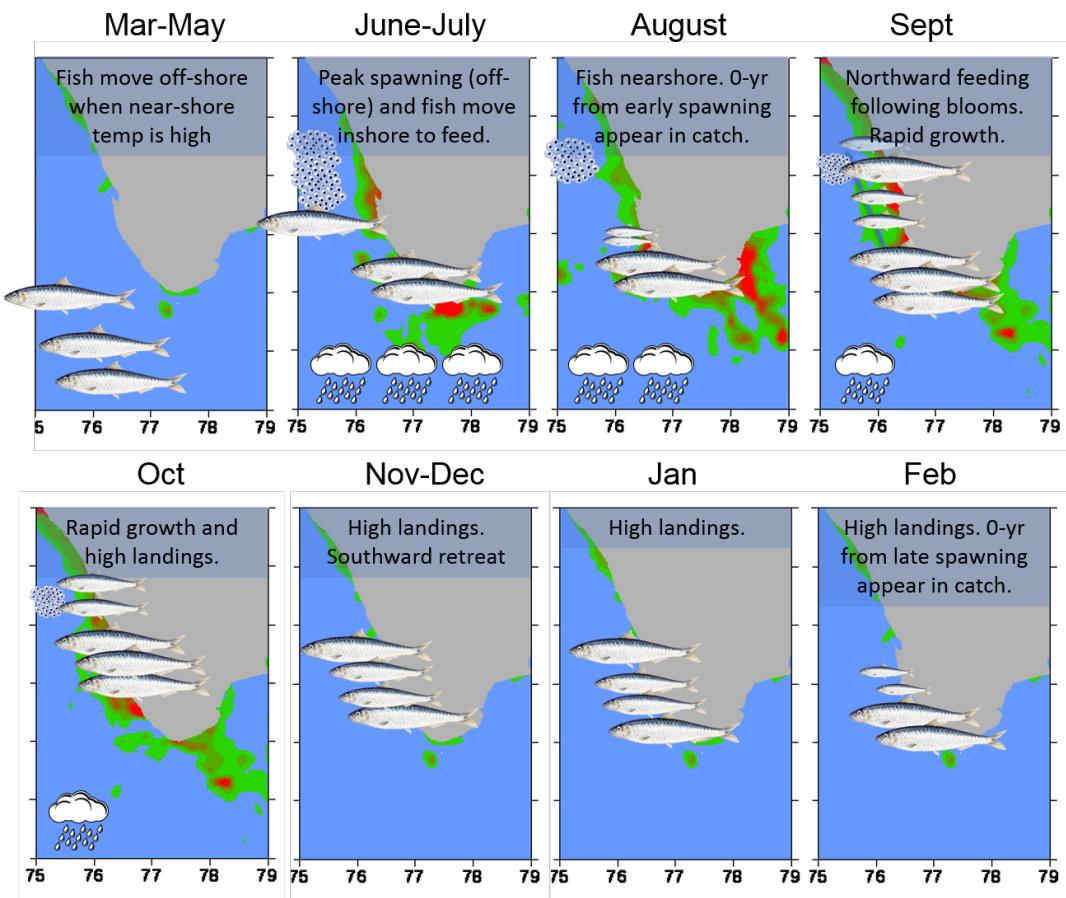


Figure 3

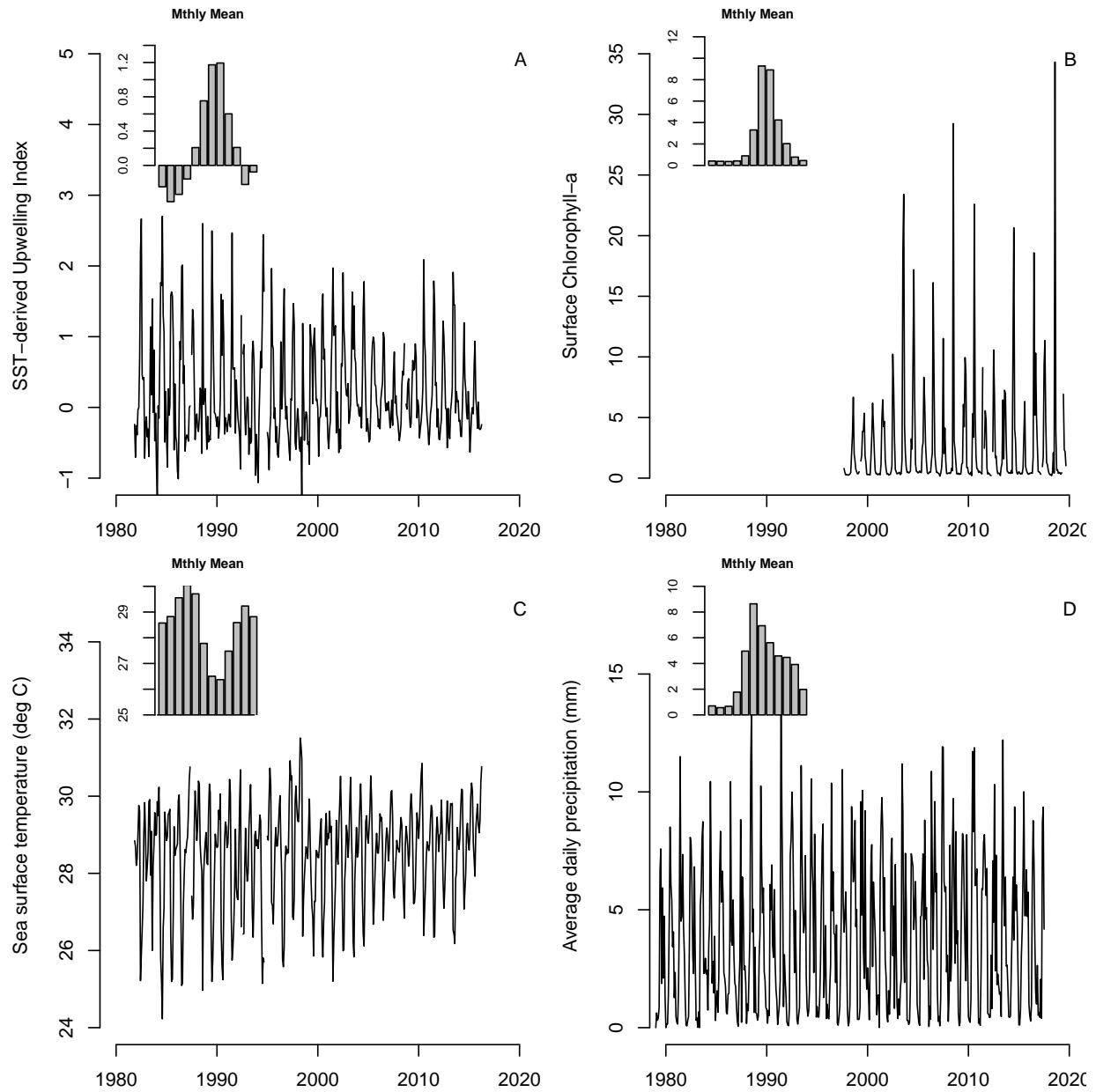


Figure 4

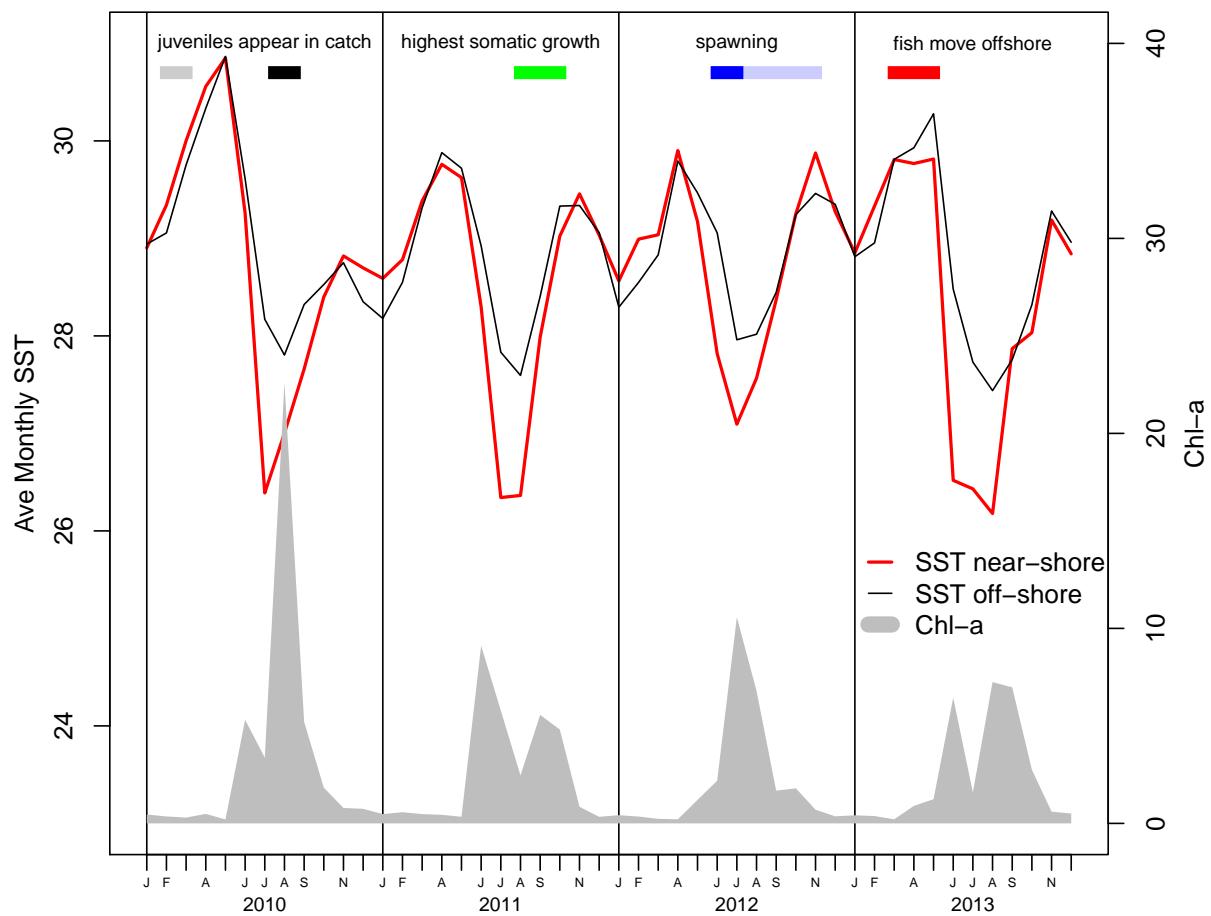


Figure 5

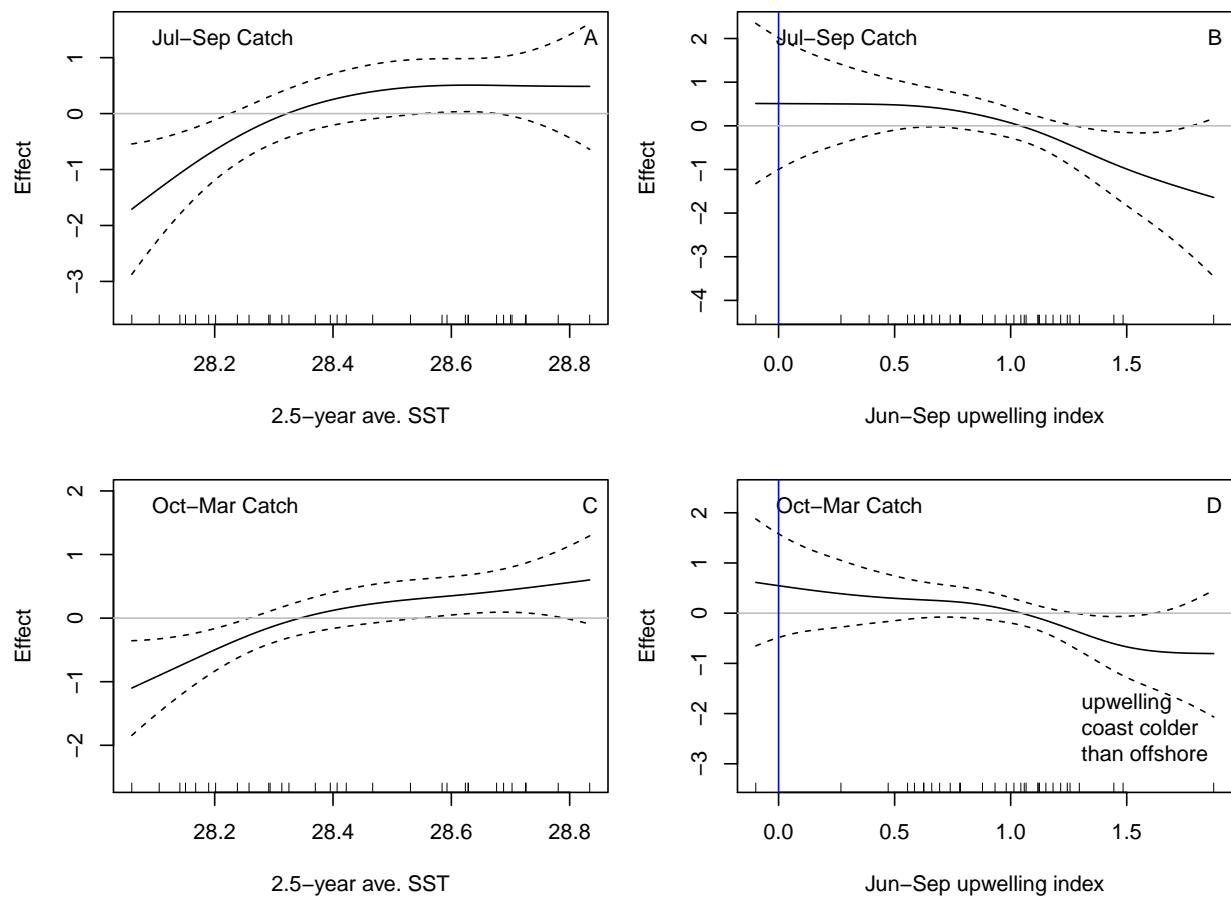


Figure 6

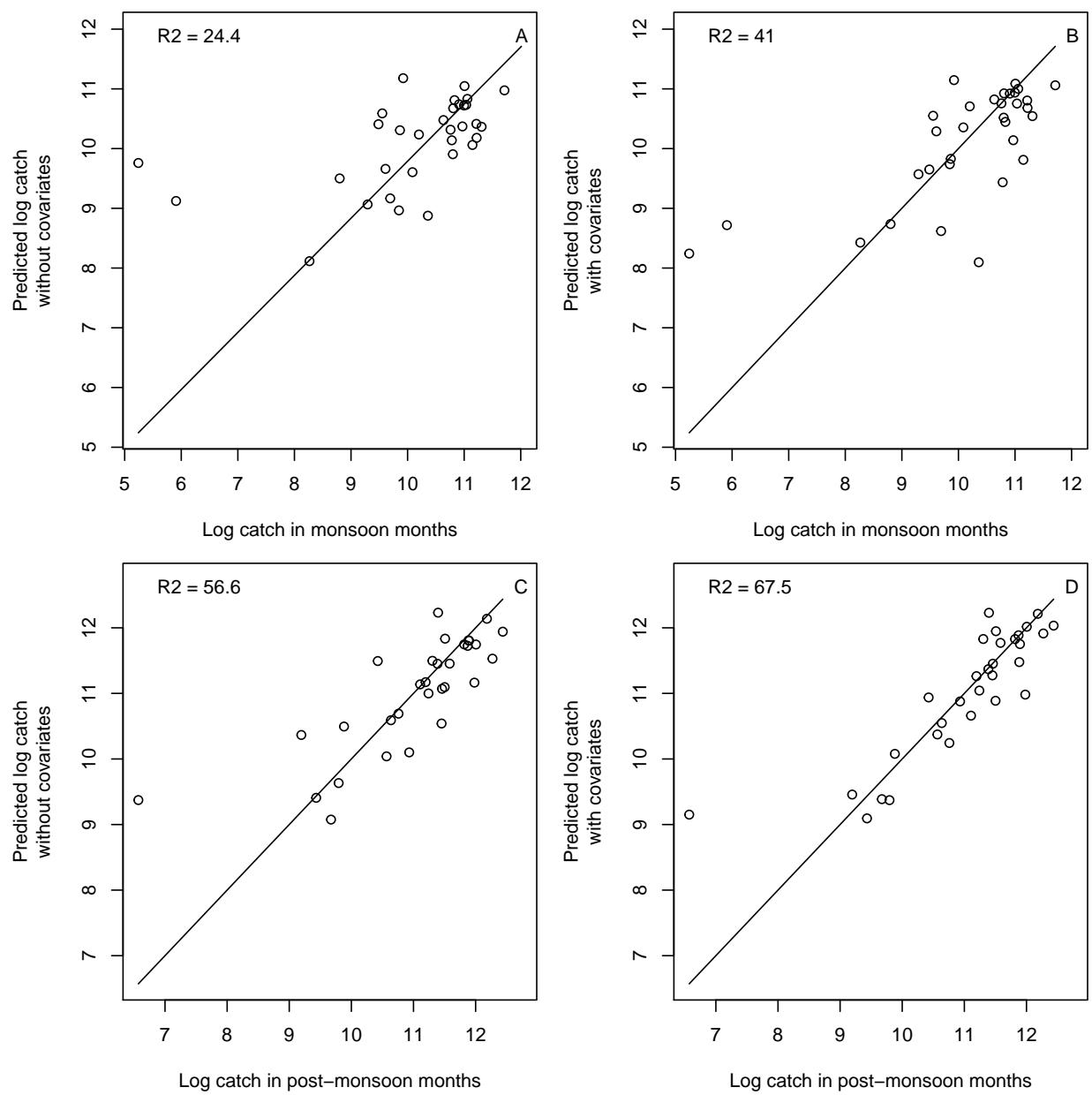


Figure 7