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1 **Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in**

2 **the California Current Ecosystem revisited and revised**

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Abstract

Small pelagic fish typically show highly variable population dynamics, due in large part to climate variability. Despite this sensitivity to climate, few stocks of pelagic species are managed with consideration of the environment. The Pacific sardine (*Sardinops sagax*) represents a notable exception, for which sea surface temperature (SST) from the Scripps Institution of Oceanography (SIO) pier has been used, until recently, to adjust exploitation pressure under warm (favorable) and cold (unfavorable) climate conditions. Recently, the previously established temperature-recruitment relationship was reassessed using different methods, resulting in abandonment of the temperature-sensitive harvest control rule in 2012. In this study, we revisit the previous temperature-recruitment relationship using the original methodology and an updated data set from 1981 to 2010. In contrast to the recent re-assessment, we find temperature explains significant variability in recruitment and recruitment success. We also show that mean annual SST averaged over the present California Cooperative Oceanic Fisheries Investigations (CalCOFI) area is a better predictor of recruitment variability than SST at the SIO pier. We propose that sustainable management of the Pacific sardine should consider climate variability and that the basis for this be periodically updated and revised, in order to inform management with the best available science.

Key words: climate, recruitment, recruitment success, sardine, management, SST, SIO, CalCOFI

Introduction

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39   Small pelagic fish comprise one of the commercially most important marine fisheries

40   resources worldwide (FAO 2011). These species typically show highly variable population

41   dynamics, both in terms of individual growth and in numbers, mainly due to direct and indirect

42   responses to climate variability (Checkley et al. 2009), a feature consistent across multiple time

43   scales, from inter-annual variability, e.g., in recruitment (Cardinale et al. 2009; Lindegren et al.

44   2011), to multi-decadal fluctuations, e.g., the pronounced cycles of sardine and anchovy

45   population size (Lluch-Belda et al. 1989; Baumgartner et al. 1992; Schwartzlose et al. 1999). In

46   addition, human exploitation has been shown to impact population dynamics of small pelagic

47   fish (e.g., Hjermann et al. 2004; Freon et al. 2008), with consequences to socio-economics

48   (Hanneson et al. 2006) and ecosystem structure and function (Cury et al. 2000; Daskalov 2007).

49   Consequently, adjusting exploitation pressures to climate variability is both a challenge and an

50   opportunity to fisheries managers seeking sustainable exploitation of these important marine

51   resources. Despite the sensitivity to climate variability, few pelagic species are managed with

52   consideration of these key factors.

53   The Pacific sardine (*Sardinops sagax*) exhibits large fluctuations in spawning stock

54   biomass (SSB), recruitment (R), and recruitment success (R/SSB) (Fig. 1). Climate mediated

55   factors, mainly related to temperature, currents and upwelling (Jacobson and MacCall 1995;

56   Lluch-Belda et al. 2001; Song et al. 2012) and/or indirect effects through lower trophic levels

57   (Lynn 2003; Reiss et al. 2008; Rykaczewski and Checkley 2008) had been shown important to

58   explaining variation and contributing an understanding of these fluctuations. Until 2012, the

59   fishery was unusual in that its management used the three-year average of sea surface

60   temperature (SST) from the Scripps Institution of Oceanography (SIO) pier to adjust the

61   exploitation rate (Hill et al. 2010). The harvestable fraction of available biomass above a cutoff

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62 (150,000 tons) ranged from 5% during cool conditions to 15% during warm conditions (PFMC

63 1998). This decision rule accounted temperature conditions favorable and unfavorable for

64 sardine recruitment (Jacobson and MacCall 1995) and, to the extent possible, buffered against

65 large fluctuations in abundance and potentially avoid rapid population collapses, e.g., as

66 observed during the 1940s (Fig. 1a). The previously established temperature-recruitment

67 relationship (Jacobson and MacCall 1995) was recently shown by McClatchie et al. (2010),

68 albeit using a different methodology, to no longer be significant, resulting in removal of

69 temperature from the harvest control rule in 2012 (Hill et al. 2011).

70   In this study, we revisit the previous stock-recruitment and temperature relationships for

71 Pacific sardine (Jacobson and MacCall 1995) using the same methodology, i.e., Generalised

72 Additive Models (GAMs; Hastie and Tibshirani 1990). In contrast to the recent re-assessment

73 (McClatchie et al. 2010), we find a significant temperature effect explaining a considerable part

74 of variability in recruitment and recruitment success, and robust to sequentially refitting and

75 updating on an annual basis. However, we show that mean annual SST averaged over the

76 California Cooperative Oceanic Fisheries Investigations (CalCOFI) area provide a better

77 predictor of recruitment variability than SST measured locally at the SIO pier, as previously

78 suggested and used by management until 2012 (PFMC 1998; Hill et al. 2011).

79 **Material and methods**

80 **Data availability**

81   In order to investigate potential temperature effects on sardine recruitment at different

82 spatial scales, a number of variables characterising the local physical conditions, as well as

4

83   regional ocean-atmospheric forcing, were collected (Table 1). In accordance with previous

84   studies of the sardine recruitment-temperature relationship (Jacobson and MacCall 1995;

85   McClatchie et al. 2010), we used the annual average of sea surface temperature (SST) measured

86   daily at the SIO pier. In addition, we averaged SST (NOAA_ERSST_V3; Smith et al. 2008) for

87   the four offshore grid squares used by McClatchie et al. (2010). As an alternative to the SIO pier

88   temperature and the NOAA_ERSST_V3, we used the annual mean 5-15m temperature (here also

89   termed SST) from the regular CalCOFI area (i.e., averaged over all stations from line 76.7 to

90   93.3), covering a large part of the southern California Bight and the main spawning area of

91   sardine (Lynn 2003; Reiss et al. 2008). Finally, the Pacific Decadal Oscillation (PDO), as well as

92   the Multivariate El Niño Southern Oscillation Index (MEI), proxies for SST variations across the

93   North and Tropical Pacific, respectively, were used as indices of large-scale climate potentially

94   forcing recruitment dynamics. In order to represent potential effects of temperature specifically

95   during spawning and early development (i.e., egg and larval stages), spring averages (March –

96   May), corresponding to the peak spawning period of Pacific sardine (Checkley et al. 2009), were

97   also included for each variable.

98   Recruitment (R) and spawning stock biomass (SSB) of Pacific sardine originated from

99   stock assessments conducted by National Oceanic and Atmospheric Administration (Hill et al.

100   2010). In order to provide an update of the previous stock-recruitment relationship (Jacobson and

101   MacCall 1995), based on virtual population analysis output from 1935 to 1963 (Murphy 1966),

102   our study focused on the period 1981 to 2010 covered by a different but consistent assessment

103   method (Hill et al. 2010) and containing a complete data set of all the climate covariates used

104   during model fitting (Table 1). In accordance with Jacobson and MacCall (1995), we used

105   recruitment at age 2. It should be noted that assessment estimates of recruitment and SSB always

5

106 include a degree of uncertainty, whether implicit or explicitly quantified. However, the long-term

107 trends and inter-annual variability in R and SSB estimates are consistent with fishery

108 independent indices, i.e., derived from long-term fish larvae surveys conducted by the CalCOFI

109 program (Moser et al. 2001; Hill et al. 2011), and may therefore be considered as representative

110 for the sardine stock throughout the period.

111

112 **Statistical analysis and recruitment modelling**

113 In order to reduce potential methodological bias originating from the choice of

114 recruitment model, we revisited the previous stock-recruitment and temperature relationship for

115 Pacific sardine by Jacobson and MacCall (1995) using the same methodology, i.e., Generalized

116 Additive Models (GAMs; Hastie and Tibshirani, 1990; Wood 2006) to examine the relationship

117 between sardine recruitment, SSB and the set of temperature-related variables chosen as possible

118 predictors during model fitting and selection. The following linearized formulations with log-

119 transformed recruitment (R) and recruitment success (R/S) estimates as responses were used:

120 $\ln(R)_t = a + s(SSB_{t-2}) + s(V_{t-2}) + \varepsilon$ (1)

121 $\ln(R/S)_t = a + s(SSB_{t-2}) + s(V_{t-2}) + \varepsilon$ (2)

122 where a is the intercept, s the thin plate smoothing function (Wood, 2003), SSB the spawning

123 stock biomass, V a number of selected predictors potentially affecting sardine recruitment (Table

124 1) and ε the error term. Note that the predictors were lagged by two years (t-2) to reflect the

125 actual year of recruitment. Although the number of regression splines is optimized (and

126 penalized) by the generalized cross validation criterion (GCV; Wood, 2004), the degrees of

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127   freedom of the spline smoother function (*s*) was further constrained to three knots (k=3) to allow

128   for potential nonlinearities, but also restrict flexibility (and ecologically unrealistic functional

129   forms) during model fitting (Cardinale et al. 2009).

130   Finally, we applied a model reduction routine based on the GCV and partial *F*-tests to

131   find the best possible set of predictors. In addition, we performed a cross validation analysis by

132   fitting the set of final models to a randomly selected subset of the data (Picard and Cook 1984),

133   i.e., amounting to 75% of the observations, and assessed the predictive accuracy of the models

134   by comparing the observed values with the predicted recruitment estimates for the remaining

135   subset. The cross-validation analysis was repeated 1000 times (i.e., with a new set of random

136   draws each time) in order to assess the range of uncertainty associated with the predictions. All

137   statistical analysis were conducted using the R software (www.r-project.org).

138

Results

140   After model fitting, annual average SST of the CalCOFI area was found the most

141   significant explanatory variable for recruitment and recruitment success (Table 2). Although

142   other variables were statistically significant, e.g., SST at the SIO pier, CalCOFI SST was the best

143   single explanatory variable of recruitment variability, demonstrating the lowest GCV and highest

144   degree of explained variance overall (80.5% and 73.7% for recruitment and recruitment success,

145   respectively). In addition to the SST effect, SSB was found significant for both recruitment and

146   recruitment success (Table 3). Furthermore, note that the lack of correlation between SST and

147   SSB (p=0.17, n=28) limits the risk of confounding effects on model estimates. Model reduction

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148 through partial *F-* tests indicated that excluding the temperature effect provided a considerably

149 worse fit for all models (Table S1). In addition, the cross-validation routine demonstrated a high

150 degree of explained variance for models fitted to a random subset of the data (i.e., an average of

151 80.9% and 74.9% for recruitment and recruitment success, respectively), as well as accuracy in

152 predicting the remaining data (i.e., an average of 62.0% and 61.5% explained variance for

153 recruitment and recruitment success, respectively; Fig. S1).

154   The final relationship between recruitment and SSB was represented by a dome-shaped

155 curve (Fig. 2a), while for recruitment success, a non-linear decreasing function was found

156 optimal (Fig. 2b). Note that the spawner-recruitment relationships proved consistent during

157 periods of both high and low temperatures, i.e., as illustrated by coloured values in scatter plots

158 for years above (red) and below (blue) average SST (Fig. 2a, b). The functional relationship

159 between recruitment and SST was also best described by a dome-shaped curve (Fig. 2c) while

160 the SST effect on recruitment success showed a non-linear positive relationship (Fig. 2d).

161 However, note that the functional relationship at extreme high temperatures is driven by a single

162 observation, i.e., consisting of a strong El Niño event in 1983 (Fig. 1b, c), causing confidence

163 intervals to widen (Fig. 2c). If 1983 is excluded during model fitting, the SST effect on

164 recruitment is still highly significant (Table S2) but demonstrates a positive effect throughout the

165 entire temperature range (Fig. S2). The final models explain well the long-term dynamics and

166 inter-annual variability in sardine recruitment and recruitment success throughout the period

167 (Fig. 2e, f), with the exception of occasional low values observed during the early 2000s.

168 Furthermore, note that the temperature effect proved consistently significant when refitting and

169 updating the S-R models on successively longer time series from 1997 to 2010 (Fig. S3). Model

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170 residuals were normally distributed and temporally uncorrelated for recruitment and recruitment

171 success (Fig. 3).

172

Discussion

174   Sardines and anchovies demonstrate large fluctuations in abundance with similar cyclical

175 patterns observed across the major upwelling areas of the world, including the California Current

176 System (Lluch-Belda et al. 1989; Baumgartner et al. 1992; Schwartzlose et al. 1999; Barange et

177 al. 2009). Natural climate variability caused by changes in large-scale ocean–atmospheric

178 forcing over the North Pacific (i.e., the strength and position of the Aleutan low and North

179 Pacific high pressure cells) affecting the strength and direction of winds, currents and upwelling,

180 as well as physical and biotic conditions (i.e., temperature, salinity, oxygen and zooplankton

181 community composition) in the CCE (Checkley and Barth 2009; Song et al. 2012) is the most

182 likely cause of fluctuations in anchovy and sardine prior to fishing inferred from deposition rates

183 of fish scales in the Santa Barbara Basin (Baumgartner et al. 1992). Fishing may have

184 contributed to and exacerbated the rapid decline and collapse of the Pacific sardine in the 1940s-

185 60s, consistent with the high exploitation rate during that period (Murphy 1966). Our results

186 show that both density dependent (SSB) and independent (environment) effects explain

187 significant variability in sardine recruitment and recruitment success and may therefore influence

188 population dynamics and multi-decadal variability of the Pacific sardine.

189   Climate generally influences recruitment and population dynamics of sardine by changes

190 in the physical environment manifest by e.g., temperature (Takasuka et al., 2008), oxygen

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191   conditions (Betrand et al. 2011) and/or inter-related changes in habitat size and food

192   composition/availability (e.g., Van der Lingen et al. 2006; Espinoza et al. 2009; Ayon et al.

193   2011). Whether related to a direct physiological response, indirectly via food availability

194   (Rykaczewski and Checkley 2008), or their combined effects on survival (Houde 1987)we show

195   that SST in the southern CCS explains variability in recruitment and recruitment success of the

196   Pacific sardine (Fig. 2c, d). Our results are consistent with the previous stock-recruitment study

197   assessing temperature effects on recruitment from 1935 to 1963 (Jacobson and MacCall 1995).

198   However, in contrast to that study, our analysis includes a greater range of temperatures and all

199   possible combinations of high and low SST and SSB values (Fig. 4a). In addition, the regional

200   SST of the CalCOFI area was a better predictor of recruitment variability than SST measured

201   specifically at the SIO pier or indices of SST over broad regions of the North and Tropical

202   Pacific (i.e., PDO and MEI, respectively).Hence, our results highlight the ecologically relevant

203   spatial scales to consider, with regional SST measurements from the main spawning area

204   providing the best proxy for recruitment (c.f., Checkley et al. 1997; Lynn 2003; Reiss et al. 2008

205   for egg production). In addition, the greater explanatory power of annual SST averages,

206   compared to three-year averages or spring averages, indicates the ecologically relevant temporal

207   scale may be the first year of life, including the egg, larva, and juvenile stages. Although the

208   underlying mechanisms of the temperature-recruitment relationship remain largely unresolved, a

209   direct (physiological) response to temperature, e.g., regulating growth and survival of early life-

210   stages (Lluch-Belda et al. 1991, Takasuka et al. 2007), and/or indirect impacts mediated through

211   upwelling and changes in lower-trophic levels, i.e., zooplankton availability and community

212   composition (e.g., Brinton and Townsend 2002; Lavaniegos et al. 2002; Rebstock 2002) are

213   likely candidates.

214   The extreme temperature observed in 1983 exerts a strong leverage influencing the

215   functional relationship between R and SST (Fig. 2; Fig. S1). The decision to include or exclude

216   this extreme year highlights a potential ecological and statistical concern. Even though the high

217   SST may be considered as a statistical outlier, i.e., from the linear relationship between SST and

218   MEI (Fig. 5b), it corresponds to a strong ENSO event in 1983 and therefore an actual physical

219   condition potentially influencing sardine recruitment. Since the high average SST is primarily

220   caused by extreme values during July-October (Fig. 5c), potential negative effects may be acting

221   on early-life survival following spawning (March-May), either directly and/or indirectly through

222   decreasing food availability caused by the 1983 El Niño event (e.g., Brinton and Townsend

223   2002; Lavaniegos et al. 2002; Rebstock 2002). It is difficult, based on the single observation

224   (1983), to evaluate whether sardine exhibits a dome-shaped relationship with SST, with a

225   downward slope at these or even higher temperature, as would be physiologically expected

226   (Lluch-Belda et al. 1991; Takasuka et al. 2007). In order to resolve this issue and provide the

227   best available knowledge for management advice (e.g., regarding the temperature-dependent

228   decision rule), experimental studies and/or comparative studies on temperature tolerance of

229   sardine throughout its distribution area should be considered (Takasuka et al. 2008).

230   Although our results are consistent with the previous stock-recruitment study by

231   Jacobson and MacCall (1995), they differ from a recent re-assessment showing no effect of

232   temperature on recruitment or recruitment success (McClatchie et al. 2010). While Jacobson and

233   MacCall (1995), as well as the present study, used a linearized Ricker model using GAMs,

234   McClatchie et al. (2010) used a standard Ricker model and recruitment anomalies (standardized

235   to zero mean and unit variance) and examined potential linear relationships between model

236   residuals and SST. Given the use of identical methodologies in both Jacobson and MacCall

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237 (1995) and the present study showing a significant, non-linear dependence of recruitment on

238 SST, the use of different methodology and the assumption of a linear relationship could partly

239 explain the lack of significant temperature effect in McClatchie et al. (2010). In addition, these

240 authors used a reanalysis of time series of gridded SST (i.e., NOAA_ERSST_v3) which has

241 undergone significant smoothing, thereby potentially limiting the degree of inter-annual

242 variability. As a result, it may explain less of the high-frequency variability in sardine

243 recruitment, i.e., as shown by our comparative analysis using the same data set (Table 2).

244   In addition to a positive effect of temperature on recruitment, our results indicate

245 pronounced density dependent regulation for Pacific sardine (Fig. 2a, b). Given the large stock

246 size and lack of a pronounced ontogenetic shift in diet (i.e., sardines remain planktivores

247 throughout their life cycle, albeit feeding on different size fractions (Checkley et al. 2009), food

248 limitation, potentially due to intra-specific competition, may limit recruitment and recruitment

249 success, especially at high population densities. Alternatively, cannibalism may occur at high

250 population size, as has been shown for northern anchovy (*Engraulis mordax*) (Hunter and

251 Kimbrell 1980), or predation by other species, e.g., by northern anchovy (Butler 1987).

252   Given the combined effects of temperature and population size on sardine recruitment in

253 the CCE, a holistic management approach is needed. We believe that the consideration of direct

254 and/or indirect temperature related factors can improve recruitment forecasts and consequently

255 the estimates of future potential stock size and production under different fisheries management

256 scenarios. To that end, sustainable management of small pelagic fish in general, and the Pacific

257 sardine in particular, should include a measure of climate variability, such as the temperature

258 effect demonstrated in this study. However, the climate-recruitment relationship should be

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259 updated and revised when necessary, in order to provide the best available science for

260 management.

261

Acknowledgement

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References

269   Ayon, P., Swartzman, G., Espinoza, P., and Bertrand, A. 2011. Long-term changes in

270 zooplankton size distribution in the peruvian humboldt current system: Conditions favouring

271 sardine or anchovy. Mar. Ecol. Prog. Ser. **422**:211-222.

272   Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., van der

273 Lingen, C., and Agostini, V. 2009. Habitat expansion and contraction in anchovy and sardine

274 populations. Prog. Oceanogr. **83**: 251-260.

275   Baumgartner. T., Soutar, A., and Ferreira-Bartrina,V. 1992. Reconstruction of the history

276 of Pacific sardine and northern anchovy populations over the past two millennia from sediments

277 of the Santa Barbara basin. CalCOFI Rep. **33**: 24–40.

13

278   Benjamini, Y., and Hochberg, Y. 1995. Controlling the false discovery rate: a practical

279   and powerful approach to multiple testing. J. R. Stat. Soc. B. **57**: 289–300.

280   Brinton, E., and Townsend, A. 2003. Decadal variability in abundances of the dominant

281   euphausiid species in southern sectors of the California Current. Deep-Sea Res. Pt. II, **50**:2449-

282   2472.

283   Butler, J., and Pickett, D. 1988. Age-Specific Vulnerability of Pacific Sardine, *Sardinops-*

284   *Sagax*, Larvae to Predation by Northern Anchovy, *Engraulis-Mordax*. Fish. B-NOAA. **86**: 163-

285   167.

286   Cardinale, M., Mollmann, C., Bartolino, V., Casini, M., Kornilovs, G., Raid, T.,

287   Margonski, P., Grzyb, A., Raitaniemi, J., Grohsler, T., and Flinkman, J. 2009. Effect of

288   environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea*

289   *harengus* populations. Mar. Ecol. Prog. Ser. **388**: 221-234.

290   Checkley, D., Ortner, P., Settle, L., and Cummings, S. 1997. A continuous, underway fish

291   egg sampler. Fish. Oceanogr, **6**: 58-73.

292   Checkley, D.M., Alheit, J., and Oozeki, Y. (*Editors*). 2009. Climate Change and Small

293   Pelagic Fish. Cambridge. Cambridge University Press.

294   Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., and

295   Verheye, H.M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural

296   changes in "wasp-waist" ecosystems. ICES J. Mar. Sys. **57**: 603-618.

14

297   Daskalov, G.M., Grishin, A.N., Rodionov, S., and Mihneva, V. 2007. Trophic cascades

298   triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc. Natl.

299   Acad. Sci. USA, **104**: 10518-10523.

300   Espinoza, P., Bertrand, A., van der Lingen, C.D., Garrido, S., and de Mendiola, B.R.

301   2009. Diet of sardine (*Sardinops sagax*) in the northern humboldt current system and comparison

302   with the diets of clupeoids in this and other eastern boundary upwelling systems. Prog.

303   Oceanogr. **83**:1-4.

304   Food and Agriculture Organization of the United Nations, FAO. 2011. Fishery and

305   Aquaculture Statistics. 2009/FAO annuaire. Rome, FAO. 2011. 78p.

306   Freon, P., Bouchon, M., Mullon, C., Garcia, C., and Niquen, M. 2008 Interdecadal

307   variability of anchoveta abundance and overcapacity of the fishery in Peru. Prog. Oceanogr. **79**:

308   401-412.

309   Hannesson. R., Barrange, M., and Herrick, Jr S.F. (*Editors*). 2006. Climate change and

310   the economics of world´s fisheries: examples of small pelagic stocks. Northampton. Edward

311   Elgar Publishing Inc.

312   Hastie, T., and Tibshirani, R. 1990. Generalized additive models. Chapman and Hall,

313   London.

314   Hill, K., Lo, N., Macewicz, B., Crone, P.R. and Felix-Uraga, R. 2010. Assessment of the

315   Pacific sardine resource in 2010 for U.S. management in 2011. National Oceanic Atmospheric

316   Administration Technical Memorandum 469, U.S Department of Commerce, La Jolla, Calif.

317   NOAA-TM-NMFS-SWFSC-469.

15

318   Hill, K., Crone, P.R., Lo, N., Macewicz, B., Dorval, E., McDaniel, J., and Gu, Y. 2011.

319 Assessment of the Pacific sardine resource in 2011 for U.S. management in 2012. Supplemental

320 attachment 8. National Oceanic Atmospheric Administration Technical Memorandum, U.S

321 Department of Commerce, La Jolla, Calif.

322   Hjermann, D.O., Ottersen, G., and Stenseth, N.C. 2004. Competition among fishermen

323 and fish causes the collapse of Barents Sea capelin. Proc. Natl. Acad. Sci. USA, **101:** 11679-

324 11684.

325   Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc.

326 Symp. **2**: 17-29.

327   Hunter, J., Kimbrell, C. 1980. Egg Cannibalism in the Northern Anchovy, *Engraulis-*

328 *Mordax*. Fish. B-NOAA. **78**: 811-816.

329   Jacobson, L., and MacCall, A. 1995. Stock-Recruitment Models for Pacific Sardine

330 (*Sardinops-Sagax*). Can. J. Fish. Aqua. Sci. **52**: 566-577.

331   Lavaniegos, B., Jimenez-Perez, L., and Gaxiola-Castro, G. 2002. Plankton response to El

332 Nino 1997-1998 and La Nina 1999 in the southern region of the California Current. Prog.

333 Oceanogr. **54**: 33-58.

334   Lindegren. M., Ostman, O., and Gardmark, A. 2011. Interacting trophic forcing and the

335 population dynamics of herring. Ecology, **92**: 1407-1413.

16

336   Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., Maccall, A.D., Parrish, R.H.,

337   Schwartzlose, R.A., and Smith, P.E. 1989. Worldwide Fluctuations of Sardine and Anchovy

338   Stocks - the Regime Problem. S. Afr. J. Mar. Sci. **8**: 195-205.

339   Lluch-Belda, D., Lluch-Cota, D.B., Hernandez-Vazquea, S. and Salina-Zavala, C.A.

340   1991. Sardine and anchovy spawning as related to temperature and upwelling in the California

341   Current system. CalCOFI Rep. **32**:105–111.

342   Lynn, R. 2003. Variability in the spawning habitat of Pacific sardine (*Sardinops sagax*)

343   off southern and central California. Fish. Oceanogr. **12**: 541-553.

344   McClatchie, S., Goericke, R., Auad, G., and Hill, K. 2010. Re-assessment of the stock-

345   recruit and temperature-recruit relationships for Pacific sardine (*Sardinops sagax*). Can. J. Fish.

346   Aqua. Sci. **67**: 1782-1790.

347   Moser, H., Charter, R., Watson, W., Ambrose, D., Hill, K., Smith, P., Butler, J.,

348   Sandknop, E., and Charter, S. 2001. The CalCOFI ichthyoplankton time series: Potential

349   contributions to the management of rocky-shore fishes. CalCOFI Rep. **42**: 112-128.

350   Murphy, G.I. 1966. Population biology of the Pacific sardine (*Serdinops caerulea*). Proc.

351   Cal. Acad. Sci. **34**: 1-84.

352   PFMC. 1998. Amendment 8 (to the northern anchovy fishery management plan)

353   incorporating a name change to: the coastal pelagic species fishery management plan. Pacific

354   Fishery Management Council, Portland, OR.

17

355   Picard, R.R., and Cook, R.D. 1984. Cross-validation of regression models. J. Am. Stat.

356 Assoc. **79**: 575-583.

357   Rebstock, G.A. 2002. Climatic regime shifts and decadal-scale variability in calanoid

358 copepod populations off southern California. Glob. Change. Biol. **8**: 71-89.

359   Reiss, C.S., Checkley, D.M., Jr., and Bograd, S.J. 2008. Remotely sensed spawning

360 habitat of Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*) within

361 the California Current. Fish. Oceanogr. **17**: 126-136.

362   Rykaczewski, R.R., and Checkley, D.M. 2008. Influence of ocean winds on the pelagic

363 ecosystem in, upwelling regions. Proc. Natl. Acad. Sci. USA, **105**: 1965-1970.

364   Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford,

365 R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota,

366 S.E., Maccall, A.D., Matsuura, Y., Nevarez-Martinez, M.O., Parrish, R.H., Roy, C., Serra, R.,

367 Shust, K.V., Ward, M.N., and Zuzunaga, J.Z. 1999. Worldwide large-scale fluctuations of

368 sardine and anchovy populations. S. Afr. J. Mar. Sci. **21**: 289-347.

369   Smith, T., Reynolds, R., Peterson, T., and Lawrimore, J. 2008. Improvements to NOAA's

370 historical merged land-ocean surface temperature analysis (1880–2006). J. Climate. **21**: 2283–

371 2296.

372   Song, H., Miller, A.J., McClatchie, S., Weber, E.D., Nieto, K.M., and Checkley, D.M.

373 2012. Application of a data-assimilation model to variability of Pacific sardine spawning and

374 survivor habitats with ENSO in the California Current System. J. Geophy. Res-Oceans. **117**:

375 C03009.
18

376   Takasuka, A., Oozeki, Y., and Aoki, I. 2007. Optimal growth temperature hypothesis:

377   Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? Can.

378   J. Fish. Aqua. Sci. **64:** 768-776.

379   Takasuka, A., Oozeki, Y., Kubota, H., and Lluch-Cota, S.E. 2008. Contrasting spawning

380   temperature optima: Why are anchovy and sardine regime shifts synchronous across the North

381   Pacific? Prog. Oceanogr. **77**: 225-232.

382   van der Lingen, C.D., Hutchings, L., and Field, J.G. 2006. Comparative trophodynamics

383   of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern benguela: Are

384   species alternations between small pelagic fish trophodynamically mediated? Afr. J. Mar. Sci.

385   **28**:465-477.Wood, S.N. 2003. Thin plate regression splines. J. R. Stat. Soc. B. **65**: 95-114.

386   Wood, S.N. (2004) Stable and efficient multiple smoothing parameter estimation for

387   generalized additive models. J. Am. Stat. Assoc. **99**: 673-686.

388   Wood, S.N. 2006. Generalized additive models. An introduction with R. Chapman &

389   Hall/CRC, Boca Raton.

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392   **Fig. 1.** Recruitment (i.e., ln(R) at age 2) and spawning stock biomass (SSB) of Pacific sardine

393   from 1981-2010, as well as average sea surface temperatures (SST) from the Scripps pier (SIO)

394   and the regular CalCOFI-region. In (c) the PDO and multivariate ENSO index (MEI) are shown.

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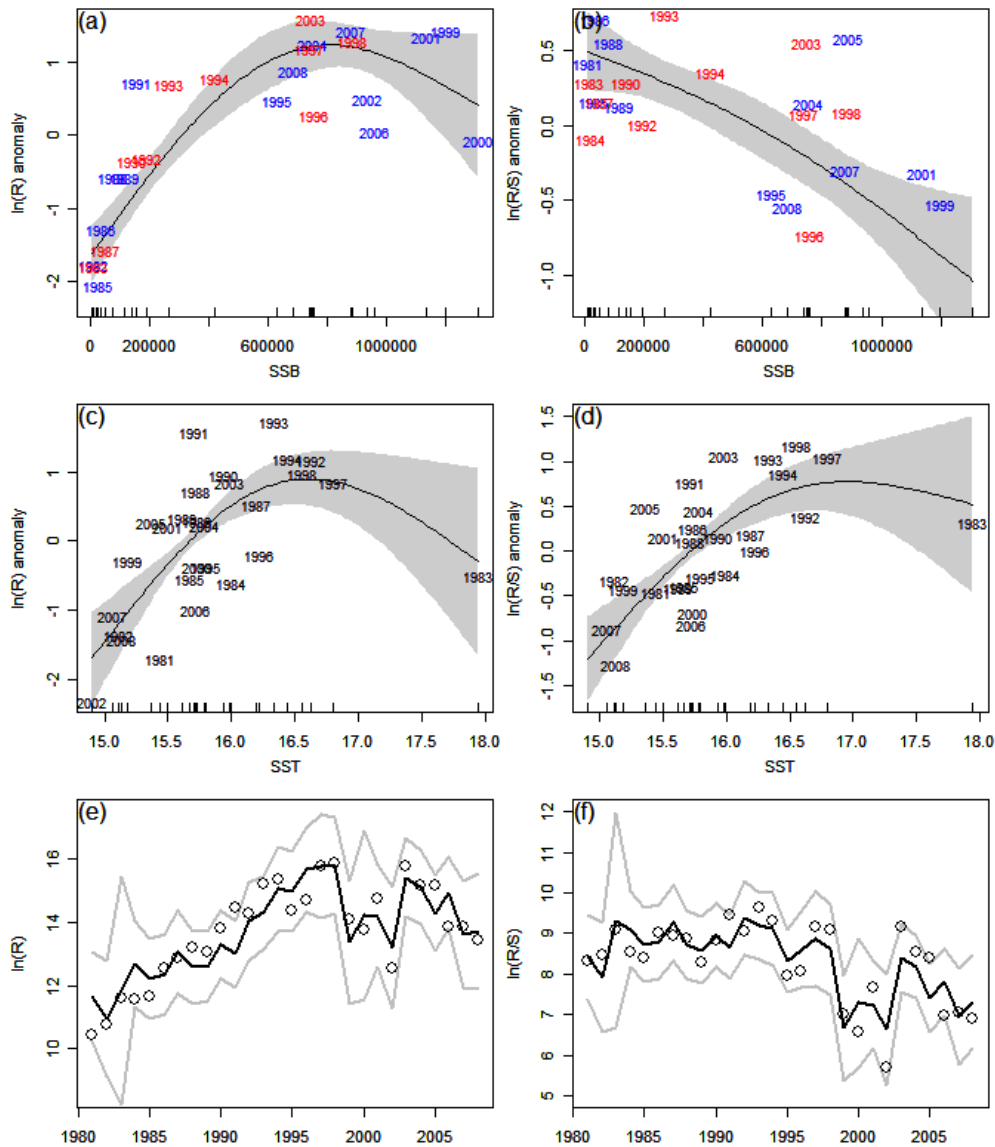
Fig. 2. The effects of predictors on recruitment with confidence intervals (grey) and residuals (i.e., coloured based on years with SST above (red) or below (blue) average) from the final GAMs, illustrating non-linear relationships between sardine recruitment and recruitment success at age 2 and SSB (a, b), as well as annual average SST (c, d). Observed (circles) and modelled recruitment (e; black) and recruitment success (f; black) with upper and lower 95% confidence intervals (grey).

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403 **Fig. 3**. Boxplots of explained variance from a cross-validation analysis of model fit on a

404 randomly selected subset, as well as the associated accuracy of recruitment and recruitment
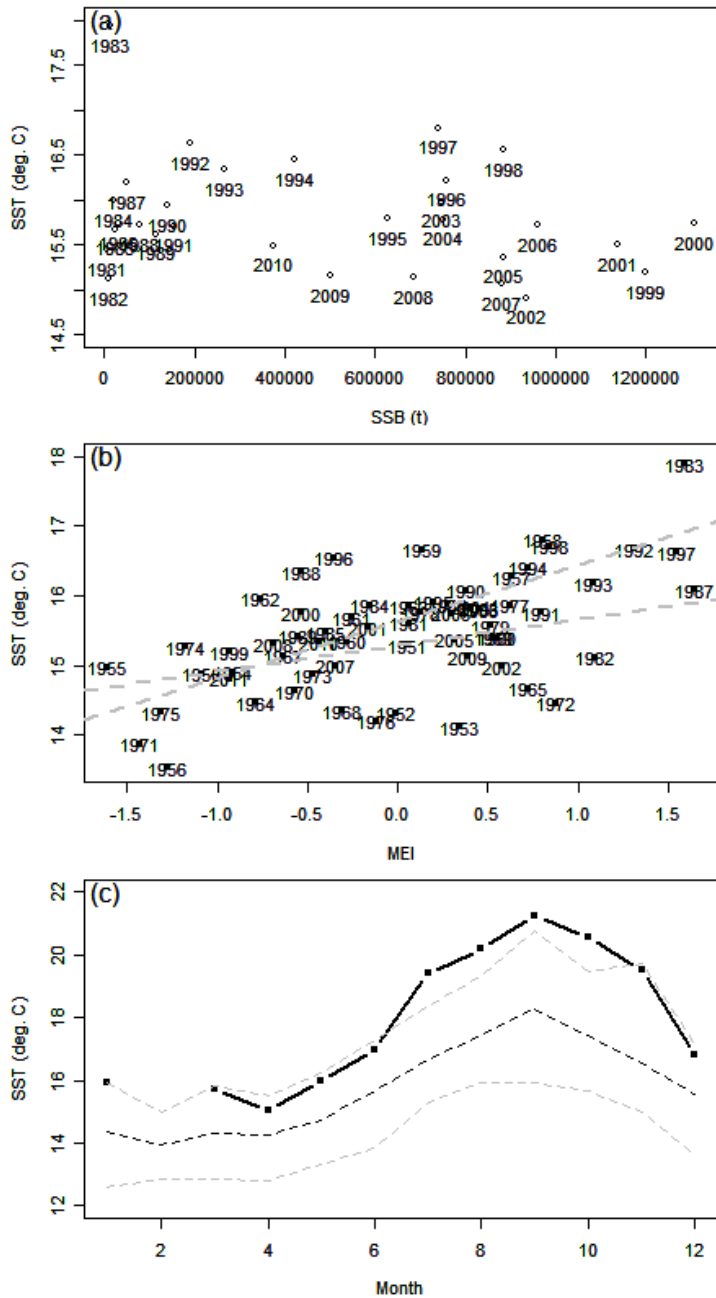
405 success predictions on the remaining data.

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408 **Fig. 4**. Significance (p-value) of the temperature effect on recruitment (solid) and recruitment

409 success (dashed) when successively fitted and annually updated on stock assessment and SST

410 data from 1997 to 2010.

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Fig. 5. Scatter plot of SST and SSB (a), as well as the degree of linear relationship between SST

and MEI (b). The positive outlier in 1983 (i.e., warmer than expected from the linear

relationship) demonstrates temperatures above the 95% confidence interval (grey dashed; based

on CalCOFI observations from 1950-2010) primarily during July to October (c).

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419 **Table 1.** Climate covariates used during model fitting.

Variable	Month	Area	Source
420			
421 SST_SIO_spring	March-May	SIO pier	http://www.shorestation.ucsd.edu/
422 SST_SIO_ann	Annual	SIO pier	http://www.shorestation.ucsd.edu/
423 SST_spring	March-May	CalCOFI	http://calcofi.org/data.html
424 SST_ann	Annual	CalCOFI	http://calcofi.org/data.html
425 ERSST_spring	March-May	McClatchie et al. (2010)	ftp://ftp.ncdc.noaa.gov/pub/data/cmb/ersst/
426 ERSST_ann	Annual	McClatchie et al. (2010)	ftp://ftp.ncdc.noaa.gov/pub/data/cmb/ersst/
427 PDO_spr	March-May	----	http://jisao.washington.edu/pdo/PDO.latest
428 PDO_ann	Annual	----	http://jisao.washington.edu/pdo/PDO.latest
429 MEI_spr	March-May	----	http://www.esrl.noaa.gov/psd/enso/mei/
430 MEI_ann	Annual	----	http://www.esrl.noaa.gov/psd/enso/mei/

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441 **Table 2.** The generalized cross validation scores (GCV), deviance explained (DEV) and p-values

442 of the climate effect after fitting the GAM stock-recruitment models to each covariate separately.

443 P-values have been modified for multiple hypotheses testing following Benjamini and Hochberg

444 (1995). (The best models are shown in bold).

445

	ln(R)			*ln(R/S)*		
446 **Age 2**	**GCV**	**DEV**	**p**	**GCV**	**DEV**	**p**
447 SST_SIO_spring	1.03	0.659	0.107	0.457	0.611	0.009
448 SST_SIO_ann	1.223	0.608	0.462	0.574	0.529	0.075
449 SST_spring	1.218	0.599	0.462	0.578	0.536	0.089
450 **SST_ann**	**0.641**	**0.805**	**0.002**	**0.343**	**0.737**	**0.002**
451 ERSST_spring	1.201	0.619	0.462	0.617	0.501	0.156
452 ERSST_ann	1.186	0.610	0.411	0.572	0.536	0.075
453 SST_SIO_spring_3	1.079	0.652	0.241	0.507	0.593	0.036
454 SST_SIO_ann3	1.231	0.594	0.462	0.624	0.478	0.148
455 SST_spring_3	1.185	0.632	0.411	0.629	0.497	0.235
456 SST_ann3	0.841	0.744	0.037	0.540	0.584	0.075
457 ERSST_spring3	1.245	0.590	0.616	0.654	0.475	0.358
458 ERSST_ann3	1.227	0.597	0.533	0.637	0.491	0.281
459 PDO_spr	1.182	0.611	0.411	0.506	0.592	0.036
460 PDO_ann	1.248	0.589	0.616	0.600	0.513	0.113
461 MEI_spr	1.124	0.63	0.357	0.529	0.572	0.049
462 MEI_ann	1.17	0.615	0.411	0.548	0.549	0.052
463 PDO_spr3	1.263	0.584	0.931	0.645	0.483	0.294
464 PDO_ann3	1.254	0.587	0.678	0.62	0.498	0.159
465 MEI_spr3	1.155	0.62	0.411	0.593	0.525	0.113
466 MEI_ann3	1.202	0.613	0.462	0.58	0.525	0.075

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468   **Table 3**. Summary statistics of parametric coefficients and smooth terms for the final stock-

469   recruitment model for Pacific sardine including, as well as excluding the strong ENSO event in

470   1983 during fitting.

471   A. Intercept

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Response	Estimate	SE	t-value	p-value
$\ln(R)$	13.71	0.14	99.68	<0.001***
$\ln(R/S)$	8.303	0.10	81.43	<0.001***
$\ln(R)_{excl.\ 1983}$	13.79	0.14	96.45	<0.001***
$\ln(R/S)_{excl.\ 1983}$	8.27	0.11	78.38	<0.001***

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478   B. Smooth terms

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Response	Predictor	edf	F-value	p-value
$\ln(R)$	SSB	1.95	28.85	<0.001***
$\ln(R)$	SST	1.47	12.72	<0.001***
$\ln(R/S)$	SSB	1.00	21.09	<0.001***
$\ln(R/S)$	SST	1.00	29.20	<0.001***
$\ln(R)_{excl.\ 1983}$	SSB	1.93	35.23	<0.001***
$\ln(R)_{excl.\ 1983}$	SST	1.93	13.62	<0.001***
$\ln(R/S)_{excl.\ 1983}$	SSB	1.39	10.28	<0.001***
$\ln(R/S)_{excl.\ 1983}$	SST	1.88	14.41	<0.001***

488   * edf is the estimated degrees of freedom for the model smooth terms where edf>1 indicates a non-linear

489   relationship

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493 **Table 4.** Model selection based on likelihood ratio tests and GCV scores. The total deviance

494 explained (DEV in %), the significance of the likelihood ratio test (p) and the number of

495 observations (n) are shown. The final models are highlighted in bold.

Nr.	Model	GCV	DEV(%)	p	n
1.	$\ln(R\ 2) \sim \alpha + s(SSB) + \varepsilon$	1.16	58.4		
2.	**$\ln(R\ 2) \sim \alpha + s(SSB) + s(SST\_ann) + \varepsilon$**	**0.64**	**80.5**	**<0.001**	**28**
1.	$\ln(R/S\ 2) \sim \alpha + s(SSB) + \varepsilon$	0.62	45.6		
2.	**$\ln(R/S\ 2) \sim \alpha + s(SSB) + s(SST\_ann) + \varepsilon$**	**0.34**	**73.7**	**<0.001**	**28**

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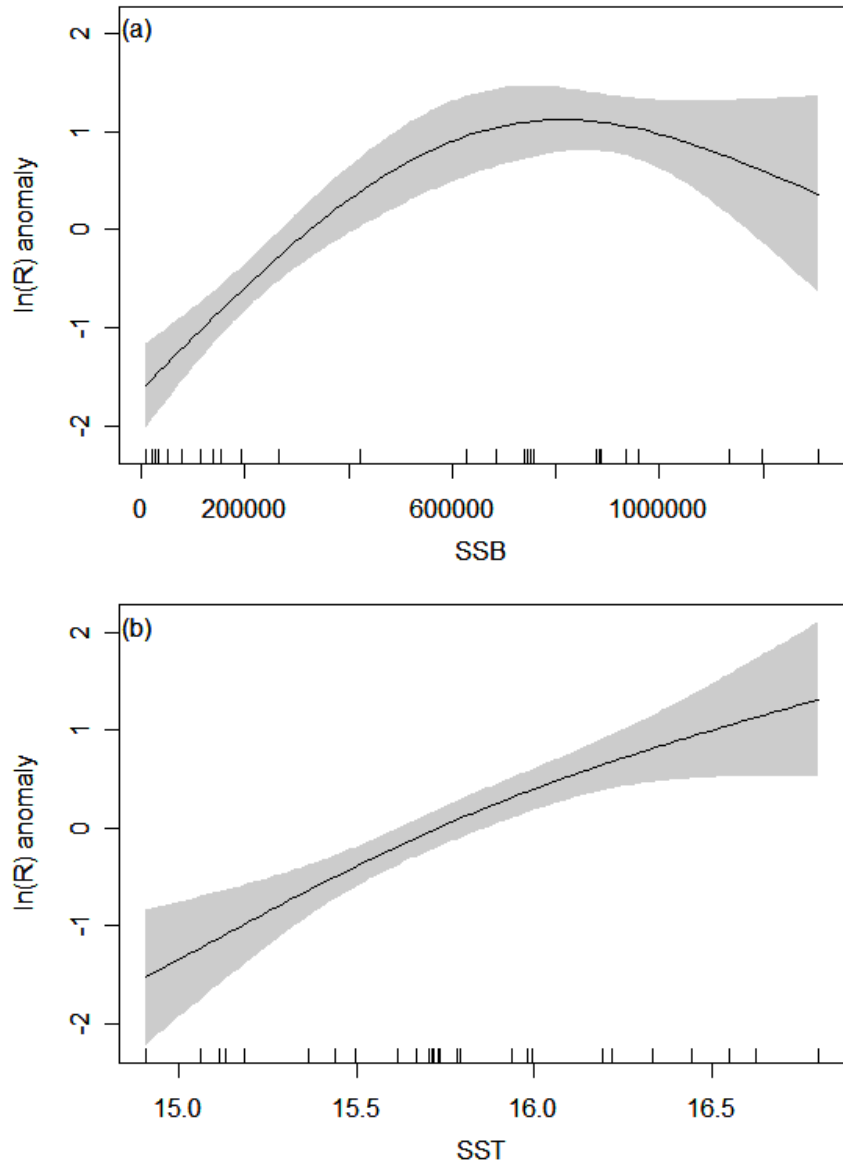
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Fig. S1. The effects SSB (a) and SST (b) on sardine recruitment at age 2 if excluding the strong

ENSO event in 1983 during model fitting.

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526   **Fig. S2.** (a-b) Normal probability plots and (c-d) partial autocorrelation plots of the final S-R

527   models for recruitment and recruitment success at age 2.

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