

¹ Influence of changing temperature and upwelling intensity on
² Indian oil sardine (*Sardinella longiceps*) landings

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⁴ Eli E. Holmes¹, Smitha B.R.², Nimit Kumar³, Sourav Maity³, David M. Checkley, Jr.⁴, Mark L. Wells⁵, Vera L. Trainer¹

⁶ 1. Northwest Fisheries Science Center, NOAA, Seattle, WA.

⁷ 2. Centre for Marine Living Resources and Ecology, MoES, Kochi, India.

⁸ 3. Indian National Centre for Ocean Information Services, Hyderabad, India.

⁹ 4. Scripps Institution of Oceanography, UC San Diego, CA.

¹⁰ 5. School of Marine Sciences, University of Maine, Orono, ME.

¹¹ **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 concentration 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 (Jul-Sep) and post-monsoon (Oct-Mar) 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 steadily increasing and the warming has been most extreme during the summer monsoon. Our work highlights that changes in sea temperature in the Southeast Indian Sea, which is warming, are likely affecting oil sardine landings.

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

51 **Introduction**

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

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

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

& Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara, 2011), with direct measures of productivity such as nearshore zooplankton and phytoplankton abundance (George et al., 2012; Madhupratap et al., 1994; Menon et al., 2019; Nair, 1952; Nair & Subrahmanyam, 1955; Piontkovski et al., 2014; Pitchaikani & Lipton, 2012), and with nearshore sea surface temperature (SST) (Annigeri, 1969; Pillai, 1991; Prabhu & Dhulkhed, 1970; Supraba et al., 2016). SST can affect both somatic growth rates and juvenile survival but in this system also can cause fish to move off-shore and away from the shore-based fishery. The multi-year average sea temperature is postulated to have effects on recruitment and the survival of larval and juvenile sardines, which affect the later overall abundance (Checkley et al., 2017; Takasuka et al., 2007). The El Niño/Southern Oscillation (ENSO) has a cascading effect on all the aforementioned environmental parameters (SST, precipitation, upwelling) and correlations have been found between ENSO indices and sardine landings (Rohit et al., 2018; Supraba et al., 2016) and coastal anoxic events which affect sardines (Vallivattathillam et al., 2017).

In this paper, we study the utility of environmental covariates from remote sensing to explain year-to-year variability using a long-term time series of quarterly Indian oil sardine landings. This time series is derived from a stratified sampling design that surveys the fishery landing sites along the southwest Indian coast and was first implemented in the 1950s (Srinath et al., 2005). The goal is to identify environmental covariates which can explain catch variability and improve the accuracy of short-term catch forecasts. Landings are a product of the biomass, the catchability, and the effort. A traditional auto-correlated catch model (ARIMA) can model smooth changes in landings, such as due to changes in fleet size or multi-year biomass changes, but the environment adds a large component of year-to-year variability that such a model does not capture. The environment affects food resources which affects recruitment through spawning and survival, and thus the biomass available to the fishery. In addition, in the Indian oil sardine system, catchability is strongly affected by the environment by affecting the inshore versus offshore distribution of sardine. The fishery is restricted to the nearshore < 50 km offshore (Rohit et al., 2018). When the sardines move offshore to spawn or to avoid hypoxic or excessively warm water, they are no longer available to the fishery. Thus, through its effects on recruitment and catchability, the environment has the potential to drive year-to-year changes in landings. The covariates which we study (Table 1) are linked to aspects of oil sardine life-history that are expected to affect catch via catchability or biomass. Covariates from remote sensing are the focus because they are available over a wide spatial extent at a daily and monthly resolution thus are practical for use in operational forecasts. A better un-

¹¹⁸ derstanding of how and whether remote sensing data explains variation in seasonal catch will
¹¹⁹ support future efforts to use satellite data to improve catch forecasts.

¹²⁰ Catch modeling versus biomass modeling

¹²¹ Modeling and forecasting landings data using statistical models fit to annual or seasonal catch
¹²² time series has a long tradition in fisheries and has been applied to many species (Cohen &
¹²³ Stone, 1987; Farmer & Froeschke, 2015; Georgakarakos et al., 2006; Hanson et al., 2006;
¹²⁴ Lawer, 2016; Lloret et al., 2000; Mendelssohn, 1981; Nobel & Sathianandan, 1991; Prista
¹²⁵ et al., 2011; Stergiou & Christou, 1996), including oil sardines (Srinath, 1998; Venugopalan
¹²⁶ & Srinath, 1998). These models can be used to identify the variables correlated with catch
¹²⁷ fluctuations and can be used to provide landings forecasts which are useful for fishery managers
¹²⁸ and the fishing industry. An example of the former is using catch forecasts to set or give
¹²⁹ warnings of seasonal fishery closures if the forecasted catch is higher than the allowed catch
¹³⁰ limits (Farmer & Froeschke, 2015). An example of the latter is the annual Gulf and Atlantic
¹³¹ menhaden forecast produced by NOAA Fisheries (Hanson et al., 2006; Schaaf et al., 1975).
¹³² This multiple regression model has been used for the last 45 years to produce an annual forecast
¹³³ of menhaden landings, which is used for planning purposes by the industry, not only the fishers
¹³⁴ but also fish catch sellers and buyers, businesses which provide fisheries gear, and banks which
¹³⁵ provide financing (Hanson et al., 2006).

¹³⁶ For the purpose of our study, the assumption of a tight relationship between landings and
¹³⁷ abundance is not necessary. The objective is to understand what drives landings variability,
¹³⁸ whether it is due to biomass or catchability variation. That said, Indian oil sardine landings are
¹³⁹ often assumed to reflect the total abundance for reasons specific to the species and the fishery
¹⁴⁰ (cf. Kripa et al., 2018). Historically, the fishery was artisanal: small boats with small motors,
¹⁴¹ no refrigeration, and limited to the near shore. The ring seine was introduced in the 1980s, but
¹⁴² widespread mechanization of the fleet is a very recent development. Fishers with small boats
¹⁴³ have limited ability to target the stock, at least not to the degree that landings remain constant as
¹⁴⁴ a stock declines. That pattern can be observed in a large, mobile, highly mechanized fleet. The
¹⁴⁵ fishery is unregulated, except for a brief closure during the monsoon months, thus the landings
¹⁴⁶ are not being affected by area closures and catch limits. Finally, the fishery is dispersed along
¹⁴⁷ the entire coastline rather than being focused from a few large ports. Again, for our objectives,
¹⁴⁸ it is not necessary that landings be a tight index of biomass, but there are many reasons to
¹⁴⁹ assume that this relationship is strong.

150 Unfortunately historical biomass estimates are not possible for the Indian oil sardine.
151 Length- or age-structured models (e.g. virtual population analysis) which produce biomass
152 estimates are not possible due to the lack of effort and catch-at-age information for the fishery.
153 The available long-term effort data are indirect (boat composition of the fishery at multi-year
154 intervals) and estimates of number of trips or hours fishing are only available in a few recent
155 years, and the data available are approximate given the vessel diversity of the fishery and sam-
156 pling constraints. Nonetheless the number and size of boats involved in the fishery has been
157 increasing. Oil sardines are caught primarily by ring seines, which were introduced in the
158 early 1980s. Ring seines of different sizes are used on both traditional small boats and on
159 large mechanized ships (Das & Edwin, 2018). Since 1985, the ring seine fishery has expanded
160 steadily in terms of horsepower, size of boats, and length of nets. There are concerns that
161 over-fishing is a factor in the most recent oil sardine declines after 2015 (Kripa et al., 2018).
162 Steadily increasing effort is assumed to have increased the landings, at least prior to 2015.
163 Our base catch model, an auto-regressive model, will capture smooth landings trends due to
164 increased effort (or multi-year changes in biomass).

165 **Study Area**

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

179 **Oil sardine life cycle and fishery**

180 The Indian oil sardine fishery is restricted to the narrow strip of the western India continental
181 shelf, within 20 km from the shore (Figure 1). The yearly cycle of the fishery begins at the
182 start of spawning during June to July, corresponding with the onset of the summer monsoon
183 (Antony Raja, 1969; Chidambaram, 1950) and the initiation of strongly cooler nearshore SST
184 due to upwelling (Figure 3). At this time, the mature fish migrate from offshore to coastal
185 spawning areas, and the spawning begins during the summer monsoon period when temper-
186 ature, salinity and suitable food availability are conducive for larval survival (Chidambaram,
187 1950; Jayaprakash & Pillai, 2000; Krishnakumar et al., 2008; Murty & Edelman, 1966; Nair et
188 al., 2016). Although peak spawning occurs in June to July, spawning continues into Septem-
189 ber (Antony Raja, 1969; Hornell, 1910; Hornell & Nayudu, 1924; Prabhu & Dhulkhed, 1970)
190 and early- and late-spawning cohorts are evident in the length distributions of the 0-year fish.
191 Spawning occurs in waters outside of the traditional range of the fishery (Antony Raja, 1964),
192 and after spawning the adults migrate closer to the coast where the spent fish become exposed
193 to the fishery.

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

210 Catches along the Kerala coast are high throughout the year except during quarter 2, Apr-
211 Jun (Figure 2). The age-distribution caught by the fishery varies through the year. The fishery

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

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). The quarterly landings (metric tons) for oil sardine landed from all gears in Kerala were obtained from CMFRI reports (1956-1984) and online databases (1985-2015); see Appendix G for data sources. The quarterly landing data were log-transformed to stabilize the variance.

Remote sensing data

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

For sea surface temperature, we used Advanced Very-High Resolution Radiometer (AVHRR) data, which provides accurate nearshore SST values. Although the ICOADS product provides SST values for earlier years, ICOADS does not provide accurate nearshore

240 temperatures. For 1981 to 2003, we used the Pathfinder Version 5.2 product on a 0.0417
241 degree grid. These data were developed by the Group for High Resolution Sea Surface
242 Temperature (GHRSSST) and served by the US National Oceanographic Data Center. For
243 2004 to 2016, we used the NOAA CoastWatch SST products derived from NOAA's Polar
244 Operational Environmental Satellites (POES).

245 We used the chlorophyll-a products developed by the Ocean Biology Processing Group in
246 the Ocean Ecology Laboratory at the NASA Goddard Space Flight Center. For 1997 to 2002,
247 we used the chlorophyll-a 2014.0 Reprocessing (R2014.0) product from the Sea-viewing Wide
248 Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite. These data are on a 0.1 degree
249 grid. For 2003 to 2017, we used the MODIS-Aqua product on a 0.05 degree grid. These CHL
250 data are taken from measurements by the Moderate Resolution Imaging Spectroradiometer
251 (MODIS) on NASA's Aqua Spacecraft. The SST and CHL data were averaged across thirteen
252 1 degree by 1 degree boxes which roughly parallel the bathymetry (Figure 1). The SST and
253 CHL satellite data were retrieved from NOAA remote-sensing data servers; see Appendix G
254 for data sources and references.

255 For an index of coastal upwelling, we used three indices. The first was the sea surface tem-
256 perature differential between near shore and 3 degrees offshore based on the index described
257 by Naidu et al. (1999) and BR et al. (2008). For SST, we used the remote sensing sea surface
258 temperature data sets described above. This SST-based upwelling index has been validated as
259 a more reliable metric of upwelling off the coast of Kerala compared to wind-based upwelling
260 indices (BR et al., 2008). The SST-based upwelling index and chlorophyll-a blooms have a
261 strong temporal association (Figure 3). The second index was simply average nearshore SST
262 along the Kerala coasts (average of boxes 2-5 in Figure 1). The third index was the Bakun
263 index based on wind stress. The index is computed from the the x- and y- components of Ekman
264 Transport. See Appendix G for data sources and references.

265 Precipitation data were obtained from two different sources. The first was an estimate
266 of the monthly precipitation (in mm) over Kerala from land-based rain gauges; these data are
267 available from the Indian Institute of Tropical Meteorology and the data are available from the
268 start of our landing data (1956). The second was a remote sensing precipitation product from
269 the NOAA Global Precipitation Climatology Project. This provides estimates of precipitation
270 over the ocean using a global 2.5 degree grid. We used the 2.5 by 2.5 degree box defined by
271 latitude 8.75 to 11.25 and longitude 73.25 to 75.75 for the precipitation off the coast of Kerala.
272 These data are available from 1979 forward. The land and nearshore ocean precipitation data
273 are highly correlated (Appendix D). See Appendix G for the precipitation data repositories and

274 references.

275 The Oceanic Niño Index (ONI) is a measure of the SST anomaly in the east-central Pacific
276 and is a standard index of the El Niño/Southern Oscillation (ENSO) cycle. The ONI index is
277 3-month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region, based on centered
278 30-year base periods updated every 5 years. The ONI was downloaded from the NOAA Na-
279 tional Weather Service Climate Prediction Center. The Dipole Mode Index (DMI) is defined
280 by the SSTA difference between the western Indian Ocean (10°S – 10°N , 50°E – 70°E) and the
281 southeastern Indian Ocean (10°S – 0° , 90°E – 110°E). The DMI has been shown to predict anoxic
282 events in our study area (Vallivattathillam et al., 2017). The DMI data were downloaded from
283 the NOAA Earth System Research Laboratory. See Appendix G for the data servers where the
284 ENSO data were downloaded and computation notes and references.

285 **Hypotheses**

286 Our statistical tests were structured around specific hypotheses (Table 1) concerning which re-
287 mote sensing covariates in which months should correlate with landings in specific quarters.
288 These hypotheses were based on biological information concerning how environmental con-
289 ditions affect sardine survival and recruitment and affect exposure of Indian oil sardines to
290 the coastal fishery. The Jul-Sep catch overlaps the summer monsoon and the main spawning
291 months. This is also the quarter where small 0-year fish from early spawning often appear in
292 the catch, sometimes in large numbers. Variables that affect or are correlated with movement of
293 sardines inshore should be correlated with Jul-Sep landings. In addition, pre-spawning (Mar-
294 May) environmental conditions should be correlated with the spawning strength as adult oil
295 sardines experience an acceleration of growth during this period along with egg development.
296 The post-monsoon catch (Oct-May) is a mix of 0-year fish (less than 12 months old) and ma-
297 ture fish (greater than 12 months old). Variables that are correlated with spawning strength and
298 larval and juvenile survival should correlate with the post-monsoon catch both in the current
299 year and in future years, one to two years after.

300 Our hypotheses (Table 1) focus mainly on two drivers: upwelling and ocean tempera-
301 ture. We also test hypotheses concerning precipitation as this has historically been an envi-
302 ronmental covariate considered to influence the timing of oil sardine landings. More recently,
303 researchers have highlighted the influence of large-scale ocean processes, specifically the El
304 Niño/Southern Oscillation, on sardine fluctuations; therefore we test the Ocean Niño Index
305 (ONI) and Dipole Mode Index (DMI) also. Chlorophyll concentration is directly correlated

306 with sardine food availability and chlorophyll fronts are known to influence sardine shoaling.
307 However our chlorophyll time series is short (1997-2015) and the statistical power for testing
308 correlation with landings is low. Tests of chlorophyll are shown in the appendices but are not
309 the focus of our analyses.

310 Statistical models

311 We modeled the catches during the late-monsoon season (Jul-Sep) separately from the post-
312 monsoon season (Oct-Mar). Thus, there is no seasonality in our catch time series as we ana-
313 lyzed a yearly time series of Jul-Sep catches separately from a yearly time series of Oct-Mar
314 catches. We divided the catch in this way for biological and statistical reasons. Catch in Jul-
315 Sep captures a mix of spawning-age fish as it overlaps with the tail end of the spawning season,
316 is affected by a fishery closure during the summer monsoon, and is periodically inflated by the
317 appearance of small 0-year fish from early summer spawning. In addition, the covariates that
318 affect the timing of spawning, movement of post-spawning mature fish inshore, and early egg
319 and larval survival may be different than those that affect later growth, survival and shoaling
320 that exposes fish to the inshore fishery. Analyzing catch and covariate time series without sea-
321 sonality also had an important statistical benefit—we removed the problem of seasonality in
322 the catch and covariates. The oil sardine life-cycle is seasonal and driven by the strong season-
323 ality in this monsoon influenced system. A simple statistical model with quarters will explain
324 much of the quarterly catch data since most of the yearly variability is due to seasonality and
325 any environmental covariate with a similar seasonality will also show high correlation with the
326 landings. Our goal was to explain year-to-year variability and thus eliminating the confounding
327 effect of seasonality in the data was important.

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

338 gous to that taken by Jacobson and MacCall (1995) in a study of the effects of SST on Pacific
339 sardine recruitment.

340 The first step in our analysis was to determine the catch model: the model for current
341 catch as a function of the past catch. We explored four classes of models: null models with a
342 simple function of prior catch, linear regressive models with one to two years of prior catch,
343 dynamic linear models (DLM) which allow the regression parameters to vary (Holmes et al.,
344 2012, using the MARSS package in R), and GAMs to allow the effect of prior catch to be
345 non-linear. One feature of GAMs is that they allow the smoothing parameter of the response
346 curve to be estimated. We fixed the smoothing parameter at an intermediate value so that
347 smooth responses were achieved. Multi-modal or overly flexible response curves would not
348 be realistic for our application. We fit GAMs with smooth terms represented by penalized
349 regression splines (Wood, 2011, using the mgcv package in R) and fixed the smoothing term
350 at an intermediate value (sp=0.6).

351 We compared the following catch models:

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

359 $\ln(C_{i,t})$ is the log catch in the current year t in season i . We modeled two different catches: S_t
360 (Jul-Sep) and N_t (Oct-Jun). The catches were logged to stabilize and normalize the variance.
361 $s()$ is a non-linear function estimated by the GAM algorithm. The model is primarily statistical,
362 meaning it should not be thought of as a population growth model. We tested models with prior
363 year and two years prior Oct-Mar catch (N_{t-1} and N_{t-2}) and Jul-Sep catch (S_{t-1} and S_{t-2}) as
364 the explanatory catch variable. S_t was not used as a predictor for N_t because S_t is the quarter
365 immediately prior to N_t and would not be available for a forecast model since time is required
366 to process landings data. The catch models were fit to 1984 to 2015 catch data, corresponding
367 to the years when the SST, upwelling and precipitation data were available. F-tests, AIC and
368 leave-one-out cross-validation (LOOCV) on nested sets of models (Wood et al., 2016) were
369 used to evaluate the support for the catch models and later for the covariate models. LOOCV

370 involves leaving out a data point, fitting the model, and then predicting the left-out data point.
371 The root mean squared error (RMSE) is reported for the set of prediction errors (one for each
372 left out data point). After selection of the best model with the 1984-2015 data, the fitting was
373 repeated with the 1956-1983 catch data to confirm the form of the catch models. An influential
374 years test was done by removing each year and repeating the model selection analysis.

375 Once the catch models were determined, the covariates were studied individually and then
376 jointly. As with the catch models, F-tests, AIC and LOOCV (leave-one-out cross-validation)
377 on nested sets of models were used to evaluate the support for models with covariates. The
378 smoothing term was fixed at an intermediate value ($sp=0.6$) instead of being treated as an
379 estimated variable. Our models for catch with covariates took the form $\ln(C_{i,t}) = M + \alpha +$
380 $s_1(V_{1,t}) + s_2(V_{2,t-1}) + \varepsilon_t$, $\ln(C_{i,t}) = M + \alpha + \beta_1 V_{1,t} + \beta_2 V_{2,t-1} + \varepsilon_t$, and $\ln(C_{i,t}) = M + \alpha +$
381 $\beta_t V_{1,t} + \varepsilon_t$ where M was the best catch model from step 1 and V is a covariate. Thus models
382 with covariates modeled as a linear, non-linear and time-varying effect were compared. The
383 covariates tested are those hypothesized to drive variability in oil sardine landings (Table 1).
384 We tested both models with one and two covariates and did not use correlated covariates in the
385 same model.

386 Results

387 Catches in prior seasons as explanatory variables

388 Using the 1984-2015 catch data, the time-period that overlaps our available environmental data,
389 the Jul-Sep catch models were compared against a “naive” model in which the forecasted Jul-
390 Sep catch is the Jul-Sep catch in the prior year. The “naive” model has no estimated parameters
391 and is a standard null model for time series modeling. Models with $\ln(N_{t-1})$ (Oct-Mar catch
392 in prior year) as the explanatory covariate were strongly supported over the naive model and
393 over models with $\ln(S_{t-1})$ (Jul-Sep catch in prior year) as the explanatory variable (Tables
394 A1 and A2). Addition of the catch two years prior, $\ln(N_{t-2})$ or $\ln(S_{t-2})$, was not supported
395 (by AIC or F-tests) for either the linear or non-linear models. We tested the support for non-
396 linearity in the effect of the prior year catch by comparing models with $\ln(N_{t-1})$ or $\ln(S_{t-1})$
397 included as a linear effect or as a non-linear effect using GAMs (Table A2). The residual error
398 decreased using a non-linear response and LOOCV decreased but at the cost increased degrees
399 of freedom. Overall there were three models with almost identical AIC and LOOCV: linear and
400 non-linear with $\ln(N_{t-1})$, and non-linear with $\ln(N_{t-1})$ and $\ln(N_{t-2})$. We choose the non-linear

401 with $\ln(N_{t-1})$ as the base catch model based on further diagnostic tests (described below) and
402 to minimize loss of degrees of freedom. The adjusted R^2 of this model was 24.4%.

403 The model selection results were similar for models of the Oct-Mar landings (N_t), but
404 the models explained much more of the variance (with a maximum adjusted $R^2 = 56.6$). The
405 most supported model for N_t (Tables A3 and A4) based on AIC and F-tests used a non-linear
406 response to Oct-Mar catch of the previous season $\ln(N_{t-1})$ plus a non-linear response to Jul-
407 Sep catch two years prior $\ln(S_{t-2})$, however the LOOCV (out of sample prediction accuracy)
408 was higher than the naive null model. The simpler model with only $\ln(N_{t-1})$ had the second
409 lowest AIC and the lowest LOOCV (and lower than the naive null model). This simpler model
410 was also included as one of the base models for the Oct-Mar catch.

411 As diagnostic checks, we repeated the model comparisons with the landings data set from
412 1956 to 1983. The results were the same for the Jul-Sep catch (Table A5) with the model
413 with $\ln(N_{t-1})$ included as a non-linear covariate giving the lowest AIC and LOOCV. For the
414 Oct-Mar catch (Table A6), the results were very similar but not identical. The model with
415 $\ln(N_{t-1})$ included as a non-linear covariate had the lowest LOOCV while the models with
416 $\ln(N_{t-1})$ and $\ln(S_{t-2})$ or $\ln(S_{t-2})$ had the lowest AIC (though less than 1 from the AIC of
417 the $\ln(N_{t-1})$ model). We also did an influential years test using leave-one-out cross-validation
418 (Appendix F). This test involved leaving out one year and repeating the model selection tests.
419 This analysis supported the selected base models using the 1984-2015 data. The dynamic
420 linear models (allowing a time-varying effect of prior catch) performed poorly for the Jul-Sep
421 catch with high AIC and LOOCV. For the Oct-Mar catch, the performance was mixed with
422 higher AIC but lower LOOCV for one of the DLMs.

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

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

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

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

426

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

427 Note that although M0 was the best model for Jul-Sep catch, it was only weakly explanatory.
428 The maximum adjusted R^2 was less than 30% (Table A2). For the Oct-Mar catch, M1 and M2

429 were more explanatory with an adjusted R^2 of 45.3% for M1 and 56.6% for M2 (Table A4).

430 Environmental covariates as explanatory variables

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

442 The sea surface temperature before spawning (March-May) has been speculated to be
443 correlated with successful egg development and spawning behavior (hypothesis S4 and S5)
444 and extreme heat events in the pre-spawning period have been associated with low recruitment.
445 This suggests that March-May in the current and prior years should be associated with low
446 catch. The sea surface temperature during larval and early juvenile development (October-
447 December) may affect survival and growth in multiple ways and thus would correlate with
448 biomass in future years (hypothesis L1). However we found no support for either of these SST
449 covariates as explanatory variables for the Jul-Sep catch and only weak support (based on AIC)
450 for March-May SST in the current season for explaining variability in Oct-Mar catch. The fall
451 average SST in the prior season did not explain variability in either Jul-Sep or Oct-Mar catch.
452 See Tables B4, B5 and B6. We also found no correlation between the ONI index (hypothesis
453 A2) for either the Jul-Sep or Oct-Mar catch (Tables B7, B8 and B9).

454 Instead we found support for the covariates indirectly and directly associated with pro-
455 ductivity and food availability: upwelling intensity and surface chlorophyll. The correlation
456 between landings and upwelling was only found for upwelling in the current season. No cor-
457 relation was found when we used the upwelling index from the prior season. The correla-
458 tion between landings and upwelling was found for both Jul-Sep and Oct-Mar landings and
459 with either SST-based upwelling index: average nearshore SST along the Kerala coast during
460 June-September or the average SST nearshore versus offshore differential (UPW) off Kochi

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

470 Chlorophyll-a concentration is speculated to be an important predictor of larval sardine
471 survival and growth. In addition, sardines shoal in response to coastal chlorophyll blooms,
472 which brings them in contact with the coastal fisheries. Thus chlorophyll-a is assumed to be an
473 important driver of future or current sardine catches. We only have chlorophyll-a remote sens-
474 ing data from 1998 onward. Our simplest covariate model required 5 degrees of freedom, thus
475 we were limited in the analyses we could conduct. In addition, the years, 1998-2014, have rela-
476 tively low variability in catch sizes; the logged catch sizes during this period range from 10-11
477 during Jul-Sep and 11-12 during the other three quarters. Second degree polynomial mod-
478 els were fit (Appendix C) to the average log chlorophyll-a concentration in July-September,
479 October-December, and January-March in the current and prior year. Chlorophyll-a concen-
480 tration was not a significant predictor for the Jul-Sep catch for any of the tested combinations
481 of current or prior season and quarter. The only significant effect was seen for Oct-Mar mon-
482 soon catches using chlorophyll-a concentration in Oct-Dec of the prior season (Table C1). This
483 is in contrast to the results with monsoon upwelling indices, which found a correlation with
484 the current season but not prior seasons.

485 The strongest correlation however was found with the multi-year average sea surface tem-
486 perature for the nearshore waters off Kerala, latitude 8 to 11 (Table 2, B7, B8 and B9). The
487 average sea surface temperature over multiple prior years has been found to be correlated with
488 sardine recruitment in Pacific sardines (Checkley et al., 2017; Jacobson & MacCall, 1995; Lin-
489 degren et al., 2013) and southern African sardines (Boyer et al., 2001). We tested as a model
490 covariate the average SST for 2.5 years prior to the Jul-Sep catch, so January-June in the cur-
491 rent calendar year and the two prior calendar years for a 30-month average. This covariate can
492 be used for forecasting since it does not overlap with either Jul-Sep or Oct-Mar catch. This
493 covariate with a non-linear response was the best covariate for both the Jul-Sep and Oct-Mar
494 catch. For Oct-Mar catch, the model with multi-year average SST had an adjusted R^2 of 67.5

495 versus 56.6 without. For the Jul-Sep catch, the adjusted R^2 was 41.0 versus 24.4 without the
496 multi-year average SST covariate. The response curve was step-like with a negative effect
497 at low temperatures and then an positive flat effect at higher temperatures (Figure 5). This
498 is similar to the step-response found in studies of the correlation between average SST and
499 recruitment in Pacific sardines (Jacobson & MacCall, 1995).

500 The only other strong correlation was found for Oct-Mar catch with the DMI in the
501 prior season. The Dipole Mode Index in the prior year has been shown to be correlated with
502 nearshore anoxia off the Kerala coast (Vallivattathillam et al., 2017). However this correlation
503 was only found with the Oct-Mar catch using the base model with both N_{t-1} and S_{t-2} . The
504 correlations with the multi-year SST average was more robust and found with both Oct-Mar
505 base models and also for Jul-Sep catch.

506 Discussion

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

517 Many studies on Pacific sardines have looked at the correlation between ocean surface
518 temperature (SST) and recruitment. Temperature can have direct effect on larval survival and
519 growth and an indirect effect on food availability. Studies in the California Current System,
520 have found that SST explains (a portion of) year-to-year variability in Pacific sardine recruit-
521 ment (Checkley et al., 2009, 2017; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012)
522 and that the average nearshore temperature over multiple seasons is the relevant explanatory
523 variable. Similar to these studies, we found that the average nearshore SST over multiple
524 seasons was the covariate that explained the most variability in catch both in the monsoon
525 and post-monsoon months. McClatchie et al. (2010) found no SST relationship with SST and

526 Pacific sardine recruitment, however their analysis used a linear relationship while the other
527 studies, and ours, that found a relationship allowed a non-linearity. Both Jacobson and Mac-
528 Call (1995) and Checkley et al. (2017) found a step-like response function for temperature:
529 below a threshold value the effect of temperature was linear and above the threshold, the effect
530 was flat and at lower temperatures the effect was negative and became positive as temperature
531 increased. Our analysis found a similar pattern with a negative effect when the 2.5-year aver-
532 age temperature was below 28.35°C and positive above and with the positive effect leveling
533 off above 28.5°C (Figure 5).

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

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

560 One of the purposes of our research was to investigate environmental covariates that would
561 improve prediction of landings, specific reduce the errors from a basic auto-correlated model
562 using only past catch. In Table 2, the out of sample prediction errors are shown in the LOOCV
563 RMSE (leave-one-out cross-validation root-mean-square error) column. The simpler catch
564 models, with only N_{t-1} as the covariate have better predictive performance than a null model
565 which uses only last years catch (in the same period) as the prediction. For Jul-Sep, the addition
566 of the best covariates only improves the predictions for one covariate, Jun-Sep SST. The Jul-
567 Sep catch is difficult to forecast. It has high variability that is poorly explained by past catch or
568 the environment. In contrast, the Oct-Mar catch is much better explained by prior catch (higher
569 R^2) and by the multi-year temperature. The multi-year average SST reduced the prediction
570 errors using either the more complex base model with two years of past catch as the covariate
571 (from LOOCV 1.062 to 0.827) and the simpler base model with only the prior year catch (from
572 LOOCV 0.966 to 0.796).

573 Conclusions

574 Remote sensing satellites can be used to detect changes in ocean physical, biological and chem-
575 ical properties, such as surface temperature, winds, surface height, surface waves, rainfall and
576 surface salinity, as well as the ecosystem and water quality changes. Unlike in-situ measure-
577 ments, environmental measures from remote-sensing can be acquired rapidly and over large
578 regions. However, which environmental covariates will improve forecasts is not obvious from
579 oil sardine life-history alone. We tested many of the covariates known or suspected to have
580 an effect on sardine spawning, growth and survival (Table 1): precipitation, upwelling indices,
581 ocean temperature and chlorophyll-a in various critical months of the sardine life-cycle. We
582 found that the multi-year average nearshore ocean temperature explained the most variability
583 in the landings. This covariate is not as directly tied to stages of the oil sardine life-cycle as
584 the other covariates we tested, though it does integrate over multiple influences (upwelling
585 strength and temperature) over multiple years.

586 The temperature of the Western Indian Ocean, of which the Southeast Arabian Sea is a
587 part, has been increasing over the last century at a rate higher than any other tropical ocean
588 (Roxy et al., 2014) and the warming has been most extreme during the summer monsoon
589 months. This ocean climate change is affecting oil sardine distributions with significant land-
590 ings now occurring north of Goa (Vivekanandan et al., 2009). Continued warming is expected
591 to affect the productivity of the region via multiple pathways, including both the direct ef-

592 ffects of temperature change on the physiology and behavior of organisms and a multiple of
593 indirect effects (Moustahfid et al., 2018). These indirect effects include changes to salinity,
594 oxygen concentrations, currents, wind patterns, ocean stratification and upwelling spatial pat-
595 terns, phenology, and intensity. Incorporating environmental covariates into landings forecasts
596 has the potential to improve fisheries management for small pelagics such as oil sardines in
597 the face of a changing ocean environment (Haltuch et al., 2019; Tommasi et al., 2016). How-
598 ever, monitoring forecast performance and covariate performance in models will be crucial as
599 a changing ocean environment may also change the association between landings and average
600 sea surface temperature.

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849 **Figure Legends**

850 Figure 1. Southwest coast of India with the latitude/longitude boxes used for the satellite data.
851 Kerala State is marked in grey and the oil sardine catch from this region is being modeled.

852 Figure 2. Quarterly catch data 1956-2014 from Kerala. The catches have a strong seasonal
853 pattern with the highest catches in quarter 4 (Oct-Dec). Note that the fishery is closed July 1 to
854 mid-August, thus the fishery is only open 1.5 months in quarter 3 (Jul-Sep). The mean catch
855 (metric tonnes) in quarters 1 to 4 are 38, 19.2, 30.9, and 59.9 metric tonnes respectively.

856 Figure 3. Key oil sardine life-history events overlaid on the monthly sea surface tempera-
857 ture in the nearshore and offshore and the nearshore chlorophyll concentration.

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

865 Figure 5. Effects of the two most influential covariates estimated from the GAM mod-
866 els: 2.5 year average SST and upwelling intensity in June-September (spawning months).
867 Panel A) Effect of the 2.5 year average SST on Jul-Sep catch (late spawning and early post-
868 spawning months). Panel B) Effect of upwelling (inshore/off-shore SST differential) during
869 June-September in the current season on Jul-Sep catch. The index is the difference between
870 offshore and inshore SST, thus a negative value indicates warmer coastal surface water than
871 off-shore. Panel C) Effect of the 2.5 year average SST on Oct-Mar catch (post-monsoon, age-
872 0, -1, -2 year fish). Panel D) Effect of upwelling (inshore/off-shore SST differential) during
873 June-September in the current season on Oct-Mar catch.

874 Figure 6. Fitted versus observed catch with models with and without the 2.5 year average
875 SST included as a covariate. The line is the one-to-one line (prediction equals observed). Panel
876 A) Fitted versus observed log catch in Jul-Sep (late monsoon) with only Oct-Mar catch in the
877 previous season as the covariate: $S_t = s(N_{t-1}) + \varepsilon_t$. Panel B) Fitted versus observed log catch in
878 Jul-Sep with the 2.5-year average SST added as a covariate to the model in panel A. This model
879 was: $S_t = s(N_{t-1}) + s(V_t) + \varepsilon_t$. Panel C) Fitted versus observed log Oct-Mar catch with only
880 Oct-Mar catch in the previous season and Jul-Sep catch two seasons prior as the covariates:

881 $N_t = s(N_{t-1}) + s(S_{t-2}) + \varepsilon_t$. Panel D) Fitted versus observed log Oct-Mar catch with 2.5-year
882 average SST (V) added. This model was $N_t = s(N_{t-1}) + s(S_{t-2}) + s(V_t) + \varepsilon_t$.

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

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

Table 1. Continued.

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

Table 2. Top covariates for the monsoon (Jul-Sep) and post-monsoon (Oct-Mar) catch (S_t and N_t) models. M0, M1 and M2 are the base models with only prior catch as covariates. To the base models, the listed environmental covariates are added. The full set of covariate models and the results of the tests on the nested models sets are given in Appendix B. The LOOCV RMSE (root mean square error) is the out-of-sample prediction error. The LOOCV RSME for the null model for Jul-Sep catch was 1.599 and the LOOCV RMSE for the null model for Oct-Mar catch was 1.015. The fitted versus observed catches from the covariate models are shown in Figure 6.

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

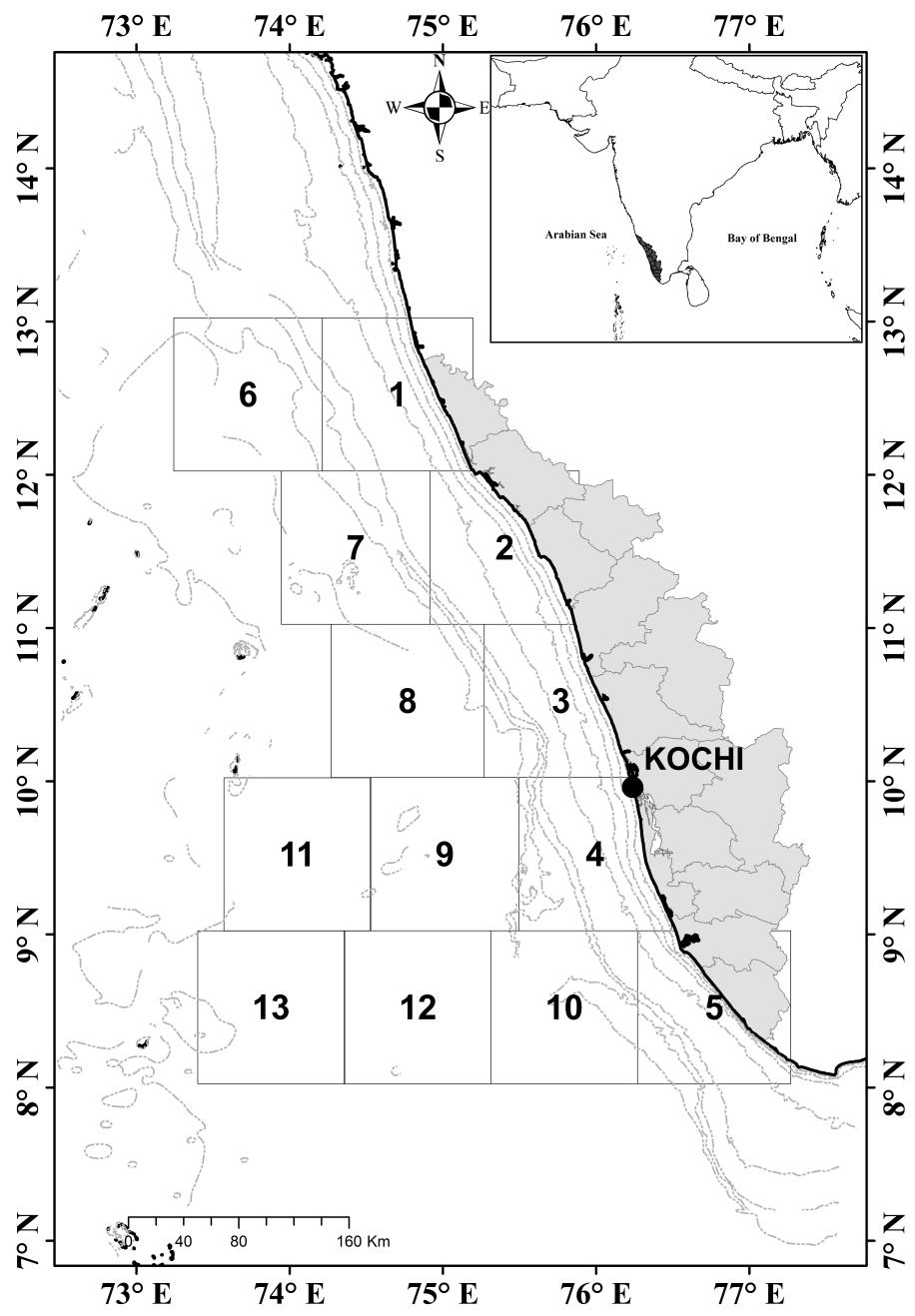


Figure 1

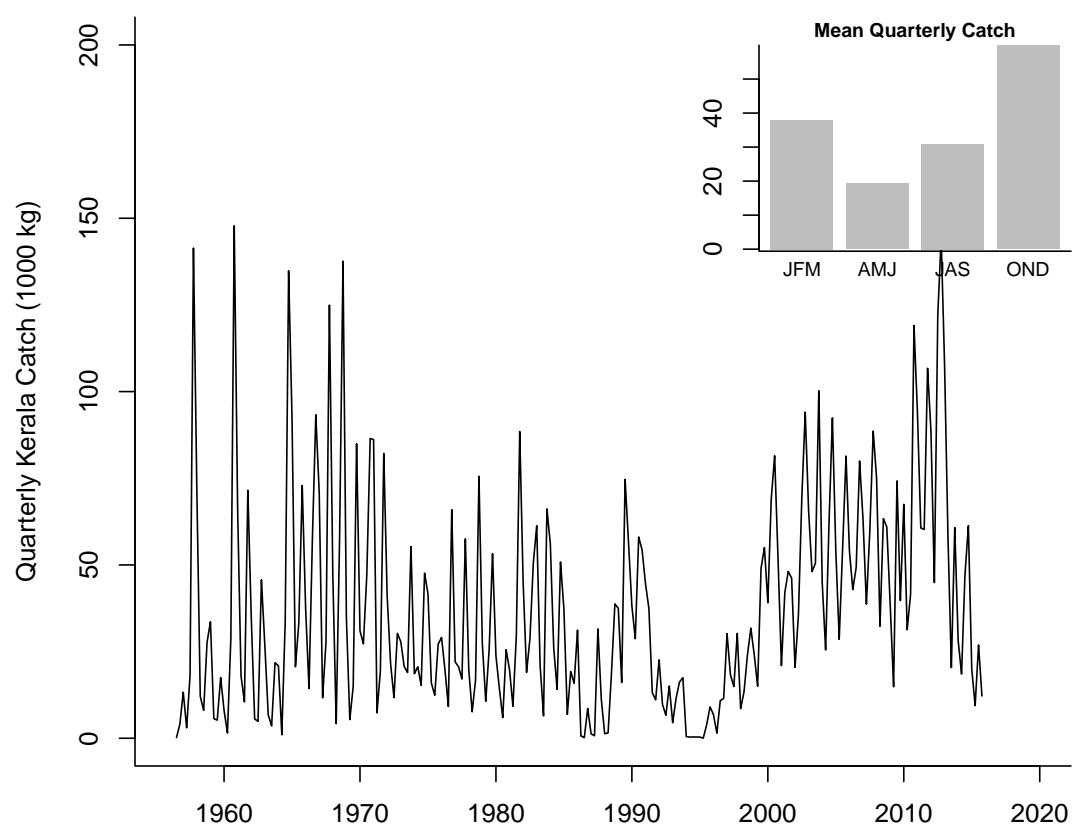


Figure 2

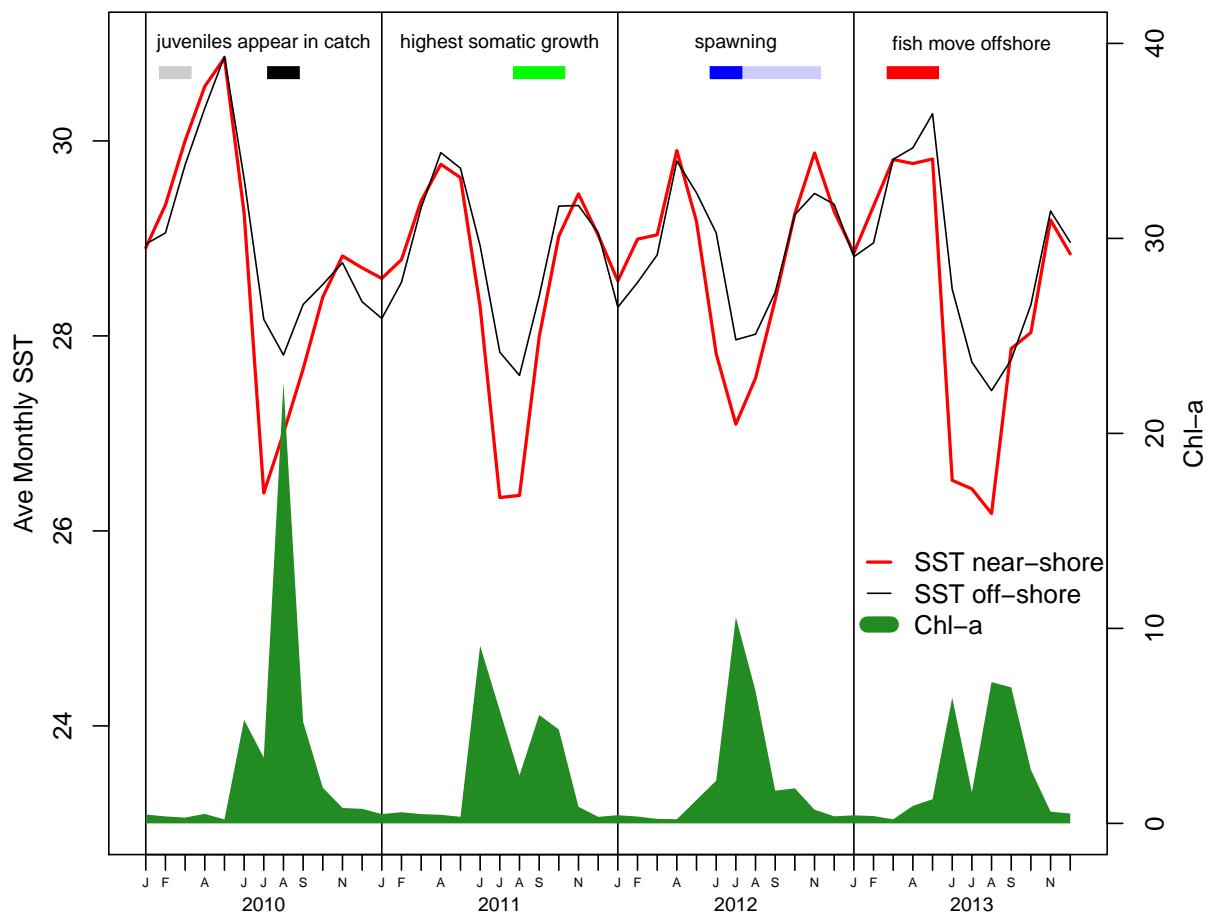


Figure 3

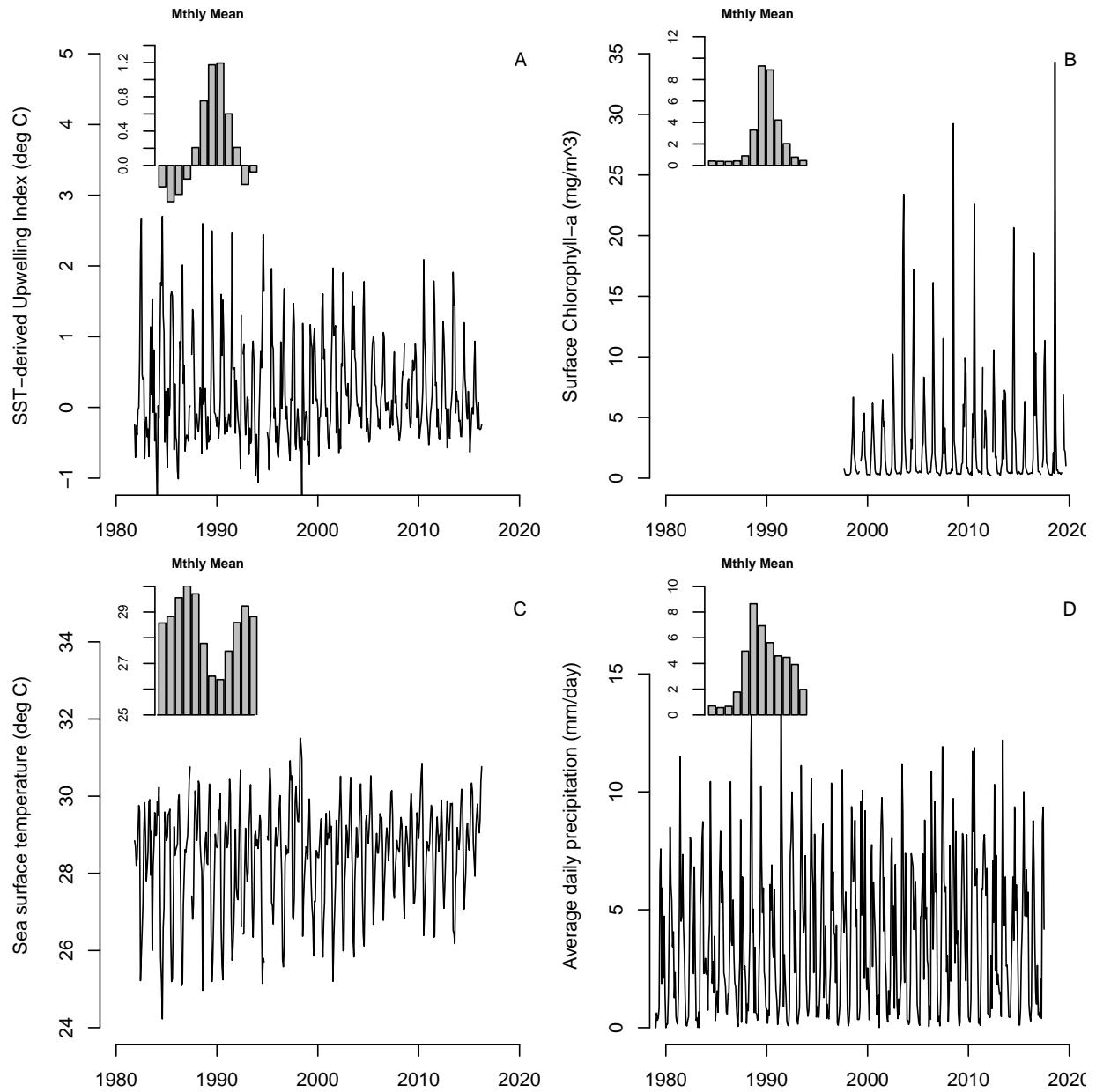


Figure 4

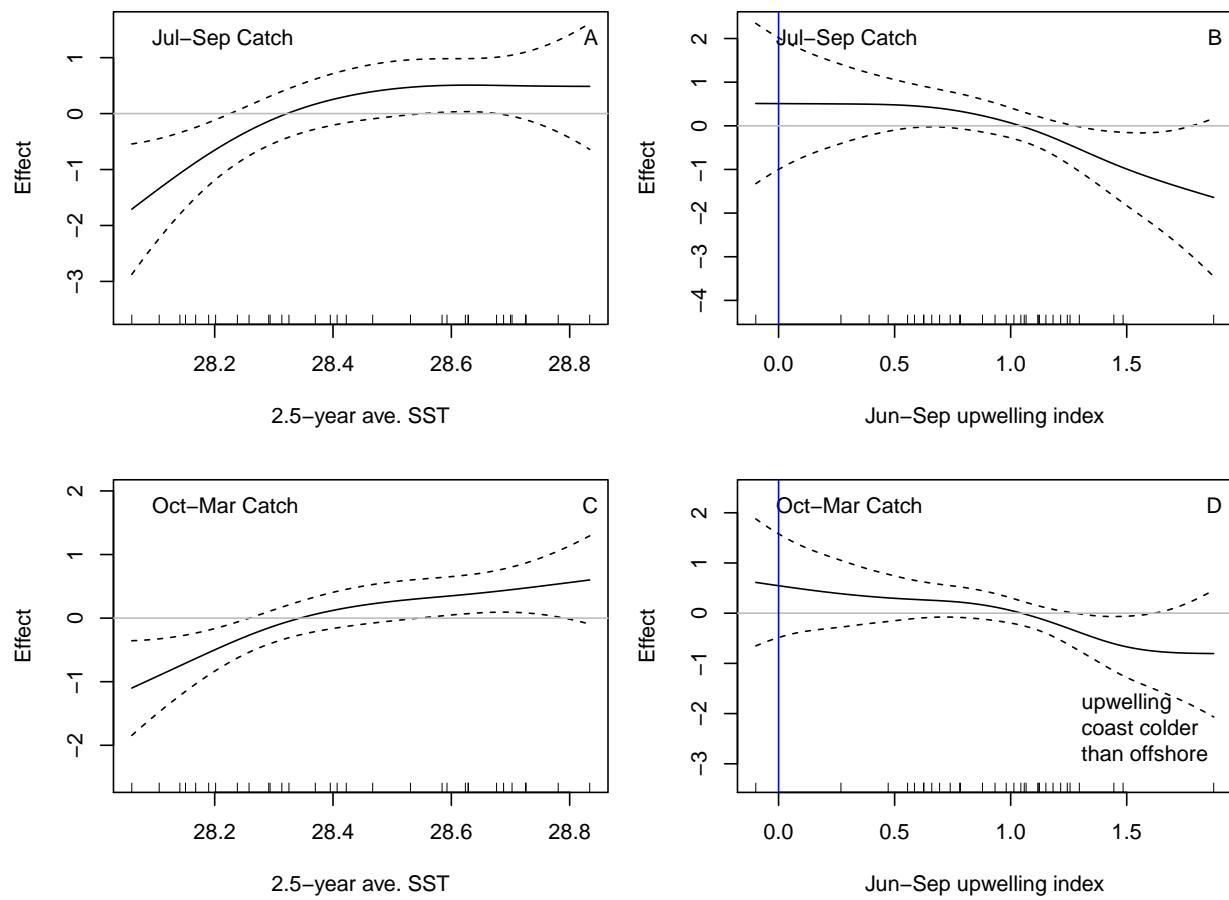


Figure 5

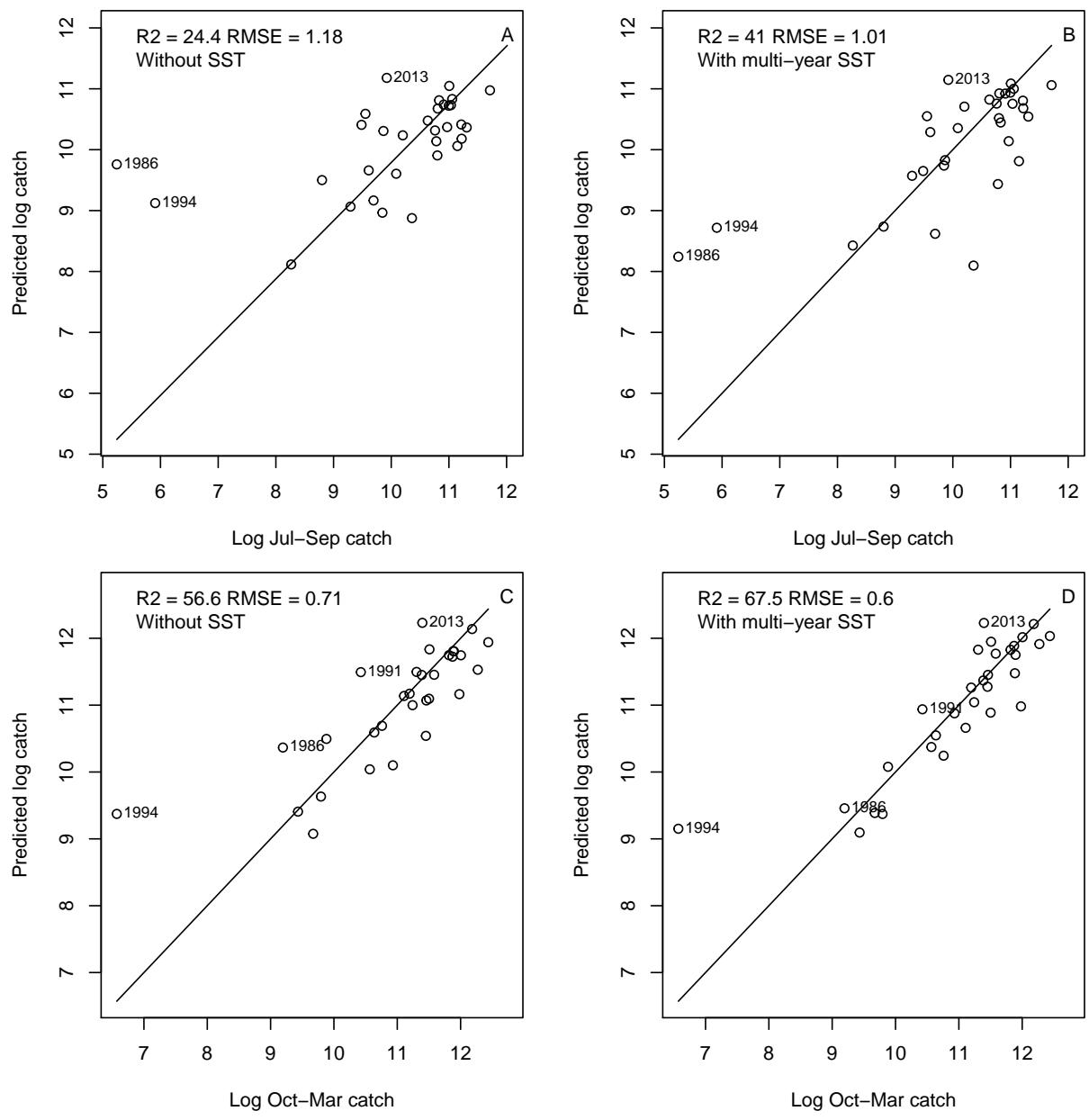


Figure 6