1 Fishing in a warming ocean: influence of changing temperature

2 and upwelling intensity on Indian oil sardine (*Sardinella*

3 *longiceps*) landings

4

5 Eli E. Holmes1, Smitha B.R.2, Nimit Kumar3, Sourav Maity3, David M.

6 Checkley4, Mark L. Wells5, Vera L. Trainer1

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

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

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

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

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

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

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25 **Abstract**

26 Commercial landings of sardine are known for strong year-to-year fluctuations. A key

27 driver is thought to be environmental variability, to which small forage fish are especially

28 sensitive. We examined the environmental drivers associated with landings fluctuations in

29 the Indian oil sardine using a 32-year time series off Kerala state. Past research suggested a

30 variety of influential variables: precipitation, upwelling intensity, ocean temperature (SST),

31 chlorophyll density and large-scale coupled atmosphere–ocean phenomena (ENSO). Using

32 the life-history of the Indian oil sardine, we developed hypotheses concerning how these

33 environmental variables might affect landings and tested them using generalized additive

34 models which allow non-linear response curves and dynamic linear models which allow

35 time-varying responses. We found significant correlation for only two variables: upwelling

36 intensity and the multi-year average nearshore SST. Both monsoon and post-monsoon

37 landings were correlated with upwelling intensity in June-September. Upwelling intensity

38 has both a positive effect (fueling higher food availability) and a negative effect at extreme

39 intensity (bringing poorly oxygenated water to the surface). However, the most significant

40 correlation (adjusted R2 of 67.5%) was between the 2.5 year average nearshore SST and

41 post-monsoon landings. The multi-year average SST also been identified as a predictor for

42 Pacific sardine and southern African sardine fluctuations, suggesting that the average SST

43 over the sardine life-span successfully captures a variety of factors which predict future

44 abundance. The temperature in the Western Indian Ocean has been increasing faster than in

45 other tropical oceans and the warming has been most extreme during the summer monsoon.

46 Our work highlights that these changes in summer upwelling intensity and sea temperature

47 are likely to affect future landings.

48

49 **Keywords**: Indian oil sardine, catch prediction, GAM modeling, climate, sea surface

50 temperature, remote sensing, Southeastern Ariabian Sea

# 51 Introduction

52 Environmental variability is known to be a key driver of population variability of small forage

53 fish such as sardines, anchovy and herring (Alheit & Hagen, 1997; Checkley et al., 2017; Cury

54 et al., 2000). In particular, ocean temperature and upwelling dynamics, along with density-

55 dependent feedback, have been identified as important in affecting recruitment success and

56 biomass of European and Pacific sardines (*Sardina pilchardus* and *Sardinops sagax*) (Alheit et

57 al., 2012; Garza-Gil et al., 2015; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012;

58 Lindegren et al., 2013; Rykaczewski & Checkley, 2008). Like other sardines, the Indian oil

59 sardine shows strong interannual fluctuations and larger decadal booms and busts. The Indian

60 oil sardine offers an instructive case study to investigate the effects of environmental variabil-

61 ity, particularly temperature and upwelling dynamics, as they occupy an ocean system that is

62 warmer than that occupied by other sardines and have a strong seasonal cycle driven by the

63 Indian summer monsoon.

64 The Indian oil sardine (*Sardinella longiceps* Valenciennes, 1847) is one of the most com-

65 mercially important fish resources along the southwest coast of India (Figure 1) and historically

66 has comprised approximately 25% of the catch biomass (Vivekanandan et al., 2003). Land-

67 ings of the Indian oil sardine are highly seasonal, peaking after the summer monsoon period in

68 October-December and reaching a nadir in spring before the summer monsoon in April-June

69 (Figure 2). At the same time, the landings of this small pelagic finfish are highly variable

70 from year to year. Small pelagics are well known to exhibit high variability in biomass due

71 to the effects of environmental conditions on survival and recruitment (Alheit & Hagen, 1997;

72 Checkley et al., 2017; Cury et al., 2000). In this fishery, environmental conditions also affect

73 exposure of sardines to the fishery. Until recently, the Indian oil sardine fishery was artisanal

74 and based on small human or low powered boats with no refrigeration. The fishery was con-

75 fined to nearshore waters, and thus migration of sardines in and out of the coastal zone greatly

76 affected exposure to the fishery.

77 Researchers have examined a variety of environmental variables for their correlation with

78 landings of the Indian oil sardine. Precipitation during the monsoon and the day of the mon-

79 soon arrival are thought to act as either a direct or indirect cue for spawning (Antony Raja,

80 1969, 1974; Jayaprakash, 2002; Murty & Edelman, 1966; Pitchaikani & Lipton, 2012; Sri-

81 nath, 1998; Xu & Boyce, 2009). Although many studies have looked for and some have found

82 correlations between precipitation and landings, the reported relationships are positive in some

83 studies and negative in others (Madhupratap et al., 1994). Researchers have also looked for and

84 found correlations with various metrics of upwelling intensity (Jayaprakash, 2002; Longhurst

85 & Wooster, 1990; Madhupratap et al., 1994; Murty & Edelman, 1966; Srinath, 1998; Thara,

86 2011), with direct measures of productivity such as nearshore zooplankton and phytoplank-

87 ton abundance (George et al., 2012; Hornell, 1910; Madhupratap et al., 1994; Menon et al.,

88 2019; Nair, 1952; Nair & Subrahmanyan, 1955; Piontkovski et al., 2015; Pitchaikani & Lip-

89 ton, 2012), and with near-shore sea surface temperature (SST) (Annigeri, 1969; Pillai, 1991;

90 Prabhu & Dhulkhed, 1970; Supraba et al., 2016). SST can affect both somatic growth rates

91 and juvenile survival but also can cause fish to move off-shore and away from the shore-based

92 fishery. The multi-year average sea temperature is postulated to have effects on recruitment and

93 the survival of larval and juvenile sardines, which affect the later overall abundance (Checkley

94 et al., 2017; Takasuka et al., 2007). The El Ni\~no/Southern Oscillation (ENSO) has a cascad-

95 ing effect on all the aforementioned environmental parameters (SST, precipitation, upwelling)

96 which in turn impact oil sardines, and correlations have been found between ENSO indices and

97 landings (Rohit et al., 2018; Supraba et al., 2016) and coastal anoxia events (Vallivattathillam

98 et al., 2017).

99 In this paper, we study the utility of environmental covariates from remote sensing to ex-

100 plain year-to-year variability in oil sardine landings using the time series of quarterly Indian oil

101 sardine landings from the southwest coast of India. This time series is derived from a stratified

102 sampling design that surveys the fishery landing sites along the southeast Indian coast and was

103 first implemented in the 1950s (Srinath et al., 2005). This is purely a landings time series.

104 Catch-at-length data are not available prior to 2001. Effort data are indirect (boat composition

105 of the fishery) and appropriate effort data (estimates of number of trips or hours fishing) are

106 only available in a few recent years. In addition, stock size estimates and fisheries independent

107 data are unavailable. Thus traditional length- or age-structured models (e.g. virtual population

108 analysis) which produce biomass estimates are not possible. Instead we use statistical models

109 with covariates to model and produce a one-year ahead forecast of landings. Unlike prior work

110 on landings models with covariates, we use non-linear time-series models and dynamic linear

111 models to allow a flexible effect of covariates and past catch on current landings. We also focus

112 on environmental covariates measured via remote sensing. Remote sensing data provide long

113 time series of environmental data over a wide spatial extent at a daily and monthly resolution.

114 A better understanding of how and whether remote sensing data explains variation in seasonal

115 catch will support future efforts to use satellite data to improve catch forecasts.

116 Modeling and forecasting landings data using statistical models fit to annual or seasonal

117 catch time series has a long tradition in fisheries and has been applied to many species (Cohen

118 & Stone, 1987; Farmer & Froeschke, 2015; Georgakarakos et al., 2006; Hanson et al., 2006;

119 Lawer, 2016; Lloret et al., 2000; Mendelssohn, 1981; Nobel & Sathianandan, 1991; Prista

120 et al., 2011; Stergiou & Christou, 1996), including oil sardines (Srinath, 1998; Venugopalan

121 & Srinath, 1998). These models can be used to identity the variables correlated with catch

122 fluctuations and can be used to provide landings forecasts which are useful for fishery managers

123 and the fishing industry. An example of the former is using catch forecasts to set or give

124 warnings of seasonal fishery closures if the forecasted catch is higher than the allowed catch

125 limits (Farmer & Froeschke, 2015). An example of the latter is the annual Gulf and Atlantic

126 menhaden forecast produced by NOAA Fisheries; the report is titled, “Forecast for the 20XX

127 Gulf and Atlantic purse-seine fisheries and review of the 20XX fishing season”. A multiple

128 regression model with environmental covaraites, similar to the model used in our paper, was

129 developed by NOAA Fisheries in the 1970s (Schaaf et al., 1975). This model has been used

130 for the last 45 years to produce an annual forecast of menhaden landings. This forecast was

131 requested by the menhaden fishing industry and has been used for planning purposes by the

132 industry, not only the fishers but also fish catch sellers and buyers, businesses which provide

133 fisheries gear, and banks which provide financing (Hanson et al., 2006).

134 The goal of the work presented here is to determine the environmental covariates which

135 explain catch variability and improve the accuracy of catch forecasts. Landings of oil sardines

136 are determined by biomass, catchability, and effort. Catchability is mainly determined by the

137 inshore versus offshore distribution of the sardine. The fishery is restricted to the nearshore

138 < 50 km offshore (Rohit et al., 2018) and when the sardines move offshore to spawn or to

139 avoid hypoxic or excessive warm water, they are no longer available to the fishery. Thus

140 the environment has a strong impact on catchibility. Recruitment and survival tied to the the

141 environmental factors which determine food resources. The covariates studied are directly

142 linked to known and conjectured connections between the environment and oil sardine that

143 are expected to affect catch. This work is part of a joint research project between US and

144 Indian research agencies: the National Marine Fisheries Service, NOAA, USA and the Indian

145 National Centre for Ocean Information Services and the Centre for Marine Living Resources

146 and Ecology, in the Ministry of Earth Sciences, India. The project objective is to develop a

147 operational forecast of sardine landings, to be used by the Indian fishery industry for planning.

148 **Study Area**

149 Our analysis focuses on the Kerala coast (Figure 1) region of India, where the majority of the

150 Indian oil sardines are landed and where oil sardines comprise ca. 40% of the marine fish catch

151 (Srinath, 1998; Vivekanandan et al., 2003). This area is in the Southeast Arabian Sea (SEAS),

152 one of world’s major upwelling zones, with seasonal peaks in primary productivity driven by

153 upwelling caused by winds during the Indian summer monsoon (Habeebrehman et al., 2008;

154 Madhupratap et al., 2001) between June and September. Within the SEAS, the coastal zone off

155 Kerala between 9◦N to 13◦N has especially intense upwelling due to the combined effects of

156 wind stress and remote forcing (BR, 2010; BR et al., 2008). The result is a strong temperature

157 differential between the near-shore and off-shore and high primary productivity and surface

158 chlorophyll in this region during summer and early fall (BR, 2010; Chauhan et al., 2011;

159 Habeebrehman et al., 2008; Jayaram et al., 2010; Madhupratap et al., 2001; Raghavan et

160 al., 2010). The primary productivity peaks subside after September while mesozooplankton

161 abundances increase and remain high in the post-monsoon period (Madhupratap et al., 2001).

162 **Oil sardine life cycle and fishery**

163 The Indian oil sardine fishery is restricted to the narrow strip of the western India continental

164 shelf, within 20 km from the shore (Figure 1). The yearly cycle of the fishery begins at the

165 start of spawning during June to July, corresponding with the onset of the southwest monsoon

166 (Antony Raja, 1969; Chidambaram, 1950) and the initiation of strongly cooler nearshore SST

167 due to upwelling (Figure 3). At this time, the mature fish migrate from offshore to coastal

168 spawning areas, and the spawning begins during the southwest monsoon period when temper-

169 ature, salinity and suitable food availability are conducive for larval survival (Chidambaram,

170 1950; Jayaprakash & Pillai, 2000; Krishnakumar et al., 2008; Murty & Edelman, 1966; Nair et

171 al., 2016). Although peak spawning occurs in June to July, spawning continues into Septem-

172 ber (Antony Raja, 1969; Hornell, 1910; Hornell & Nayudu, 1923; Prabhu & Dhulkhed, 1970)

173 and early- and late-spawning cohorts are evident in the length distributions of the 0-year fish.

174 Spawning occurs in shallow waters outside of the traditional range of the fishery (Antony Raja,

175 1964), and after spawning the adults migrate closer to the coast and the spent fish become ex-

176 posed to the fishery.

177 After eggs are spawned, they develop rapidly into larvae (Nair, 1959). The phytoplankton

178 bloom that provide sardine larvae food is dependent upon nutrient influx from coastal up-

179 welling and runoff from rivers during the summer monsoon and early fall. The blooms start in

180 the south near the southern tip of India in June, increase in intensity and spread northward up

181 the coast (BR, 2010). Variation in the bloom initiation time and intensity leads to changes in

182 the food supply and to corresponding changes in the growth and survival of larvae and in the

183 later recruitment of 0-year sardines into the fishery (George et al., 2012). Oil sardines grow

184 rapidly during their first few months, and 0-year fish (40mm to 100mm) from early spawn-

185 ing appear in the catch in August and September in most years (Antony Raja, 1970; Nair et

186 al., 2016). As the phytoplankton bloom spreads northward, the oil sardines follow, and the

187 oil sardine fishery builds from south to north during the post-monsoon period. Oil sardines

188 remain inshore feeding throughout the winter months, until March to May when the inshore

189 waters warm considerably and sardines move off-shore to deeper waters (Chidambaram, 1950).

190 Catches of sardines are correspondingly low during this time for all size classes. The age at

191 first maturity occurs at approximately 150 mm size (Nair et al., 2016), which is reached within

192 one year. When the summer monsoon returns, the oil sardine cycle begins anew.

193 Catches along the Kerala coast are high throughout the year except during quarter 2, April-

194 June (Figure 2). The age-distribution caught by the fishery varies through the year. The fishery

195 is closed during June to mid-July during the monsoon and peak spawning, and when it resumes

196 in mid-July, it is first dominated by 1-2.5 year old mature fish (Antony Raja, 1969; Bensam,

197 1964; Nair et al., 2016). In August or September a spike of 0-year (40mm) juveniles from

198 the June spawning typically appears in the catch (Antony Raja, 1969; Nair et al., 2016) and

199 another spike of 0-year fish is sometimes seen in February from the late fall spawning (Prabhu

200 & Dhulkhed, 1967, 1970). From October through June, the catch is dominated by fish from

201 120mm-180mm (Antony Raja, 1970; Nair et al., 2016; Prabhu & Dhulkhed, 1970) which is a

202 mix of 0-year, 1-year and 2-year fish (Nair et al., 2016; Rohit et al., 2018).

## 203 Contrast between catch modeling versus biomass modeling

204 Detailed yearly effort data for the individual gears is not available for the entire catch time

205 series and the data available on size of the fleet are a coarse metric of effort and thus are

206 difficult to use to compute catch-per-unit effort stastistics. Nonetheless the number of boats and

207 fishers involved in the fishery has been increasing as the population in Kerala has increased.

208 Oil sardines are caught primarly by ring seines, which were introduced in the early 1980s.

209 Ring seines of different sizes are used both both traditional small boats with a small outboard

210 motor and large mechanized ships (Das & Edwin, 2018). Since 1985, the ring seine fishery

211 has expanded steadily in terms of horsepower, size of boats, length of nets. There are concerns

212 that overfishing and especially catch of juveniles, which are at times discarded (Das & Edwin,

213 2018) is a factor in the most recent oil sardine declines (Kripa et al., 2018).

214 The relationship between the oil landings and the stock abundance is complex. It depends

215 both on the fleet size and composition, but also depends on the proximity of the stock to the

216 shore-based fishery. Although the landings are not a direct proxy for the overall abundance of

217 oil sardines, landings are often assumed to reflect the total abundance in most years for reasons

218 specific to the species and the fishery (Kripa et al., 2018): For most of the period of analysis,

219 the fishery was artisanal: small boats with small motors, no refridgeration, and limited to the

220 near shore. The ring seine was introduced but widespread mechanization of the fleet is a recent

221 developement. The artisanal fisherman have limited ability to target the stock, at least not to the

222 degree that landings can remain constant as a stock declines, a pattern than can be observed in

223 a large, mobile, highly mechanized fleet. The fishery is unregulated, except for a brief closure

224 during the monsoon months. Unlike some species, oil sardine shoals do not perform long

225 distance migrations that take them out of contact with the fishery. However for the purpose

226 of our study, the assumption of a tight relationship between landings and abundance is not

227 necessary. The objective is to understand what drives landings variability, whether it be due to

228 abundance variability or due to exposure to the fishery (by being closer to shore).

# 229 Materials and Methods

## 230 Sardine landing data

231 Quarterly fish landing data have been collected by the Central Marine Fisheries Research In-

232 stitute (CMFRI) in Kochi, India, since the early 1950s using a stratified multi-stage sample

233 design (Srinath et al., 2005). The survey visits the fish landing centers along the entire south-

234 east coast of India and samples the catch from the variety of boat types and gear types used

235 in the coastal fishery. Landings estimates are available for all the coastal states, however we

236 model the catch for the state of Kerala only, where the longest time series is available and the

237 overwhelming majority of oil sardines are landed (Figure 2). Kerala contributes a remarkable

238 14.4% of the total marine production (CMFRI, 2017) and Major resources contributing to the

239 pelagic landings were oilsardine (57.4%). The quarterly landings (metric tons) for oil sardine

240 landed from all gears in Kerala were obtained from CMFRI reports (1956-1984) and online

241 databases (1985-2015) (CMFRI, 1969, 1995, 2016; Jacob et al., 1987; Pillai, 1982). The quar-

242 terly landing data were log-transformed to stabilize the variance. Yearly effort data for the

243 individual gears is not available for the entire catch time series and the data available on size of

244 the fleet are a coarse metric of effort and thus are difficult to use to compute catch-per-unit ef-

245 fort stastistics. However the goal in this study is to describe and forecast landings, not biomass,

246 and our analysis uses landings data as is standard in landings modeling.

## 247 Remote sensing data

248 We analysed monthly composites of the following environmental data derived from satellite

249 data: sea surface temperature (SST), chlorophyll-a (CHL), upwelling (UPW), the Oceanic

250 Niño Index (ONI) and precipitation. The monthly means of the covariate time series are shown

251 in Figure 4.

252 For sea surface temperature, we used Advanced Very-High Resolution Radiometer

253 (AVHRR) data, which provides accurate nearshore SST values. Although the ICOADS

254 product provides SST values for earlier years, ICOADS does not provide accurate nearshore

255 temperatures. For 1981 to 2003, we used the Pathfinder Version 5.2 product on a 0.0417

256 degree grid. These data were developed by the Group for High Resolution Sea Surface

257 Temperature (GHRSST) and served by the US National Oceanographic Data Center. For

258 2004 to 2016, we used the NOAA CoastWatch SST products derived from NOAA’s Polar

259 Operational Environmental Satellites (POES).

260 For chlorophyll-a, we used the chlorophyll-a products developed by the Ocean Biology

261 Processing Group in the Ocean Ecology Laboratory at the NASA Goddard Space Flight Cen-

262 ter. For 1997 to 2002, we used the chlorophyll-a 2014.0 Reprocessing (R2014.0) product from

263 the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite. These data

264 are on a 0.1 degree grid. For 2003 to 2017, we used the MODIS-Aqua product on a 0.05 de-

265 gree grid. These CHL data are taken from measurements by the Moderate Resolution Imaging

266 Spectroradiometer (MODIS) on NASA’s Aqua Spacecraft. The SST and CHL data were aver-

267 aged across thirteen 1 degree by 1 degree boxes which roughly parallel the bathymetry (Figure

268 1). The SST and CHL satellite data were retrieved from the NOAA ERDDAP server (Simons,

269 2017).

270 For an index of coastal upwelling, we used the sea-surface temperature differential be-

271 tween near shore and 3 degrees offshore as described by Naidu et al. (1999) and Smitha et

272 al. (2008). The index was computed as the average SST in box 4 off Kochi (Figure 1) minus

273 the average SST in box 13. For SST, we used the remote sensing sea-surface temperature data

274 sets described above. This SST-based upwelling index has been validated as a more reliable

275 metric of upwelling off the coast of Kerala compared to wind-based upwelling indices (BR et

276 al., 2008). The SST-based upwelling index and chlorophyll-a blooms are strongly correlated

277 (Figure 3).

278 Precipitation data were obtained from two different sources. The first was an estimate

279 of the monthly precipitation (in mm) over Kerala from land-based rain gauges (Kothawale &

280 Rajeevan, 2017); these data are available from the Indian Institute of Tropical Meteorology

281 and the data are available from the start of our landing data (1956). The second was a remote

282 sensing precipitation product from the NOAA Global Precipitation Climatology Project (Adler

283 et al., 2016). This provides estimate of precipitation over the ocean using a global 2.5 degree

284 grid. We used the 2.5 by 2.5 degree box defined by latitude 8.75 to 11.25 and longitude 73.25

285 to 75.75 for the precipitation off the coast of Kerala. These data are available from 1979

286 forward (NCEI, 2017). The land and nearshore ocean precipitation data are highly correlated

287 (Appendix E), supporting the use of the land time series as a proxy for the precipitation over

288 the ocean off the Kerala coast.

289 The Oceanic Niño Index (ONI) is a measure of the SST anomaly in the east-central Pacific

290 and is a standard index of the El Niño/Southern Oscillation (ENSO) cycle. The ONI index is 3-

291 month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region, based on centered 30-

292 year base periods updated every 5 years. The ONI was downloaded from the NOAA National

293 Weather Service Climate Prediction Center.

294 **Hypotheses**

295 Our statistical analyses were structured around specific hypotheses (Table 1) concerning which

296 remote sensing covariates in which months should correlate with landings in specific quarters.

297 These hypotheses were based on biological information concerning how environmental condi-

298 tions affect sardine survival and recruitment and affect exposure of Indian oil sardines to the

299 coastal fishery as reviewed in the introduction. The quarter 3 (Jul-September) catch overlaps

300 the summer monsoon and the main spawning months. This is also the quarter where small

301 0-year fish from early spawning (June) often appear in the catch, sometimes in large numbers.

302 Variables that affect or are correlated with movement of sardines inshore should be correlated

303 with quarter 3 landings. In addition, pre-spawning (March-May) environmental conditions

304 should be correlated with the spawning strength as adult oil sardines experience an accel-

305 eration of growth during this period along with egg development. The post-monsoon catch

306 (October-May) is a mix of 0-year fish (less than 12 months old) and mature fish (greater than

307 12 months old). Variables that are correlated with spawning strength and larval and juvenile

308 survival should correlate with the post-monsoon catch both in the current year and in future

309 years, one to two years after.

310 Our hypotheses (Table 1) focus mainly on two drivers: upwelling and ocean tempera-

311 ture. We also test hypotheses concerning precipitation as this has historically been an envi-

312 ronmental covariate considered to influence the timing of oil sardine landings. More recently,

313 researchers have highlighted the influence of large-scale ocean processes, specifically the El

314 Niño/Southern Oscillation, on sardine fluctuations; therefore we test the Ocean Niño Index

315 (ONI) also. Chlorophyll density is directly correlated with sardine food availability and chloro-

316 phyll fronts are known to influence sardine shoaling. However our chlorophyll time series is

317 short (1997-2015) and the statistical power for testing correlation with landings is low. Tests

318 of chlorophyll are shown in the appendices but are not the focus of our analyses.

## 319 Statistical models

320 We modeled the catches during the late-monsoon season (quarter 3, July-September) separately

321 from the post-monsoon season (October-March). Thus there is no seasonality in our catch time

322 series, as we analyzed a yearly time series of quarter 3 catches separately from a yearly time

323 series of post-monsoon catches. We divided the catch in this way for biological and statistical

324 reasons. Catch in quarter 3 (July-September) captures a mix of spawning age fish as it overlaps

325 with the tail end of the spawning season, is affected by a fishery closure from July to mid-

326 August during the summer monsoon, and is periodically inflated by the appearance of small

327 0-year fish from early summer spawning. In addition, the covariates that affect the timing of

328 spawning, movement of post-spawning mature fish inshore, and early egg and larval survival

329 may be different than those that affect later growth, survival and shoaling that exposes fish

330 to the inshore fishery. Analyzing catch and covariate time series without seasonality also had

331 an important statistical benefit—we removed the problem of seasonality in the catch and all

332 the covariates. The oil sardine life-cycle is seasonal and driven by the strong seasonality in

333 this monsoon influenced system. A simple statistical model with quarters will explain much

334 of the quarterly catch data since most of the yearly variability is due to seasonality and any

335 environmental covariate with a similar seasonality will also show high correlation with the

336 landings. Our goal was to explain year-to-year variability thus eliminating the confounding

337 effect of seasonality in the data was important.

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

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

We compared the following catch models:

* null: *ln*(*Ci,t* ) = *ln*(*Cj,t*−1)
* random walk: *ln*(*Ci,t* ) = *α* + *ln*(*Cj,t*−1)) + *εt*
* linear AR-1: *ln*(*Ci,t* ) = *α* + *φln*(*Cj,t*−1)) + *εt*
* linear AR-2: *ln*(*Ci,t* ) = *α* + *φ*1*ln*(*Cj,t*−1)) + *φ*2*ln*(*Ck,t*−2)) + *εt*
* DLM AR-1: *ln*(*Ci,t* ) = *αt* + *φt ln*(*Cj,t*−1)) + *εt*
* GAM AR-1: *ln*(*Ci,t* ) = *α* + *s*(*ln*(*Cj,t*−1)) + *εt*
* GAM AR-2: *ln*(*Ci,t* ) = *α* + *s*1(*ln*(*Cj,t*−1)) + *s*2(*ln*(*Ck,t*−2)) + *εt*

*ln*(*Ci,t* ) is the log catch in the current year *t* in season *i*. We modeled two different catches:

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monsoon catch *St* (July-September), which is during the late part of the summer monsoon, and post-monsoon catch *Nt* (October-June). The catches were logged to stabilize and normalize the variance. *s*() is a non-linear function estimated by the GAM algorithm. The model is primarily statistical, meaning it should not be thought of as being a population growth model. We tested models with prior year post-monsoon catch (*Nt*−1) and 3rd quarter catch (*St*−1) as the explanatory catch variable. *St* was not used as a predictor for *Nt* ; *St* is the quarter immediately prior to *Nt* and would not be available for a forecast model since time is required to process landings data. The catch models were fit to 1982 to 2015 catch data, corresponding to the years where the SST, upwelling and precipitation data were available. F-tests and AIC on nested sets of models (Wood et al., 2016) were used to evaluate the support for the catch models and later for the covariate models. After selection of the best model with the 1982-2015 data, the fitting was repeated with the 1956-1981 and 1956-2015 catch data to confirm the form of the catch models.

Once the catch models were determined, the covariates were studied individually and then jointly. As with the catch models, F-tests, AIC and LOO (leave-one-out cross-validation) on nested sets of models were used to evaluate the support for models with covariates. The smoothing term was fixed at an intermediate value (sp=0.6) instead of treated as an estimated variable. Our models for catch with covariates typically took the form *ln*(*Ci,t* ) = *M* + *s*1(*V*1*,t* )+ *s*2(*V*2*,t*−1) + *εt* or *ln*(*Ci,t* ) = *M* + *β*1*V*1*,t* + *β*2*V*2*,t*−1 + *εt* where *M* was the best catch model from step 1. Thus models with covariates modeled both as a linear and non-linear effect were com- pared. The covariates tested are those discussed in the section on covariates that have been hypothesized to drive the size of the sardine biomass exposed to the fishery. We tested both models with one and two covariates, and did not use correlated covariates in the same model.

394 **Results**

## 395 Catches in prior seasons as explanatory variables

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Using the 1984-2015 catch data, which is the time-period that overlaps our available environ- mental data, the Jul-Sep catch models were compared against a “naive” model in which the forecasted Jul-Sep catch was simply the Jul-Sep catch in the prior year. The “naive” model has no estimated parameters and is a standard null model for time series modeling. Models with *ln*(*Nt*−1) (Oct-Mar catch in prior year), whether linear or non-linear, as the explanatory covariate were strongly supported over the naive model and over models with *ln*(*St*−1) (Jul-

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Sep catch in prior year) as the explanatory variable (Tables A1 and A2). Addition of the catch two years prior, *ln*(*Nt*−2) or *ln*(*St*−2), did not reduce AIC or LOOCV for either the linear or non-linear models. We tested the support for non-linearity in the effect of the prior year catch by comparing models with *ln*(*Nt*−1) or *ln*(*St*−1) included as a linear term or as a non-linear function *s*() using GAMs (Table A2). 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 LOOCV.

The results on model structure were similar for models of the Oct-Mar landings (*Nt* ), but the models explained much more of the variance (with a maximum adjusted *R*2 = 56*.*6). The most supported model for *Nt* (Tables A3 and A4) based on AIC and F-tests used a non- linear response to Oct-Mar catch of the previous season *ln*(*Nt*−1) plus a non-linear response to Jul-Sep catch two years prior *ln*(*St*−2). However the simpler model with only *ln*(*Nt*−1) had the lowest LOOCV (out of sample prediction accuracy). Thus this simpler model was also included as one of the base models for the Oct-Mar catch. Models with Jul-Sep catch in the current fishing season were not used as these data would not be available by Oct of the current season (for forecast purposes).

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

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

*M*0 : *ln*(*St* ) = *α* + *s*(*ln*(*Nt*−1)) + *εt .*

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

*M*1 : *ln*(*Nt* ) = *α* + *s*1(*ln*(*Nt*−1)) + *s*2(*ln*(*St*−2)) + *εt*

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*M*2 : *ln*(*Nt* ) = *α* + *s*(*ln*(*Nt*−1)) + *εt*

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

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

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

## 436 Environmental covariates as explanatory variables

437 There was no support for using precipitation during the summer monsoon (June-July) or pre-

438 monsoon period (April-May) as an explanatory variable for the quarter 3 (July-September) or

439 post-monsoon (October-March) catch (hypotheses S1 and S2; Tables B1 and B2). This was

440 the case whether precipitation in the current or previous season was used, if precipitation was

441 included as non-linear or non-linear effect, and if either precipitation during monsoon (June-

442 July) or pre-monsoon (April-May) were used as the covariate. Quarter 3 overlaps with the

443 spawning period and precipitation is often thought to trigger spawning, however we were un-

444 able to find any consistent association of catch during these spawning and early-post spawning

445 months with precipitation. Raja (1974) posited that the appropriate time period for the affect

446 of rainfall is the weeks before and after the new moon when spawning is postulated to occur

447 and not the total rainfall during the monsoon season. Thus the lack of correlation may be due

448 to using too coarse of a time average for the precipitation.

449 The sea-surface temperature before spawning (March-May) has been speculated to be cor-

450 related with successful egg development and spawning behavior (hypothesis S4 and S5) and

451 extreme heat events pre-spawning have been associated with low recruitment. This suggests

452 that March-May in the current and prior years should be associated with low catch. The sea-

453 surface temperature during larval and early juvenile development (October-December) may

454 affect survival and growth in multiple ways and thus could correlated with biomass in future

455 years (hypothesis L1). However we found no support for either of these SST variates as ex-

456 planatory variables for the July-September catch and only weak support (based on AIC) for

457 March-May SST in the current season for explaining variability in post-monsoon catch. The

458 fall average SST in the prior season did not explain variability in either July-September or

459 October-March catch. See Tables B3 and B4.

460 We also found no correlation between the ONI index (hypothesis A2) for either July-

461 September or post-monsoon catch (Tables B1 and B2).

462 Instead we found with the covariates indirectly and directly associated with productiv-

463 ity and food availability: upwelling intensity and surface chlorophyll. The correlation between

464 landings and upwelling was only found for upwelling in the current season. No correlation was

465 found when we used the upwelling index from the prior season. The correlation between land-

466 ings and upwelling was found for both July-September and October-March landings and with

467 either upwelling index: average nearshore SST along the Kerala coast during June-September

468 or the average SST nearshore versus offshore differential (UPW) off Kochi in June-September

469 (Table 2, Table B3 and Table B4). These two upwelling indices are correlated but not identical.

470 The model with average June-September nearshore SST was more supported than the model

471 using the SST differential off Kochi. For July-September catch, this model with a non-linear

472 response had an adjusted *R*2 of 41.0 versus an adjusted *R*2 of 24.4 for the model with no co-

473 variates (Table B3), and for October-March catch, the adjusted *R*2 was 61.8 versus 56.6 (Table

474 B4). Note, that this covariate is June-September in the current season and overlaps with the

475 July-September catch. Thus this model cannot be used to forecast July-September catch but

476 does help us understand what factors may be influencing catch during the monsoon.

477 Chlorophyll-a density is speculated to be an important predictor of larval sardine sur-

478 vival and growth. In addition, sardines shoal in response to coastal chlorophyll blooms, which

479 brings them in contact with the coastal fisheries. Thus chlorophyll-a density is assumed to be

480 an important driver of future or current sardine catches. We had chlorophyll-a remote sensing

481 data only from 1998 onward. Our simplest covariate model required 5 degrees of freedom,

482 thus we were limited in the analyses we could conduct. In addition, the years, 1998-2014,

483 have relatively low variability in catch sizes; the logged catch sizes during this period range

484 from 10-11 during quarter 3 and 11-12 during the other three quarters. Second degree polyno-

485 mial models were fit (Appendix C) to the average log chlorophyll-a density in the current and

486 prior season from quarter 3 (July-September), 4 (October-December), and 1 (January-March).

487 Chlorophyll-a density was not a significant predictor for the July-September catch for any of

488 the tested combinations of current or prior season and quarter. The only significant effect was

489 seen for post-summer monsoon catches using chlorophyll-a density in October-December of

490 the prior season (Table C1). This is in contrast to the results with monsoon upwelling indices,

491 which found a correlation with the current season but not prior seasons.

492 The strongest correlation however was found with the multi-year average sea surface tem-

493 perature for the nearshore waters off Kerala (latitude 8 to 11). The average sea surface tem-

494 perature over multiple prior years has been found to be correlated with sardine recruitment in

495 Pacific sardines (Checkley et al., 2017; Jacobson & MacCall, 1995; Lindegren et al., 2013)

496 and southern African sardines (Boyer et al., 2001). We tested as a model covariate the average

497 SST for 2.5 years prior to the July-September catch, so January-June in the current calendar

498 year and the two prior calendar years for a 30-month average. This covariate can be used

499 for forecasting since it does not overlap with either July-September or October-March catch.

500 This variate with a non-linear response was best covariate for both the July-September and the

501 post-monsoon catch. For post-monsoon catch, the model with SST had an adjusted *R*2 of 67.5

502 versus 56.6 without. For the July-September catch, the adjusted *R*2 was 41.0 with SST and 24.4

503 without. The response curve was step-like with a negative effect at low temperatures and then

504 an positive flat effect at higher temperatures (Figure 5). This is similar to the step-response

505 found in studies of the correlation between average SST and recruitment in Pacific sardines

506 (Jacobson & MacCall, 1995).

507 **Discussion**

508 Sardines in all the world’s ecosystems exhibit large fluctuations in abundance (Baumgartner et

509 al., 1992). These small forage fish are strongly influenced by natural variability in the ocean

510 environment. Upwelling, influenced by both large-scale forces such as regimes shifts and El

511 Ni\~{n}o/Southern Oscillation patterns (Alheit & Hagen, 1997; Schwartzlose et al., 2010)

512 and by seasonal wind and current patterns, brings nutrient rich and oxygen rich waters to the

513 surface. This drives the seasonal variability in phytoplankton resources and in turn sardine

514 prey (Bakun et al., 2008). Local variability in temperature, salinity, and oxygen levels have

515 both direct and indirect on sardine reproduction, recruitment and survival (Checkley et al.,

516 2017). Sardines are also influenced by competition and predation by other species and well-

517 known for their sensitivity to over-fishing which has been linked to many fishery collapses

518 (Kripa et al., 2018).

519 Many studies on Pacific sardines have looked at the correlation between ocean temperature

520 (SST) and recruitment. Temperature can have direct effect on larval survival and growth and

521 an indirect effect on food availability. Studies in the California Current System, have found

522 that SST explains year-to-year variability in Pacific sardine recruitment (Checkley et al., 2009,

523 2017; Jacobson & MacCall, 1995; Lindegren & Checkley, 2012) and that the average nearshore

524 temperature over multiple seasons is the explanatory variable. Similar to these studies, we

525 found that the average nearshore SST over multiple seasons was the covariate that explained

526 the most variability in catch both in the monsoon and post-monsoon months. McClatchie et

527 al. (2010) found no SST relationship with SST and Pacific sardine recruitment, however their

528 analysis used a linear relationship while the other studies, and ours, that found a relationship

529 (Checkley et al., 2017; Jacobson & MacCall, 1995) allowed a non-linear relationship. Both

530 Jacobson and MacCall (1995) and Checkley et al. (2017) found a step-like response function

531 for temperature: below a threshold value the effect of temperature was linear and above the

532 threshold, the effect was flat and at lower temperatures the effect was negative and became

533 positive as temperature increased. Our analysis found a similar pattern with a negative effect

534 when the 2.5-year average temperature was below 28*.*35◦C and positive above and with the

535 positive effect leveling off above 28*.*5◦C (Figure 5).

536 There were four outlier years when catch were much lower than expected based on prior

537 catches: 1986, 1991, 1994 and 2013. The 2.5-year average SST predicted the collapses in

538 1986 and 1991 (Figure 6); the size of the residual with the covariate was much smaller than

539 without the covariate. The largest collapse was in 1994 and the most recent, in our dataset,

540 was 2014. The 2.5-year average SST did not predict the 1994 nor 2013 collapse. There was

541 no change in the size of the residual with and without the covariate. In fact, none of the

542 covariates we tested changed the size of the model residuals for 1994 nor 2013. The causes of

543 these unusual declines appear either unrelated to the environmental factors we studied. This

544 suggests either that other factors, biological or anthropogenic, drove these declines or that a

545 particular combination of environmental factors led to the declines. It should also be noted

546 that our upwelling indices captured on one aspect of upwelling: the nearshore intensity. Other

547 aspects of upwelling also affect oil sardines, such as the spatial extent both along the coast and

548 off the coast and the timing of the start of upwelling.

549 Seasonal productivity in the SE Arabian Sea upwelling is driven the summer monsoon,

550 which causes strong coastal upwelling that moves from the south to the north over the summer.

551 This drives a strong seasonal pattern of zooplankton abundance (Figure 3). Despite the strong

552 connection between sardine recruitment, growth and survival with upwelling, we found no

553 correlation upwelling in the prior season with landings. We did find a correlation between

554 upwelling in the current season with landings in the current season. The biological reasons

555 behind a positive relationship with upwelling are clear. Upwelling drives productivity and

556 higher food resources in the current season leads to higher recruitment and higher numbers

557 of 0-year fish in the landings or may bring sardines into the nearshore to feed where they are

558 exposed to the fishery. However, the explanatory power of the upwelling indices was mainly

559 due to the negative effect of extremely high upwelling (Figure 5). Extremely high upwelling

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

561 **Conclusions**

562 Remote sensing satellites can be used to detect changes in ocean physical, biological and chem-

563 ical properties, such as surface temperature, winds, surface height, surface waves, rainfall and

564 surface salinity, as well as the ecosystem and water quality changes. Unlike in-situ measure-

565 ments, environmental measures from remote-sensing can be acquired rapidly and over large

566 regions. However, which environmental covariates will improve forecasts is not obvious from

567 oil-sardine life-history alone. We tested using many of the covariates known or suspected to

568 have a effect on sardine spawning, growth and survival: precipitation, upwelling indices, ocean

569 temperature and chlorophyll-a in various critical months of the sardine life-cycle. We found

570 that the multi-year average nearshore ocean temperature explained the most variability in the

571 landings. This covariate is not as directly tied to stages of the oil-sardine life-cycle as the other

572 covariates we tested, though it does integrate over multiple influences (upwelling strength and

573 temperature) over multiple years.

574 The temperature of the Western Indian Ocean, of which the Southeast Arabian Sea is a

575 part, has been increasing over the last century at a rate higher than any other tropical ocean

576 (Roxy et al., 2014) and the warming has been most extreme during the summer monsoon

577 months. This ocean climate change is affecting oil sardine distributions with significant land-

578 ings now occurring north of Goa (Vivekanandan et al., 2009). Continued warming is expected

579 to affect the productivity of the region via multiple pathways, including both the direct effects

580 of temperature change on the physiology and behavior of organisms and a multiple of indirect

581 effects (Moustahfid et al., 2018). These indirect effects includes changes to salinity, oxygen

582 concentrations, currents, wind patterns, ocean stratification and upwelling spatial patterns, phe-

583 nology, and intensity. Incorporating environmental covariates into landings forecasts has the

584 potential to improve fisheries management for small pelagics such as oil sardines in the face of

585 a changing ocean environment (Haltuch et al., 2019; Tommasi et al., 2016). However, moni-

586 toring forecast performance and covariate performance in models will be crucial as a changing

587 ocean environment may also change the association between landings and average sea surface

588 temperature.

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861 **Figure Legends**

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

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

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

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

Figure 5. Effects of covariates estimated from the GAM models. Panel A) Effect of the

2.5 year average nearshore SST on catch during the catch during July-September (late spawn- ing and early post-spawning) months. Panel B) Effect of upwelling (inshore/off-shore SST differential) during June-September in the current season on July-September catch. The index is the difference between offshore and inshore SST, thus a negative value indicates warmer coastal surface water than off-shore. Panel C) Effect of the 2.5 year average nearshore SST on catch during the catch during October-March (post-monsoon, age-0, -1, -2 year fish). Panel

D) Effect of upwelling (inshore/off-shore SST differential) during June-September in the cur- rent season on October-March catch. Strong upwelling (positive upwelling index) in the larval and juvenile high growth period (Oct-Dec) is associated with higher early survival and larger cohorts of age-0 fish in the catch.

Figure 6. Fitted versus observed catch with models with and without environmental co- variates. Panel A) Fitted versus observed log catch in the spawning months with only non- spawning catch in the previous season as the covariate: *St* = *s*(*Nt*−1) + *εt* . Panel B) Fitted versus observed log catch in July-September with the 2.5-year average nearshore SST added

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as a covariate to the model in panel A. This model was: *St* = *s*(*Nt*−1) + *s*(*Vt* ) + *εt* . Panel

C) Fitted versus observed log catch in the post-monsoon months with only post-monsoon catch in the previous season and July-September catch two seasons prior as the covariates: *Nt* = *s*(*Nt*−1) + *s*(*St*−2) + *εt* . Panel D) Fitted versus observed log catch in the post-monsoon

months with 2.5-year average nearshore SST (*V* ) added as covariates. This model was *Nt* =

*s*(*Nt*−1) + *s*(*St*−2) + *s*(*Vt* ) + *εt* .

Table 1. Hypotheses for covariates affecting landings. *St* is Jul-Sep catch in the current season, *St*−1 is Jul-Sep catch in the previous season. *Nt* is the Oct-Mar catch in the current season and *Nt*−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.

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| --- | --- |
| Hypothesis | Description |
| DD1  *St* ∼ *Nt*−1 | *St* is age 1+ age fish and reflects the 0-2yr fish in *Nt*−1  which have aged 3-6 months (Nair et al. 2016). |
| DD2  *St* ∼ *St*−1 + *St*−2 *Nt St*−1 + *St*−2 | *St* is age 1+ fish and is dominated by spent  post-spawning fish (Nair et al. 2016). *St* 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  *Nt* ∼ *Nt*−1 | *Nt*−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  *Nt* landings. |
| S1  *St* ∼ 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  *St* ∼ 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  *Nt* ∼ 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  *St* ∼ 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  *St* ∼ Mar-May r-SST in *t Nt* ∼ 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.

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| Hypothesis | Description |
| L1  *St* ∼ Oct-Dec ns-SST *t* − 1  *Nt* ∼ 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  *St* ∼ Jun-Sep UPW in *t* − 1 & *t Nt* ∼ 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  *St* ∼ CHL in *t* − 1 & *t Nt* ∼ 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  *St* ∼ 2.5-yr ave. ns-SST  *Nt* ∼ 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  *St* ∼ ONI in *t* − 1  *Nt* ∼ 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  *St* ∼ DMI in *t* − 1  *Nt* ∼ DMI in *t* − 1 & *t* | Negative Dipole Mode Index (DMI) values in Sep-Nov  are associated with anoxic events on the Kerala coast while positive values are associated with a absence of such events (Vallivattathillam et al. 2017). |

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

Residual

Adj.

LOOCV

*ln*(*Nt* ) = *M*1 + *s*(*Vt* ) 22 63 0.628 76.01 1.002

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| --- | --- | --- | --- | --- | --- |
| Model | df | R2 | RMSE | AIC | RMSE |
| Jul-Sep catch models with covariates |  |  |  |  |  |
| *Vt* = Jun-Sep SST current season |  |  |  |  |  |
| *Wt* = Jun-Sep Bakun-UPW current season |  |  |  |  |  |
| *Zt* = 2.5-year average SST  M0: *ln*(*St* ) = *α* + *s*(*ln*(*Nt*−1)) + *εt ln*(*St* ) = *M*0 + *s*(*Vt* )  *ln*(*St* ) = *M*0 + *βWt*  ⇒ *ln*(*St* ) = *M*1 + *s*(*Zt* )  Oct-Mar catch models with covariates | 28.6  25.9  27.6  26.2 | 24  41  28  41 | 1.184  1.007  1.133  1.011 | 109.52  103.43  108.66  103.26 | 1.299  1.192  1.404  1.338 |
| *Vt* = Mar-May SST current season *Wt* = Jun-Sep SST current season *Zt* = 2.5-year average SST  *Xt* = fall DMI prior season  M1: *ln*(*Nt* ) = *α* + *s*(*ln*(*Nt*−1)) + *s*(*ln*(*St*−2)) + *εt* | 24.8 | 57 | 0.713 | 79.53 | 1.062 |

*ln*(*Nt* ) = *M*1 + *βWt* 23.8 63 0.648 75.57 1.042

⇒ *ln*(*Nt* ) = *M*1 + *s*(*Zt* ) 22.7 67 0.597 71.88 0.827

*ln*(*Nt* ) = *M*1 + *s*(*Xt* ) 21.1 68 0.58 72.69 0.89

M2: *ln*(*Nt* ) = *α* + *s*(*ln*(*Nt*−1)) + *εt* 27.6 45 0.836 84.75 0.966

*ln*(*Nt* ) = *M*2 + *s*(*Vt* ) 24.8 47 0.791 85.9 0.981

*ln*(*Nt* ) = *M*2 + *βWt* 26.6 52 0.772 81.79 0.927

⇒ *ln*(*Nt* ) = *M*2 + *s*(*Zt* ) 25.3 60 0.688 76.34 0.796

*ln*(*Nt* ) = *M*2 + *s*(*Xt* ) 23.7 43 0.8 88.43 0.969

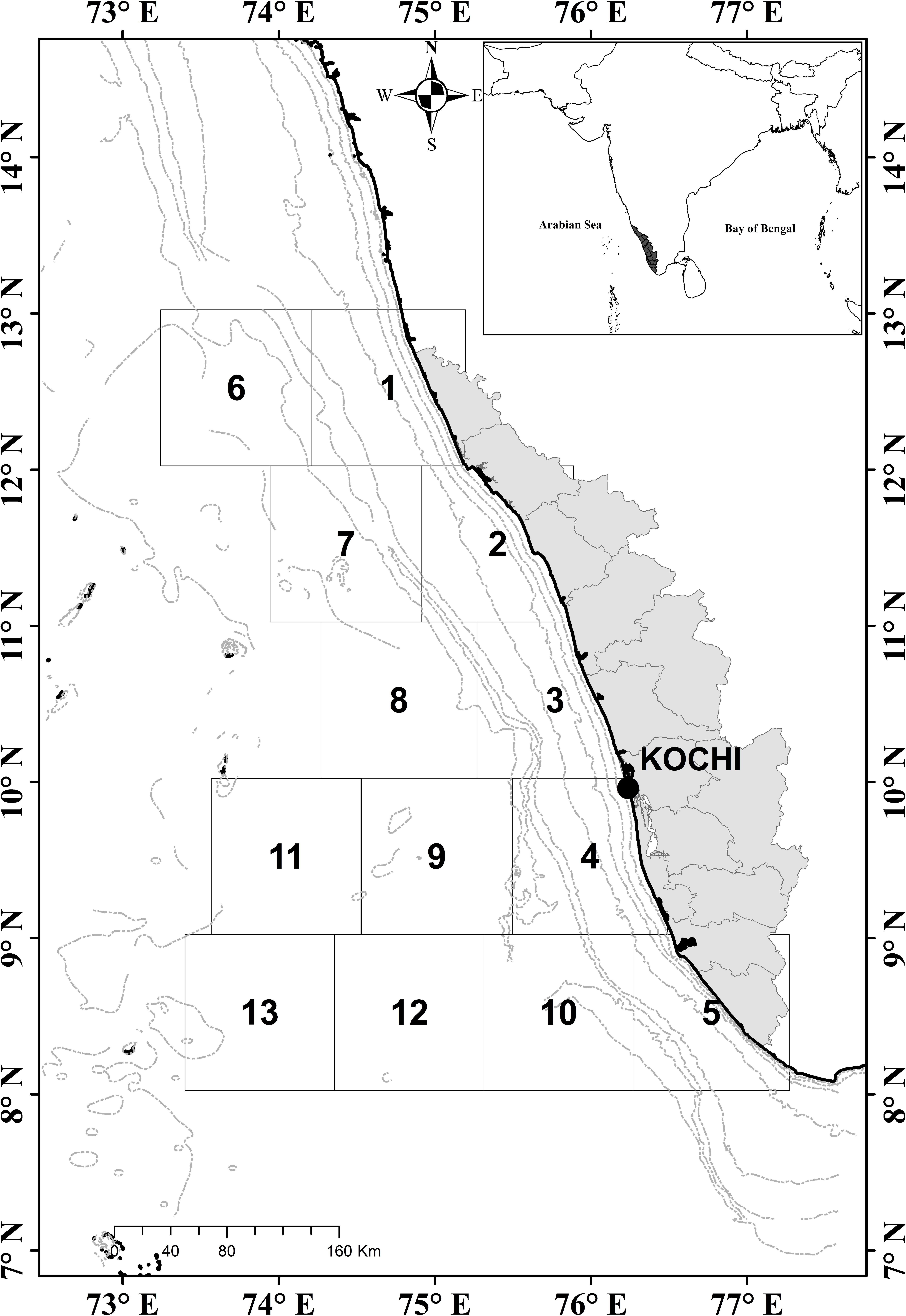


Figure 1

100

150

0

20

40

1960 1970 1980 1990 2000 2010 2020

**Mean Qtrly Catch**

JFM

JAS

Quarterly Kerala Catch (1000 kg)

0

50

Figure 2

Ave Monthly SST

26

28

30

20

Chl−a

30

40

J F A J J A S N J F A J J A S N J F A J J A S N J F A J J A S N

juveniles appear in catch highest somatic growth

spawning

fish move offshore

SST near−shore SST off−shore Chl−a

24

0

10

2010 2011 2012 2013

Figure 3

**Mthly Mean**

**Mthly Mean**

B

1990

**Mthly Mean**

1990

**Mthly Mean**

2000

2010

2020

D

1990

1990

2000

2010

2020

38

Sea surface temperature (deg C) SST−derived Upwelling Index

24 26 28 30 32 34 −1 0 1 2 3 4 5

1980

1980

25 27 29 0.0 0.4 0.8 1.2



Average daily precipitation (mm) Surface Chlorophyll−a

A

2000

2010

2020

C

2000

2010

2020

Figure 4

0 5 10 15 0 5 10 15 20 25 30 35



0 2 4 6 8 10

1980

1980

0 2 4 6 8 12



28.2 28.4 28.6 28.8 0.0 0.5 1.0 1.5

Jul−Sep Catch

A

Jul−Sep Catch

B

Effect

−3

−2

−1

0

Effect

−4 −3 −2 −1 0

1 2

2.5−year ave. SST Jun−Sep upwelling index

0

1

2

1

2

28.2 28.4 28.6 28.8 0.0 0.5 1.0 1.5

Oct−Mar Catch

C

Oct−Mar Catch

D

upwelling coast colder than offshore

Effect

−2

−1

Effect

−3 −2 −1 0

2.5−year ave. SST

Figure 5

Jun−Sep upwelling index

1

5 6 7 8 9 10 11 12 5 6 7 8 9 10 11 12

R2 = 24.4

A

R2 = 41

B

Predicted log catch without covariates

5

6

7

8

Predicted log catch with covariates

5

6

7

8

Log catch in monsoon months Log catch in monsoon months



R2 = 56.6

C

R2 = 67.5

D

Predicted log catch without covariates

10

11

12

Predicted log catch with covariates

10

11

12

7 8 9 10 11 12 7 8 9 10 11 12

7

8

9

7

8

9

Log catch in post−monsoon months

9

10

11

12

9

10

11

12

Figure 6

Log catch in post−monsoon months