
The relative importance of environmental stochasticity, interspecific interactions, and observation error: Insights from sardine and anchovy landings

Geoffrey R. Hosack^{a,*}, Verena M. Trenkel^b, Jeffrey M. Dambacher^a

^a CSIRO Mathematics, Informatics and Statistics, GPO Box 1538, Hobart, Tasmania 7001, Australia

^b Ifremer, rue de l'île d'Yeu, BP 21105, 44311 Nantes cedex 3, France

*: Corresponding author : Geoffrey R. Hosack, email address : geoff.hosack@csiro.au

Abstract:

Long-term time series of sardine and anchovy landings often suggest negative dependence between these species, and an array of mechanisms have been proposed as explanations. We reduce these propositions to four basic hypotheses of (1) independence, (2) correlated process noise, (3) interspecific interactions, and (4) correlated observational error. We use a Bayesian approach to develop priors for parsimonious state space models with both process noise and observation error that represent each of these hypotheses, and apply this approach to five long-term time series of landings collected from the Pacific and Atlantic Oceans. Model comparison criteria suggest that the hypothesis of correlated process noise has the broadest support, where the temporal dependence of anchovy and sardines may be caused in part by either direct environmental influence on their physiology, or indirect bottom-up effects on their prey. However, all hypotheses find some degree of support within the five time series, and in general, the sardine and anchovy landings suggest weak intraspecific density dependence and susceptibility to both environmental and anthropogenic perturbation. Results additionally suggest that the best fitting hypothesis depends on the choice of geographic scale, temporal scale, and stock definition of the recorded landings.

Highlights

► Test four hypotheses of temporal dependence in sardine and anchovy landings. ► Using state space models, model comparison finds support for all hypotheses. ► Correlated process noise finds the broadest support. ► Support for hypotheses depends on spatiotemporal scale and stock definition.

Keywords: Adaptive Metropolis ; Bayes factors ; DIC ; Gompertz model ; Hyperstability ; Kalman filter; Model comparison ; Reactivity ; Small pelagic fishes ; Stability

1. Introduction

Forage fish such as sardine and anchovy play a key trophodynamic role in many upwelling systems even as the last sixty years show an increasing trend in their global landings (Smith et al., 2011). The large, seemingly antagonistic, low-frequency fluctuations of anchovy and sardine landings observed in marine upwelling systems around the world have attracted much attention in the literature (e.g., Lluch-Belda et al., 1989; Schwartzlose et al., 1999). Several explanations for this phenomena have been put forward, with various studies attempting to identify the ecological mechanisms that explain the putative negative dependence in anchovy and sardine (e.g., MacCall, 2009). In this vein, environmental forcing through direct physiological impacts (e.g., Bertrand et al., 2004; Takasuka et al., 2008; Takahashi et al., 2009) or indirect impacts through phytoplankton or zooplankton (e.g., Cury and Shannon, 2004; Yatsu et al., 2005; van der Lingen et al., 2006) has been proposed to explain the negative dependence of anchovy and sardine landings in these upwelling systems. However, interspecific interactions between sardine and anchovy may also drive this negative dependence (Bakun and Cury, 1999; Irigoien and de Roos, 2011). Alternatively, non-biological explanations, such as data quality issues for landings data, have been proposed (Barange et al., 2009a; Finney et al., 2010), as have combinations of the above; for example, Beverton (1990) concluded that some of the spectacular stock crashes of small pelagics might have been accelerated by both increasing catchability as stock size decreased in addition to concomitant recruitment failures. The overall emerging picture is one of various biological and non-biological mechanisms that operate individually or together in different areas and over various time periods.

The diversity of postulated environmental, biological, and anthropogenic mechanisms reflects a long-term interest in the apparently antagonistic fluctuations of sardine and anchovy landings. In this paper, we seek to conceptually simplify the proposed mechanisms into competing hypotheses that can be compared using available long term records of landings collected from around the world. The published evidence leads to four main hypotheses for joint anchovy and sardine dynamics that we consider here:

H_{ind}: *Independence hypothesis*—Under this hypothesis, apparent negative dependence between the two species is spurious. Indeed, both species

36 have been simultaneously abundant in the 1980s in the Humboldt Current
37 (Gutiérrez et al., 2007) and in the early 2000s in the southern Benguela
38 (Barange et al., 2009a); both were low around Japan in the early 20th century
39 (Lluch-Belda et al., 1989). Paleoecological fish scale data from the South At-
40 lantic and the Pacific suggest that fluctuations of anchovy and sardine may
41 sometimes exhibit independence or weak positive dependence (Soutar and
42 Isaacs, 1974; Baumgartner et al., 1992; Finney et al., 2010).

43 *H_{pro}*: *Process noise dependence hypothesis*—Environmental conditions may
44 cause one species to predominate over the other either directly or indirectly
45 (Barange et al., 2009b). Direct effects that can favor one species over another
46 include temperatures that differentially affect recruitment (Takasuka et al.,
47 2008), climatically influenced shifts in spawning habitat (Bertrand et al.,
48 2004), and oceanographic processes that impact nursery areas for larvae and
49 juveniles (Takahashi et al., 2009). Indirect effects that favor a species by shift-
50 ing the composition of phytoplankton or zooplankton have been identified
51 as initiating and maintaining factors in the northern and southern Benguela
52 ecosystem (Cury and Shannon, 2004; van der Lingen et al., 2006), in Japanese
53 sardine (Yatsu et al., 2005), and in the Humboldt Current system, where high
54 zooplankton abundance seems to have contributed to maintain high anchovy
55 abundance during the 1960s (Alheit and Niquen, 2004). Alternatively, both
56 species may be impacted similarly by changes in environmental conditions
57 (Nakata et al., 1994), which could produce positive process dependence.

58 In addition, process noise dependence could potentially be created by
59 the fisheries. Geographical distributions of stocks may shift in response to
60 environmental conditions such that catchability is affected (e.g., Rodríguez-
61 Sánchez et al., 2002; Alheit and Niquen, 2004; Bertrand et al., 2004; Barange
62 et al., 2009a), thus introducing dependent process error into the landings
63 data. Alternatively, from a purely economic standpoint, a shift in market
64 forces, processing capacity, or management policy may lead to more landings
65 of one species over the other.

66 *H_{com}*: *Community interactions hypothesis*—Interspecific density depen-
67 dence may arise from the predation of anchovy on sardine eggs (Butler,
68 1991; Valdés Szeinfeld, 1991) or vice versa (Valdés Szeinfeld, 1991; Tudela
69 and Palomera, 1997). Alternatively, according to the school-trap hypothesis,
70 a species at low population abundance that schools with another abundant
71 species may be trapped at low abundance, if conditions are worse for the
72 rarer species in the mixed school (Bakun and Cury, 1999).

73 *H_{obs}*: *Observation error dependence hypothesis*—In the process dependence

74 hypothesis, changes in the exploitation rate that result from environmental
75 conditions, effective effort, or catchability affect stock abundance. In Section
76 3.1, we show that such factors can also impact how catch functions as a proxy
77 index for the stocks. Such factors that covary can thus introduce dependence
78 into the observation error.

79 We use landings data of sardine and anchovy from several stocks in up-
80 welling areas in the Pacific and Atlantic Oceans (Section 2) to test the above
81 hypotheses as follows. First, for each hypothesis H_i we develop a Bayesian
82 state space model M_i (Section 3.1) with priors that correspond to each hy-
83 pothesis (Sections 3.2, 3.3, 3.4). We use this statistical framework to jointly
84 estimate both process noise and unknown observation error that is intro-
85 duced by processes such as fishery management impacts, fishing effort and
86 catchability. Second, we use model selection criteria to identify models that
87 best explain the observed long-term fisheries landings of anchovy and sardine
88 (Section 3.5). In Section 4, we test the sensitivity of these conclusions to al-
89 ternative choices of model priors for both synthetically generated data, for
90 which the true model is known, and the time series of landings data, for which
91 the true model is unknown, and use this modeling framework to identify the
92 hypotheses that most likely explain the potential temporal dependence of
93 sardine and anchovy landings.

94 2. Sardine and anchovy landings data

95 Barange et al. (2009b) present landings data for spatially overlapping
96 sardine and anchovy stocks that exhibit asynchronous fluctuations in abun-
97 dance from four areas around the world over 40–50+ years. All of the stocks
98 in these four areas have fishery independent surveys in recent years (Barange
99 et al., 2009b). However, for three of the four areas, substantial periods with
100 missing data exist with respect to both fishery independent surveys and effort
101 for one or both species (an exception is California, Barange et al., 2009a).
102 Below we provide a short description of the landings data recorded for the
103 stocks included in our analyses as presented by Barange et al. (2009b). Fur-
104 ther descriptions of these stocks are found in Barange et al. (2009a). After
105 considering these data, we then describe for comparison a 100-year time se-
106 ries of sardine and anchovy landings from Japan (Figure 1, Yatsu et al., 2005;
107 Takasuka et al., 2008) that exhibit antagonistic fluctuations (Takasuka et al.,
108 2007). The data sets are presented below in order of increasing length.

109 *California*—The California data set covers the northern subpopulation
110 of California sardine (*Sardinops sagax caerulea*) that extends from central
111 Baja California to southeastern Alaska, and the central subpopulation of
112 the California anchovy (*Engraulis mordax*) that extends from central Baja
113 California to central California. This data set covers the period from 1950
114 to 2007. However there are years with nearly zero landings of anchovy in
115 the years 1950-1963, and also 2005-2007 because of poor market conditions
116 (Barange et al., 2009a). Landings of sardine in the years 1966-1982 are
117 also near zero because this fishery had collapsed after catches peaked earlier
118 in the 20th century (Barange et al., 2009a). We restrict our analysis to the
119 period 1983-2004 when there are non-negligible recorded landings from active
120 fisheries that target each species; this is the shortest series of landings data
121 considered in this paper.

122 *Peru*—This data set contains landings of Humboldt sardine (*Sardinops*
123 *sagax*) from the north-central Peru stock and the southern Peru and northern
124 Chile stock, and the Humboldt anchovy (*Engraulis ringens*) stock in north-
125 central Peru, for the years 1960-2003.

126 *South Africa*—This data set has recorded landings for both anchovy (*En-*
127 *graulis encrasicolus*) and sardine (*Sardinops sagax*) in South Africa for the
128 period 1964 to 2005; it is also referred to as the southern Benguela stock
129 (Barange et al., 2009a)

130 *Japan (Pacific)*—This data is from the Northwest Pacific stock of anchovy
131 that contributes 75% of Japanese landings (Barange et al., 2009a), and the
132 Pacific stock of sardine. Landings of both species are from 1951 to 2004.
133 These are a subset of the stocks contained in the longer time series of Japan
134 (Combined) landings data, described below.

135 *Japan (Combined)*—This data set covers all landings of Japanese anchovy
136 (*Engraulis japonicus*) and sardine (*Sardinops melanostictus*) stocks for the
137 period 1905-2004 (Figure 1). It was originally compiled by the Japanese
138 Statistics of Agriculture, Forestry and Fisheries, and later arranged by Yatsu
139 et al. (2005); the data presented here were updated by Takasuka et al. (2008),
140 and constitute the longest data series considered. Takasuka et al. (2008)
141 found that the landings data are correlated with biomass estimates over the
142 last few decades when such estimates are available.

143 **3. State Space Models (SSMs) of sardine and anchovy landings**

144 *3.1. Motivation and model formulation*

145 A parsimonious process model that includes environmental stochasticity
146 and both intra- and interspecific density dependence between two species is
147 given by a Gompertz model (Ives et al., 2003),

$$B_t^{(i)} = l^{(i)} \left(B_{t-1}^{(i)} \right)^{G^{(i,i)}} \left(B_{t-1}^{(j)} \right)^{G^{(i,j)}} e^{\epsilon_t^{(i)}}, \quad (1)$$

148 where $B_t^{(i)}$ is the biomass of species i in year t , $l^{(i)}$ controls density indepen-
149 dent growth and natural mortality, $G^{(i,i)}$ controls intraspecific density depen-
150 dence, $G^{(i,j)}$ controls interspecific density dependence, and process noise is
151 independently and identically distributed, and marginally normal with mean
152 zero and standard deviation $\sigma_\epsilon^{(i)}$, $\epsilon_t^{(i)} \sim \mathcal{N} \left(0, \left(\sigma_\epsilon^{(i)} \right)^2 \right)$.

153 The goal is to infer whether or not sardine and anchovy exhibit temporal
154 dependence in Eq. (1) using landings data. Clearly, changes made to a
155 fishery’s effective effort or regulations over time will affect landings data.
156 Nevertheless, a stock’s landings probably provide *some* information on a
157 stock’s size in regions with active fisheries, although the story is incomplete.
158 For example, with the usual caveats, trends in landings data from sardine and
159 anchovy are often compared with sardine and anchovy stock estimates (e.g.,
160 Lluch-Belda et al., 1989; Schwartzlose et al., 1999; Barange et al., 2009a, and
161 many others).

162 The next step might be to consider that a species’ annual catch C is
163 proportional to effort E multiplied by biomass B , $C = qEB$, and include
164 effort of commercial fisheries in the analyses. Although this approach may
165 be useful, it does pose three major problems for small pelagic fisheries. First,
166 effort data is notoriously difficult to correct for the difference in observable
167 versus effective effort (e.g., Pascoe and Robinson, 1996) and is particularly so
168 for long time series without reference time series that have relatively constant
169 fishing power (e.g., Marchal et al., 2001). Also, even nominal effort data does
170 not extend over the full time period of recorded landings for some of the
171 stocks considered here (Barange et al., 2009a). Second, catchability, which is
172 defined as $q = f/E$ where f is the exploitation rate (defined as the fraction of
173 biomass B that contributes to the fishery’s catch C such that $f = C/B$), of
174 a small pelagic fishery increases with decreasing stock size (Beverton, 1990);
175 this concomitant increasing relationship between catchability and stock size

176 is referred to as hyperstability (Hilborn and Walters, 1992), and catch per
 177 unit effort is a poor index for stock size in this situation. Third, using a
 178 linear state space model, Reed and Simons (1996) show that the degree of
 179 hyperstability is difficult to estimate. This problem can be overcome by using
 180 fishery independent surveys, however, until recent years such data are limited
 181 for many small pelagic fisheries (Barange et al., 2009a).

182 Beverton (1990), on the other hand, notes that the exploitation rate f
 183 of small pelagic fisheries is often sustained at a high level even while the
 184 estimated stock sizes vary by orders of magnitude. This occurs because of
 185 hyperstability: small pelagic species tend to shoal at low abundance, and this
 186 increases the probability of detection and capture by the fishery (Beverton,
 187 1990). When this is the case, then catch is roughly proportional to biomass
 188 since $C = B \times f$ with f sustained at a high level. However, this presupposes
 189 an active fishery that targets the stock.

190 Variability in the exploitation rate is introduced because of changes in
 191 vulnerability, effective effort, and management regulations over the years.
 192 Noise therefore affects how catch functions as a proxy indicator of the stock
 193 and also how catch affects the annual change in the stock's abundance. This
 194 suggests two sources of error to consider: (1) observation error, which en-
 195 compasses not only measurement error in catch records but also all random
 196 variation that affects catch as a proxy indicator of stock size, and (2) process
 197 noise that now includes annual variation in the exploitation rate, in addition
 198 to the environmental stochasticity introduced in Eq. (1).

199 Incorporating catch into Eq. (1), under the assumption of a relatively
 200 constant exploitation rate, produces for the i^{th} species the state space model,

$$\begin{aligned}
 C_t^{(i)} &= f^{(i)} B_t^{(i)} e^{\omega_t^{(i)}} \\
 B_t^{(i)} &= l^{(i)} \left(B_{t-1}^{(i)} - f^{(i)} B_{t-1}^{(i)} \right)^{G^{(i,i)}} \left(B_{t-1}^{(j)} - f^{(j)} B_{t-1}^{(j)} \right)^{G^{(i,j)}} e^{\epsilon_t^{(i)}} \\
 &= m^{(i)} \left(B_{t-1}^{(i)} \right)^{G^{(i,i)}} \left(B_{t-1}^{(j)} \right)^{G^{(i,j)}} e^{\epsilon_t^{(i)}},
 \end{aligned} \tag{2}$$

201 where observation error is marginally normal, $\omega_t^{(i)} \stackrel{\text{i.i.d.}}{\sim} \mathcal{N} \left(0, \left(\sigma_\omega^{(i)} \right)^2 \right)$. In
 202 the second line of Eq. (2), the parameter $m^{(i)}$ contains both the density
 203 independent and density dependent parameters from Eq. (1) and also the
 204 exploitation rates, $m^{(i)} = l^{(i)} \left(1 - f^{(i)} \right)^{G^{(i,i)}} \left(1 - f^{(j)} \right)^{G^{(i,j)}}$. Note that the
 205 density dependent parameters in Eq. (1) retain this role in Eq. (2).

206 Variability in the exploitation rates evidently affects both the process
 207 noise and the observation error in Eq. (2), as expected. This suggests that
 208 the process noise and observation error are correlated. On the log scale, how-
 209 ever, Eq. (2) is a dynamic linear model, and such a model with correlated
 210 process noise and observation error can always be transformed to a model
 211 with independent process noise and observation error to assist interpretation
 212 (West and Harrison, 1997). If the sources of stochasticity are uncorrelated,
 213 then observation error is interpreted as randomness that affects the obser-
 214 vations but not the underlying dynamics. Process noise, on the other hand,
 215 is randomness that affects how the trajectory of the unobserved dynamics
 216 changes over time.

217 Substituting $X_t^{(i)} = f^{(i)} B_t^{(i)}$, which we refer to as the latent (unobserved)
 218 state, and transforming to the log scale obtains,

$$\begin{aligned} \log \mathbf{C}_t &= \log \mathbf{X}_t + \boldsymbol{\omega}_t \\ \log \mathbf{X}_t &= \mathbf{G} \log \mathbf{X}_{t-1} + \mathbf{h} + \boldsymbol{\epsilon}_t, \end{aligned} \quad (3)$$

219 where vectors of random variables (catch and latent states) are in bold upper
 220 case with year subscripts, matrices of parameters (i.e., \mathbf{G} , which contains the
 221 density parameters) are in bold upper case, and vectors of parameters (\mathbf{h})
 222 and realisations of random variables (noise terms) are in bold lower case.
 223 The density independent parameter of species i is now,

$$h^{(i)} = \log (f^{(i)} l^{(i)}) + G^{(i,i)} \log \left(\frac{1 - f^{(i)}}{f^{(i)}} \right) + G^{(i,j)} \log \left(\frac{1 - f^{(j)}}{f^{(j)}} \right).$$

224 Again, the relationships with the density dependent parameters and the stock
 225 sizes are unaffected. The matrix \mathbf{G} then corresponds to density dependent
 226 interactions between and within the stocks (e.g., the community interactions,
 227 see Ives et al., 2003). The SSM given by Eq. (3) has the desired interpretation
 228 of stochasticity with independence between process noise and observation
 229 error, such that both sources of randomness are distributed bivariate normal
 230 with independent covariance matrices $\boldsymbol{\Sigma}_\omega$ and $\boldsymbol{\Sigma}_\epsilon$, $\boldsymbol{\omega}_t \stackrel{\text{i.i.d.}}{\sim} \mathcal{N}(\mathbf{0}, \boldsymbol{\Sigma}_\omega)$ and
 231 $\boldsymbol{\epsilon}_t \stackrel{\text{i.i.d.}}{\sim} \mathcal{N}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon)$.

232 3.2. Prior specification for models

233 For each of the hypotheses H_i , $i \in \{ind, pro, com, obs\}$, we develop a
 234 corresponding model M_i with weakly informative priors that constrain the

235 parameters of Equation (3) to reasonable values that are consistent with its
 236 respective hypothesis.

237 *M_{ind}: Independence*—In this model, both the process and observation er-
 238 rors are uncorrelated and there is no interspecific density dependence; that is,
 239 the off-diagonal entries of Σ_ϵ , Σ_ω , and \mathbf{G} are set to zero. Intraspecific density
 240 dependence, on the other hand, occurs if the diagonal entries $G^{(i,i)} < 1$ for
 241 species i . Intraspecific negative density dependence may result from canni-
 242 balism (e.g., Valdés Szeinfeld, 1991), predation (e.g., Kishida and Matsuda,
 243 1993), and competition for food or other factors that lead to negative density-
 244 dependence (e.g., van der Lingen et al., 2006). Moreover, if $G^{(i,i)} < 0$, then
 245 species i will exhibit overcompensation with potentially drastic overcorrec-
 246 tions due to overly strong intraspecific density dependence.

247 Analyses based on linear state space models fit to population census data
 248 suggest that only half present clear evidence of density dependence (Knappe
 249 and de Valpine, 2012). We choose a prior that places a 50% chance that neg-
 250 ative density dependence occurs, and favors undercompensatory intraspecific
 251 density dependence, but still allows for overcompensation, by using a normal
 252 distribution with mean (mode) set to one, $G^{(i,i)} \sim \mathcal{N}(\mathbf{1}, \sigma_{G^{(i,i)}}^2)$. This prior
 253 specifies that the process model is in the general region of stability by setting
 254 the standard deviation $\sigma_{G^{(i,i)}}$ equal to 1; in the absence of interspecific den-
 255 sity dependence, Equation (3) is only stable when $-1 < G^{(i,i)} < 1$ (Harvey,
 256 1989). We use this prior for the diagonal entries of \mathbf{G} in all model structures.

257 *M_{pro}: Process noise dependence*—In this model, the off-diagonal entries of
 258 Σ_ϵ are equal to $\rho_\epsilon \sigma_\epsilon^{(i)} \sigma_\epsilon^{(j)}$, where ρ_ϵ is the correlation coefficient of the process
 259 noise. We allow for either positive or negative correlations using a uniform
 260 prior, $\rho_\epsilon \sim \mathcal{U}(-1, 1)$.

261 *M_{com}: Community interactions*—Density dependent, interspecific interac-
 262 tions are modeled with non-zero off-diagonal entries in the matrix \mathbf{G} . We
 263 allow for either positive or negative density-dependent interactions using a
 264 normal prior centered at zero, $G^{(i,j)} \sim \mathcal{N}(0, \sigma_{G^{(i,j)}}^2)$ for $i \neq j$. The Jury test
 265 (Jury, 1962) provides the following criteria for stability:

$$\begin{aligned} (1) \quad & G^{(i,i)}G^{(j,j)} - G^{(i,j)}G^{(j,i)} < 1 \\ (2) \quad & G^{(i,j)}G^{(j,i)} + G^{(i,i)} + G^{(j,j)} - G^{(i,i)}G^{(j,j)} < 1, \\ & G^{(i,j)}G^{(j,i)} - G^{(i,i)} - G^{(j,j)} - G^{(i,i)}G^{(j,j)} < 1. \end{aligned}$$

266 These criteria show, for example, that increasing either interspecific com-
 267 petition or predation too much will lead to instability. We expect that the

268 sardine and anchovy populations are either stable or in the vicinity of stability
 269 and set $\sigma_{G^{(i,j)}} = 1$, which allows for competition, mutualism, ammensalism,
 270 commensalism, or predation among sardine and anchovy.

271 *M_{obs}: Observation error dependence*—Rather than specify dependence
 272 through the process model, here we allow correlated observation error and
 273 set the off-diagonal entries of the observation error covariance matrix Σ_ω to
 274 $\rho_\omega \sigma_\omega^{(i)} \sigma_\omega^{(j)}$. Similar to the correlated process noise model, we assume a uniform
 275 prior that permits either positive or negative dependence, $\rho_\omega \sim \mathcal{U}(-1, 1)$.

276 3.3. Prior specification for noise processes

277 The problem of identifying the relative ratio between the process vari-
 278 ance and the observation variance is a well-known issue for fisheries state
 279 space models (Kimura et al., 1996; Schnute and Kronlund, 2002). Even in a
 280 univariate state space model with a Gompertz process model, a multimodal
 281 likelihood surface often occurs with potentially global maximums on one or
 282 more of the boundaries $\sigma_\epsilon, \sigma_\omega = 0$ (Dennis et al., 2006). We choose priors that
 283 allow a wide range of observation and process error magnitudes while placing
 284 constraints on the values of σ_ϵ and σ_ω that ensure non-negligible observation
 285 and process error consistent with the state space model framework.

286 We assume that the observations have at least a 95% chance of being
 287 within an order of magnitude above or below a realized value of the latent
 288 state for species i , denoted $x_t^{(i)}$, such that,

$$P\left(x_t^{(i)}/10 < C_t^{(i)} < 10x_t^{(i)}\right) > 0.95$$

$$P(-\log 10 < \log C_t^{(i)} - \log x_t^{(i)} < \log 10) > 0.95,$$

289 and, because $P(-1.96 \times \sigma_\omega^{(i)} < \log C_t^{(i)} - \log x_t^{(i)} < 1.96 \times \sigma_\omega^{(i)}) = 0.95$ for the
 290 Gaussian observation model, this sets the upper bound $\sigma_\omega^{(i)} < \log 10/1.96$. On
 291 the other hand, we also include the assumption of nonnegligible observation
 292 error such that the chance that $y_t^{(i)}$ is roughly within 10% of $x_t^{(i)}$ is never
 293 more than 95% (recall that observation error is not just measurement error
 294 in the recorded catch data but all sources of random variation that affect
 295 catch as a proxy index of stock size, see Section 3.1). This means that,

$$P\left(x_t^{(i)}/1.1 < C_t^{(i)} < 1.1x_t^{(i)}\right) < 0.95$$

$$P(-\log 1.1 < \log C_t^{(i)} - \log x_t^{(i)} < \log 1.1) < 0.95,$$

296 and, again because $P(-1.96 \times \sigma_\omega^{(i)} < \log C_t^{(i)} - \log x_t^{(i)} < 1.96 \times \sigma_\omega^{(i)}) = 0.95$,
 297 this sets the lower bound $\sigma_\omega^{(i)} > \log 1.1/1.96$. These assumptions thus imply
 298 that $\log 1.1 \leq 1.96 \times \sigma_\omega^{(i)} \leq \log 10$.

299 A similar argument is made for the process error, where we consider the
 300 year to year variation in the latent states. For the development of this prior,
 301 we consider the simplified case where the annual variation in the true pop-
 302 ulation state is dominated by the process error and then proceed as above
 303 to specify identical constraints on σ_ϵ . These constrain the year-to-year vari-
 304 ation in the latent states to have less than a 5% chance of fluctuating by
 305 more than an order of magnitude, and less than a 95% chance of varying by
 306 $\sim 10\%$ or less (conversely, this latter restriction says that there is more than
 307 a 5% chance that the population fluctuates by at least $\sim 10\%$).

308 Given the above constraints on the standard deviation of the noise pro-
 309 cesses and based on arguments presented by Gelman (2006), we place uniform
 310 priors on the standard deviation of the process and observation noise with
 311 limits determined by the bounds above. These weakly informative priors thus
 312 capture a wide range of magnitudes for the process and observation errors.
 313 We also consider alternative prior specifications in Section 3.5.

314 3.4. *Prior specification for density independent parameters and initial states*

315 Following the above discussion on the process error, we place a normal
 316 prior on $\mathbf{h} \sim \mathcal{N}(\mathbf{0}, \mathbf{I}\sigma_{\mathbf{h}}^2)$ with $\sigma_{\mathbf{h}} = \log 10/1.96$. In the deterministic process
 317 model and in the absence of density dependence (i.e., low noise and low
 318 population abundance), the prior on the intrinsic rate of growth says that
 319 there is less than a 5% chance that the latent population state will change
 320 by more than an order of magnitude. For the initial states, we assume
 321 independent normal priors, $\log \mathbf{X}_0 \sim \mathcal{N}(\mathbf{0}, \mathbf{I}\sigma_{\log \mathbf{X}_0}^2)$, with mean zero and
 322 standard deviation $\sigma_{\log \mathbf{X}_0} = 2$.

323 3.5. *Model comparison*

324 Our goal is to determine the relative fits of each of the above model-
 325 hypotheses of sardine-anchovy dependence to the time series of landings
 326 data. We used two approaches for model comparison, Bayes factors and
 327 the Deviance Information Criterion (DIC). The Bayes factor is a pairwise
 328 comparison of two models, say M_i and M_j , and if the models M_i and M_j are
 329 equally likely before seeing the data, then the Bayes factor gives the poste-
 330 rior odds in favor of M_i , $BF_{ij} = p(\mathbf{y}|M_i)/p(\mathbf{y}|M_j)$ (Kass and Raftery, 1995),

331 where \mathbf{y} are all observations from the first to the last year of the time series,
 332 $t \in \{1, \dots, T\}$. The marginal likelihood $p(\mathbf{y}|M_i) = \int p(\mathbf{y}|\boldsymbol{\theta}_i, M_i)p(\boldsymbol{\theta}_i|M_i)d\boldsymbol{\theta}_i$,
 333 where $\boldsymbol{\theta}_i$ is the vector of unknown parameters under M_i , gives the proba-
 334 bility of the data under model M_i . The Bayes factors may be interpreted
 335 as evidence against a particular model with the following categories on the
 336 logarithmic scale (modified from Jeffreys, 1961; Kass and Raftery, 1995),

$\log_{10}(BF_{ij})$	Evidence against M_j
0 to 1/2	Weak
1/2 to 1	Substantial
1 to 2	Strong
> 2	Decisive

338 Bayes factors are known to exhibit sensitivity to the priors. We address
 339 this feature in two ways. First, we investigated the sensitivity of both meth-
 340 ods for model comparison under alternative choices of priors: a “broad prior”,
 341 with double the default standard deviations for priors of non-noise static pa-
 342 rameters; and a “half-Cauchy prior”, with a half-Cauchy for the process noise
 343 standard deviation. For the latter option, we set the scale parameter such
 344 that 99% of the prior probability mass is less than the upper bound of the
 345 process noise standard deviation given above (Section 3.3). Gelman (2006)
 346 suggests considering the half-Cauchy as an alternative prior to the uniform
 347 distribution; this option removes the upper bound on the process noise while
 348 placing greater support for low values of process noise.

349 Second, we also considered the Deviance Information Criterion (DIC)
 350 (Spiegelhalter et al., 2002). DIC is defined by $DIC = \overline{D(\boldsymbol{\theta})} + p_D$, where
 351 $D(\boldsymbol{\theta}) = -2 \log p(\mathbf{y}|\boldsymbol{\theta})$ is the deviance, $D(\bar{\boldsymbol{\theta}})$ uses the posterior mean as a
 352 point estimate of $\boldsymbol{\theta}$, $\overline{D(\boldsymbol{\theta})}$ is the deviance averaged over the posterior, and
 353 $p_D = \overline{D(\boldsymbol{\theta})} - D(\bar{\boldsymbol{\theta}})$ is the estimated effective number of parameters.

354 3.6. Synthetic Data

355 To test that the model-comparison approach can potentially detect the
 356 correct hypothesis from all alternatives, we generated a synthetic dataset
 357 under H_{pro} of length $T = 100$ years with parameter values: $\log \mathbf{x}_0 = [0, 0]'$,
 358 $G^{(i,i)} = G^{(j,j)} = 0.4$, $\mathbf{h} = [-1, -1]'$, $\sigma_\omega^{(i)} = 0.2$, $\sigma_\omega^{(j)} = 0.4$, $\sigma_\epsilon^{(i)} = 0.3$, $\sigma_\epsilon^{(j)} =$
 359 0.5 , and $\rho_\epsilon = 0.5$. We then fit models M_i for $i \in \{ind, pro, isi, obs\}$ under
 360 the default prior choice, the broad prior, and the half-Cauchy prior. Bayes
 361 factors and DIC were calculated for each prior choice. Similarly, we evaluated

362 model comparison under each prior choice for every empirical dataset to test
 363 the sensitivity of conclusions to the choice of priors.

364 3.7. Estimation

365 The state space model (Eq. 3) is linear and has Gaussian noise. We
 366 therefore used the Kalman filter to estimate the latent states conditional on
 367 the static parameters (Harvey, 1989; Schnute, 1994). We used an adaptive
 368 MCMC (AdMCMC) random-walk Metropolis algorithm with an acceptance
 369 probability that is jointly determined by the priors for the static parameters
 370 (Section 3), denoted by $p(\boldsymbol{\theta})$, and the likelihood conditional on the proposed
 371 set of static parameters, denoted by $p(\mathbf{y}_{1:T}|\boldsymbol{\theta}) = p(\mathbf{y}_1|\boldsymbol{\theta}) \prod_{t=2}^T p(\mathbf{y}_t|\mathbf{y}_{1:(t-1)}, \boldsymbol{\theta})$,
 372 that is derived from the Kalman filter (Harvey, 1989; Schnute, 1994). The target
 373 posterior distribution is then $p(\boldsymbol{\theta}|\mathbf{y}_{1:T}) \propto p(\mathbf{y}_{1:T}|\boldsymbol{\theta}) p(\boldsymbol{\theta})$. The Metropolis-
 374 Hastings acceptance probability at iteration j for the proposed static param-
 375 eters $\boldsymbol{\theta}_j^*$ is given by,

$$\alpha(\boldsymbol{\theta}_{j-1}, \boldsymbol{\theta}_j^*) = \min\left(1, \frac{p(\mathbf{y}_{1:T}|\boldsymbol{\theta}_j^*) p(\boldsymbol{\theta}_j^*)}{p(\mathbf{y}_{1:T}|\boldsymbol{\theta}_{j-1}) p(\boldsymbol{\theta}_{j-1})}\right),$$

376 where $\boldsymbol{\theta}_j^*$ is generated from a multivariate normal proposal distribution, de-
 377 noted $q(\boldsymbol{\theta}_{j-1}, \boldsymbol{\theta}_j^*)$, centered at $\boldsymbol{\theta}_{j-1}$.

378 We used an adaptive proposal $q_j(\boldsymbol{\theta}_{j-1}, \cdot)$ at iteration j for the proposed
 379 static parameters $\boldsymbol{\theta}_j^*$ that satisfies theoretical properties for ergodicity (Roberts
 380 and Rosenthal, 2009) and consisted of the mixture,

$$q_j(\boldsymbol{\theta}_{j-1}, \cdot) = \gamma \mathcal{N}\left(\boldsymbol{\theta}_j^*; \boldsymbol{\theta}_{j-1}, \frac{1}{d} \boldsymbol{\Sigma}_{j-1}\right) + (1 - \gamma) \mathcal{N}\left(\boldsymbol{\theta}_j^*; \boldsymbol{\theta}_{j-1}, \frac{0.1^2}{d} I_{d,d}\right), \quad (4)$$

381 where $\boldsymbol{\Sigma}_{j-1}$ is the empirical covariance matrix of the static parameters for
 382 all iterations up to and including iteration $j - 1$, d is the number of static
 383 parameters, $I_{d,d}$ is the $d \times d$ identity matrix, and γ is the weighting of the
 384 adaptive portion, here set equal to 0.95. The scaling coefficients were set
 385 to values proposed by Roberts and Rosenthal (2009) that approximate a
 386 theoretically optimal proposal for a multivariate normal posterior (Gelman
 387 et al., 2003), except that we have adjusted the scaling of the covariance matrix
 388 of the adaptive mixture component from $2.38^2/d$ to $1/d$ to help increase
 389 mixing.

390 We initialized the static parameters by sampling from the priors and
 391 started the AdMCMC algorithm with 600 iterations from the nonadaptive

392 mixture component in Equation (4) (i.e., with $\gamma = 0$). We then ran the
 393 algorithm for 1 million samples using the proposal Equation (4) with $\gamma =$
 394 0.95, thinned to every 50th sample, and monitored trace plots for suitable
 395 mixing. We report the posterior means and 95% credible intervals (CIs) of
 396 the static parameters based on the last half of the adaptive phase, which
 397 after thinning provided 10,000 samples drawn from the posterior.

398 The marginal likelihoods are required for calculation of the Bayes factors
 399 and are defined as $p(\mathbf{y}_{1:T}|M_i) = \int p(\mathbf{y}_{1:T}|\boldsymbol{\theta}_i, M_i) p(\boldsymbol{\theta}_i, M_i) d\boldsymbol{\theta}_i$, where $\boldsymbol{\theta}_i$ de-
 400 notes the vector of static parameters for model M_i . We used the importance
 401 sampling estimator $\hat{p}(\mathbf{y}_{1:T}|M_i) = N^{-1} \sum_{j=1}^N p(\mathbf{y}_{1:T}|\boldsymbol{\theta}_i^j, M_i) p(\boldsymbol{\theta}_i^j, M_i) / g(\boldsymbol{\theta}_i^j)$
 402 (e.g., Sinharay and Stern, 2005), where the density $g(\boldsymbol{\theta}_i^j) = \mathcal{T}(\boldsymbol{\theta}_i^j; \delta = \bar{\boldsymbol{\theta}}_i, \boldsymbol{\Sigma}_{\boldsymbol{\theta}_i},$
 403 $\nu = 2)$ is a Student's t distribution centered at the posterior mean, $\bar{\boldsymbol{\theta}}_i$, with
 404 $\nu = 2$ degrees of freedom and $\boldsymbol{\Sigma}_{\boldsymbol{\theta}_i}$ defined by the empirical covariance ma-
 405 trix of the posterior samples. The N samples $\boldsymbol{\theta}_i^j$ were drawn from this same
 406 distribution, $\boldsymbol{\theta}_i^j \sim \mathcal{T}(\delta = \bar{\boldsymbol{\theta}}_i, \boldsymbol{\Sigma}_{\boldsymbol{\theta}_i}, \nu = 2)$. We used $N = 100,000$ samples,
 407 which provided a level of accuracy sufficient to interpret the Bayes factors
 408 on the logarithmic scale.

409 4. Results

410 4.1. Synthetic data analyses

411 In accord with the synthetic dataset generated under H_{pro} , both Bayes
 412 factors and DIC ranked the true model M_{pro} as the best-fitting model (Ap-
 413 pendix A). Moreover, the 95% CI intervals for M_{pro} models under all priors
 414 contained the true parameters that generated the synthetic dataset. The
 415 observation model was the second best fitting model. Across all prior choices
 416 (default, “broad” and “half-Cauchy” priors, Table A.1), the relative rank-
 417 ings provided by Bayes factors and DIC were unchanged with M_{pro} and M_{obs}
 418 closely ranked together as the best fitting models.

419 4.2. Real data analyses

420 For a given species and dataset, the standard deviations of both the
 421 process and observation error were similar across all models (Figure 2, Table
 422 B.1). There was some evidence that process noise is higher for California
 423 anchovy than sardine, where the probability that $\sigma_\epsilon^{(s)} > \sigma_\epsilon^{(a)}$ was greater than
 424 0.90 for every model but M_{com} . The estimated observation error was higher
 425 for anchovy than sardine in Peru with $P(\sigma_\omega^{(a)} > \sigma_\omega^{(s)}) > 0.95$ for all models.

426 Process noise and observation error magnitudes were relatively similar for
427 South Africa. In Japan, the estimated process noise was significantly higher
428 for sardine compared to anchovy (Figure 2), and the Japanese data sets had
429 the lowest observation noise.

430 Estimates of intraspecific density dependence appeared weaker for sardine
431 than anchovy (Figure 3, Table B.1). For sardine, the 95% CI for $G^{(s,s)}$
432 admitted density independence for all models in every data set but California.
433 For anchovy, the 95% CI for $G^{(a,a)}$ excluded density independence for all
434 models from Peru, South Africa, and Japan (Pacific). Differences between
435 the two species were most apparent in Peru. There, $G^{(s,s)}$ was significantly
436 higher than $G^{(a,a)}$ and $h^{(s)}$ significantly less than $h^{(a)}$ for all models but M_{com} .
437 On the other hand, a significant difference was seen for model M_{com} in the
438 short Japan series. Although these are the only significant differences among
439 these parameters, it is notable that the posterior means for $G^{(a,a)}$ were less
440 than $G^{(s,s)}$ in every analysis, which suggests that anchovy may have stronger
441 intraspecific density dependence than sardine.

442 We now step through the model selection results and present the esti-
443 mated latent path spaces for the top ranked models of each location. The
444 estimated latent path space for the best fitting models from each dataset are
445 shown in Figure 4.

446 *California*—The Bayes factors suggested that M_{pro} was the best-fitting
447 model with substantial support over the other models (Table 1). Whereas the
448 Bayes factors suggested that all of the other models have equivalent support,
449 DIC instead ranked the model with interspecific competition (M_{com}) very
450 closely with M_{pro} as the best-fitting models.

451 This is the shortest data series considered in the paper, and in Figure 5
452 the marginal posterior distributions and prior distributions are plotted for the
453 best fitting model M_{pro} . We note that although the posterior distributions
454 for the standard deviations of the noise processes were broad, their modes
455 fell well within the bounds specified by the uniform priors. Comparatively
456 narrow marginal posterior distributions were evident for both \mathbf{G} and \mathbf{h} . The
457 posterior mode of ρ_ϵ was strongly negative, which suggests some evidence for
458 negative dependence in the process noise between the two species.

459 *Peru*—The Bayes factors suggested that M_{pro} was the best model, but
460 with weak support relative to M_{ind} and M_{obs} . The DIC rankings suggested
461 that no particular model dominates.

462 *South Africa*—The Bayes factors suggested that model M_{pro} was the best
463 fitting model, but with only weak support over M_{ind} and M_{obs} . Model M_{com}

464 was the worst. DIC ranked M_{pro} and M_{obs} as the best models.

465 *Japan (Pacific)*—The Bayes factors showed weak support for M_{com} relative
466 to the other models, except for M_{obs} with which it was tied. M_{pro} was the
467 worst-fitting model but the evidence against it was weak. The DIC ranking
468 on the other hand favored M_{com} over the other models.

469 *Japan (Combined)*—The Bayes factors suggested that the best-fitting model
470 was M_{pro} , but with only weak support over M_{ind} and M_{obs} . M_{com} was the
471 worst-fitting model. The DIC values suggested that M_{pro} was the best model
472 and M_{com} the worst. A complementary analysis on the subset of this dataset
473 for the years that match those of the Japan (Pacific) series suggested strong
474 support for M_{pro} over M_{ind} and M_{obs} (Table C.1).

475 For the best-fitting model M_{pro} of this time series, which was the longest
476 considered in this paper, we considered the bivariate relationships from the
477 posterior (Figure 6). For both species, negative dependence existed between
478 $h^{(i)}$ and $G^{(i,i)}$. This corresponds to a trade-off between density dependence
479 and density independence seen in Gompertz process models (Dennis et al.,
480 2006). Negative dependence also existed between the magnitude of the envi-
481 ronmental and observational noise; this dependence was stronger for anchovy
482 than sardine.

483 4.3. Prior sensitivity

484 For the Bayes factor model comparison with the real data sets, the relative
485 rankings of M_{pro} and M_{com} for the Japan (Pacific) and California analyses
486 depended on the choice of prior. In the M_{pro} comparison to M_{com} , the broad
487 prior choice provided less support for M_{com} in the Japan (Pacific) series
488 relative to the default prior choice. This may have occurred because overly
489 broad priors in a Bayes factor comparison favor the simpler model (Kass
490 and Raftery, 1995), which is M_{pro} in this case. In contrast, the Bayes factor
491 comparison for California under the half-Cauchy prior choice provided less
492 support for M_{pro} than the default prior. This may have occurred because
493 the half-Cauchy prior provides less support for moderately high values of
494 $\sigma_\epsilon^{(i)}$ than the default prior. Posterior means for $\sigma_\epsilon^{(i)}$ were lower under the
495 half-Cauchy prior than the default prior (a reduction of 70% for anchovy
496 and 40% for sardine). Pairwise model comparisons that have substantial
497 evidence in favor of one model were consistent in the sense that there was
498 never substantial evidence for the other model under an alternative prior
499 choice (Tables 1, Appendix D).

500 The DIC rankings were also broadly consistent, and had identical rankings
501 across prior choices for the Japanese and South African datasets. The rank
502 order for the California dataset did depend on the prior choice with the half-
503 Cauchy prior leading to M_{com} having a very low value of DIC; however, the
504 posterior distribution for this model showed evidence for multimodality, and
505 the simple application of DIC to the posterior means of the parameters may
506 not be appropriate (Spiegelhalter et al., 2002). For the Peru data set, the half-
507 Cauchy prior also led to better performance by M_{pro} and M_{obs} relative to the
508 other models, whereas the DIC ranked M_{com} , which again had a multimodal
509 posterior, as the best model.

510 5. Discussion

511 The process dependence hypothesis H_{pro} had the broadest support out of
512 the four hypotheses considered. Model M_{pro} either shared or solely occupied
513 the top rank for all time series. Nevertheless, the independence hypothe-
514 sis (H_{ind}) and the observational dependence hypothesis (H_{obs}) could not be
515 discounted for four of the five time series. Moreover, the community in-
516 teractions hypothesis (H_{com}) had some support for the Japan (Pacific) time
517 series, which is based on a subset of the Japan (combined) data. A secondary
518 analysis performed on the Japan (combined) series for the same period as
519 the shorter Japan (Pacific) series found strong support for M_{pro} over M_{com} .
520 Conclusions for the Japanese stocks were evidently affected by geographical
521 scale, temporal scale, stock composition, or a combination of these factors.
522 Thus, although the environmental dependence hypothesis performed best in
523 most of the analyses considered, all hypotheses found some support.

524 As expected, the Bayes factors exhibited some sensitivity to the choice of
525 priors, but not enough to draw the main conclusions into question. Pairwise
526 model comparisons that had substantial evidence in favor of one model were
527 consistent in the sense that there was never substantial evidence for the
528 other model under an alternative prior choice. The relative rankings of the
529 different models as given by DIC were preserved under each prior choice in
530 most cases. However, comparatively low DIC values were seen if the posterior
531 distribution exhibited multimodality; in this case, simply applying DIC using
532 the posterior mean as a point estimate may be inappropriate (Spiegelhalter
533 et al., 2002). Excepting those analyses that exhibited a multimodal posterior,
534 M_{pro} remained among the top ranked models for four of the five data sets for
535 both DIC and Bayes factors no matter the prior choice.

536 We take the success of M_{pro} to most likely signal the effect of dependent
537 environmental stochasticity that arise from one or more underlying common
538 factors. Process noise dependence could theoretically be introduced by fish-
539 eries management or economics that affect the exploitation rates, but this
540 seems less likely than the environmental hypotheses that receive the most at-
541 tention in the literature. The negative fluctuations between Japanese sardine
542 and anchovy landings, for instance, are thought to be driven by changes in
543 stock abundance rather than the fisheries alternately targeting the different
544 species (Hayasi, 1967).

545 There was some evidence that intraspecific density dependence may be
546 stronger for anchovy than sardine (Figure 3). The 95% CIs for $G^{(s,s)}$ in the
547 sardine populations admitted the possibility of no negative density depen-
548 dence for every model in every data set but California (Table B.1). These
549 small pelagic systems may thus exhibit susceptibility to environmental and
550 anthropogenic perturbations in line with the sentiment of Beverton (1990).

551 Small pelagic fishes may be susceptible to perturbations because of their
552 short lifespan and young age at maturity (Yatsu et al., 2008). Reactivity
553 provides a useful metric for measuring transitory susceptibility to perturba-
554 tions; in general, it is a nonlinear function of the density dependent param-
555 eters given by \mathbf{G} (Caswell and Neubert, 2005). If the system described by \mathbf{G}
556 is reactive then some perturbations will be amplified by the process model
557 and the system response can be difficult to predict. Neubert et al. (2009)
558 provide a frequentist test for the null hypothesis that reactivity is exactly
559 zero. In our Bayesian approach, we have obtained posterior samples for each
560 model, and so it is easy to not only evaluate the probability that any model
561 is reactive but also to examine conditional probabilities with other nonlinear
562 functions of the process model parameters. For instance, M_{com} was the best
563 ranked model for the Japan (Pacific) data set, and there was a posterior
564 probability of 0.8 that this system is reactive. However, we could also look
565 at the conditional probability that the system is reactive, given that the sys-
566 tem is also stable. Returning to the analysis of M_{com} for the Japan (Pacific)
567 data, we found that ~ 0.88 probability that the system was stable. Given
568 that the system was stable, there was a conditional probability of ~ 0.77
569 that the system was reactive, and 0.68 joint probability that the system was
570 both stable and reactive.

571 The sometimes dramatic nature of the antagonistic fluctuations of sar-
572 dine and anchovy has prompted discussions of regime shifts (e.g., Lluich-Belda
573 et al., 1989; Alheit and Niquen, 2004). We did not consider the added compli-

574 cation of a model developed specifically for regime shifts, although the models
575 can and do capture transitions between sardine and anchovy dominated ma-
576 rine ecosystems. The success of the correlated environmental stochasticity
577 could be interpreted as support for regime shifts, in that it suggested that
578 negative dependence between sardine and anchovy is environmentally forced
579 (deYoung et al., 2004), but this external forcing may be driven by oscillating
580 mechanisms such as the El Niño-Southern Oscillation that are not typically
581 considered regime shifts (Alheit and Niquen, 2004).

582 One explanation for oceanic regime shifts suggests that positive feedbacks
583 generated by biological mechanisms may maintain alternative stable states
584 (e.g., Scheffer et al., 2001). The process model (Equation 3) is linear and so
585 does not admit alternative stable states. However, this process model may
586 approximate nonlinear systems (Ives et al., 2003; Neubert et al., 2009). If
587 so considered, the sign of the off-diagonal elements of the matrix \mathbf{G} provides
588 evidence of whether or not feedback cycles may assist in maintaining regime
589 change. In our analyses, only the Japan (Pacific) data set provided some
590 support for a biological model M_{com} with non-zero interspecific interactions
591 between sardine and anchovy. Moreover, using samples from the posterior
592 of this analysis (M_{com} for the Japan (Pacific) dataset) to consider joint de-
593 pendence among the entries of \mathbf{G} , the posterior probability of competitive
594 interactions, and hence positive feedback between sardine and anchovy, was
595 only 0.10. This analysis thus suggested that regime shifts are not sustained
596 by positive feedback among sardine and anchovy.

597 To test the four general hypotheses considered in this paper with the
598 diverse landings data, we used a parsimonious state space model that did
599 not explicitly include fishing effort or aspects of catchability for the three
600 reasons discussed in Section 3.1. Instead, our simple model is based on
601 the observation of Beverton (1990) that the exploitation rate f for small
602 pelagic fisheries is often sustained at relatively high levels across changes
603 in stock abundance of more than an order of magnitude. The observation
604 error captures variation in the exploitation rate that affects catch as a proxy
605 index of the latent states. Moreover, process noise captures the variation
606 in the exploitation rate that affects the trajectory of the latent states over
607 time, in addition to the environmental stochasticity introduced by processes
608 that affect recruitment and mortality. Whether or not this is a valid model
609 depends on the nature of the fishery; at a minimum, it requires an active
610 fishery that targets the stocks.

611 Some evidence of a catch–abundance relationship, for instance, is sug-

612 gested for the Japanese stocks of anchovy and sardine, where the estimates
613 of biomass available in recent years are correlated with landings data (Taka-
614 suka et al., 2008). Borges et al. (2003) also correlated annual recruitment of
615 Portuguese sardine with variation in the catch for the following year. They
616 attributed this association to changes in effective effort that track the sar-
617 dine population over time. However, this result is also consistent with a
618 relatively constant f , which also absorbs the problem of changing catcha-
619 bility as discussed in Section 3.1. Nevertheless, inferences from commercial
620 catch or catch-effort data of small pelagic fisheries will always be limited
621 without annual fishery independent surveys that can help identify changes
622 in catchability (Reed and Simons, 1996). Many small pelagic fisheries have
623 ongoing fishery independent surveys (Barange et al., 2009a) that will assist
624 analyses of temporal dependence among stocks as longer time series become
625 available.

626 The estimation procedure used here (Section 3.7) may also be extended to
627 accommodate nonlinear process models using a particle filter representation
628 of the likelihood and MCMC over the static parameters (Andrieu et al., 2010).
629 Combining this approach with the adaptive Metropolis proposal presented
630 in Section 3.7 provides a flexible methodology to include nonlinear process
631 models for flexible negative density dependence or depensation (Peters et al.,
632 2010, submitted manuscript). Such an approach can also accommodate non-
633 Gaussian observation error (Hosack et al., In Press), which Knappe et al.
634 (2011) notes may affect estimates of density dependence in Gompertz state
635 space models.

636 6. Conclusion

637 Four hypotheses of temporal dependence between sardine and anchovy
638 landings were tested using five different data sets of sardine and anchovy
639 landings. The hypotheses were independence, process dependence, commu-
640 nity interactions, and observation dependence. The hypothesis of process
641 dependence found the broadest support, however, some support was found
642 for all hypotheses depending on the specificities of the sardine and anchovy
643 time series. In general, sardine and anchovy landings suggest strong process
644 dependence with susceptibility to environmental and anthropogenic pertur-
645 bations and undercompensating intraspecific density dependence. Results
646 suggest that for specific stocks the best fitting hypothesis may depend on
647 the geographic scale, temporal scale, and stock composition of the time se-

648 ries. Further developments should consider a refined specification of model
649 structure and the identification of appropriate scales of analysis relevant to
650 both biological and fisheries dynamics of small pelagics.

651 **Acknowledgments**

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Figure 1: A 100 year time series of annual landings of Japanese stocks of anchovy (black line) and sardine (grey line), as reported by Yatsu et al. (2005) and Takasuka et al. (2008), for the years 1905-2004.

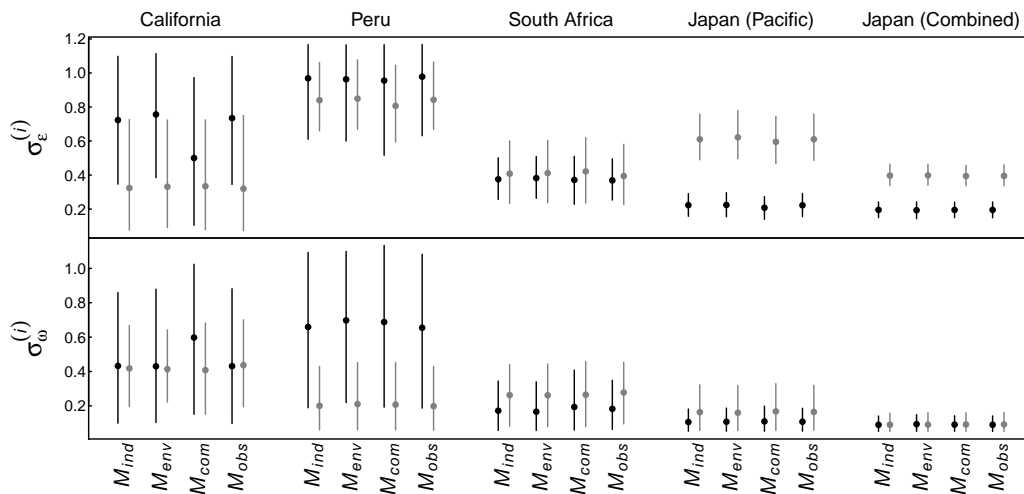


Figure 2: Posterior means (points) and 95% CI (lines) for (*top*) standard deviation of process error $\sigma_\epsilon^{(a)}$ (anchovy in black) and $\sigma_\epsilon^{(s)}$ (sardine in grey) and (*bottom*) standard deviation of observation error $\sigma_\omega^{(a)}$ (black) and $\sigma_\omega^{(s)}$ (grey).

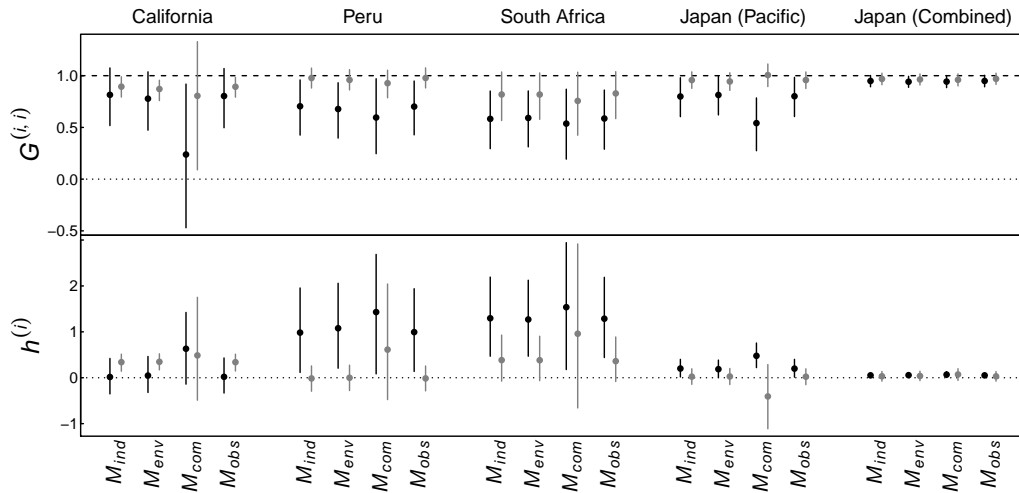


Figure 3: Posterior means (points) and 95% CI (lines) for (*top*) intraspecific density dependence $G^{(a,a)}$ (black) and $G^{(s,s)}$ (grey). The horizontal dashed line corresponds to a random walk for models without intraspecific density dependence (i.e., excluding M_{com}); for these same models, estimates of density dependence below the dotted line correspond to overcompensating density dependence and the region in between the lines corresponds to undercompensating negative density dependence. *Bottom*: density independent parameters $h^{(a)}$ (black) and $h^{(s)}$ (grey).

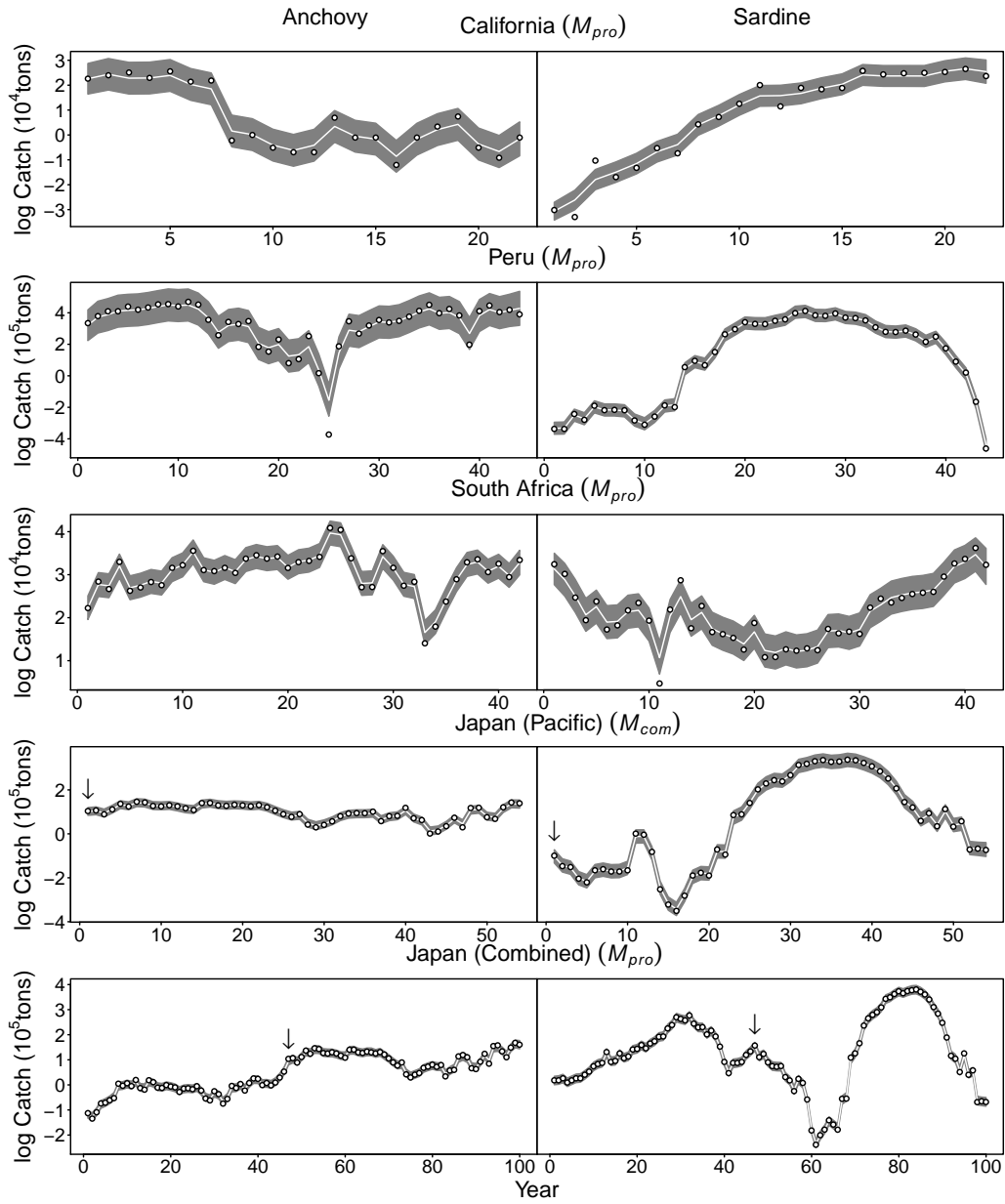


Figure 4: Minimum mean square estimates of the smoothed mean for the latent path space (white line) with ± 2 smoothed standard deviations. Observations are overlaid points. Latent path space estimates are based on the best fitting model for each series (Table 1). The x-axes are given in years beginning with the first observation of both anchovy and sardine landings. For the two related Japan series, the arrows denote the year in which the shorter Japan (Pacific) series begins.

Table 1: Bayes factors and DIC results under the default choice of priors. For a given dataset, the entry $\log_{10}(BF_{ij})$, which corresponds to the logarithm of the Bayes factor for the i^{th} row and the j^{th} column, gives the evidence for M_i and the evidence against M_j . Thresholds for interpreting the Bayes factors on the log scale are given in Section 3.5. Note that the Bayes factor table for a given dataset is antisymmetric. Bayes factors with substantial evidence for or against M_i are in bold.

		M_{ind}	M_{pro}	M_{com}	M_{obs}	DIC
California	M_{ind}	0	-0.6	0	0.1	94.9
	M_{pro}	0.6	0	0.6	0.7	90.7
	M_{com}	0	-0.6	0	0.1	90.6
	M_{obs}	-0.1	-0.7	-0.1	0	95.0
Peru	M_{ind}	0	-0.2	1.1	0	261.6
	M_{pro}	0.2	0	1.3	0.2	261.1
	M_{com}	-1.1	-1.3	0	-1.1	261.0
	M_{obs}	0	-0.2	1.1	0	261.4
South Africa	M_{ind}	0	-0.4	1.5	-0.2	112.8
	M_{pro}	0.4	0	1.9	0.2	110.2
	M_{com}	-1.5	-1.9	0	-1.8	117.7
	M_{obs}	0.2	-0.2	1.8	0	110.9
Japan (Pacific)	M_{ind}	0	0.2	-0.1	-0.1	114.3
	M_{pro}	-0.2	0	-0.3	-0.2	115.0
	M_{com}	0.1	0.3	0	0	107.8
	M_{obs}	0.1	0.2	0	0	114.1
Japan (Combined)	M_{ind}	0	-0.4	2.7	-0.1	97.1
	M_{pro}	0.4	0	3.1	0.3	94.6
	M_{com}	-2.7	-3.1	0	-2.8	99.4
	M_{obs}	0.1	-0.3	2.8	0	96.5

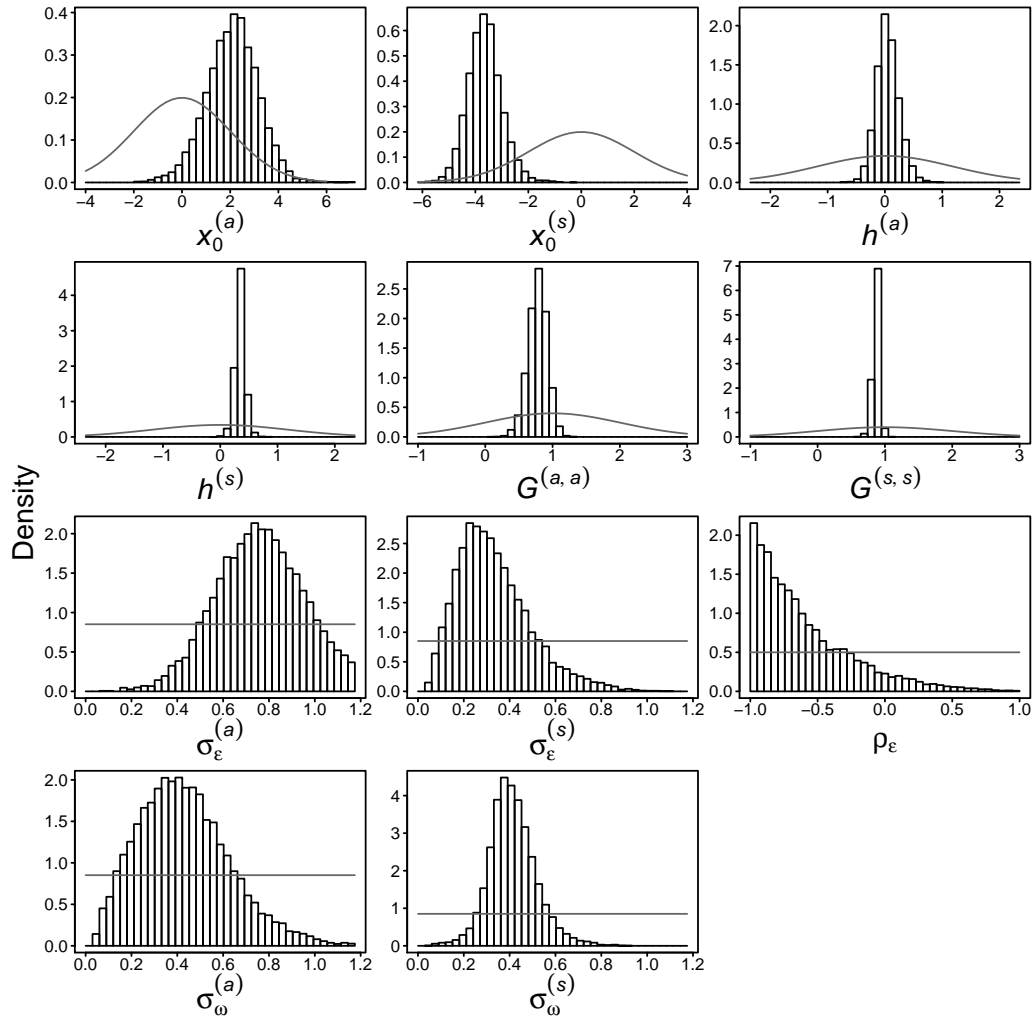


Figure 5: Marginal posterior distributions (histograms) and prior densities (grey lines) of the static parameters of the best-fitting model M_{pro} for the California landings data.

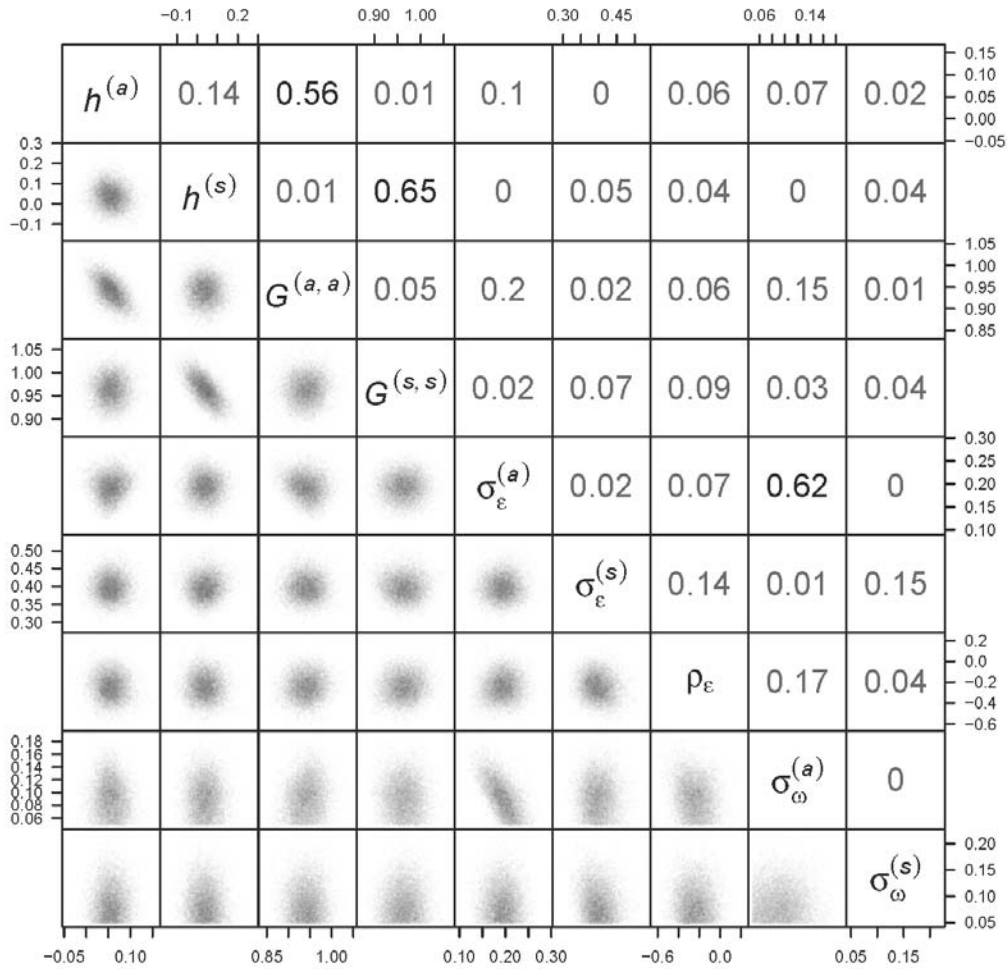


Figure 6: Bivariate marginal posterior distributions of the static parameters of the best-fitting model M_{pro} for the Japan (combined) landings data. The lower diagonal shows pairwise samples drawn from the posterior. The upper diagonal shows the linear correlation coefficients with those greater than 0.5 in bold. For legibility, the initial state parameters \mathbf{x}_0 are not shown.

657 **References**

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840 **Appendix A. Synthetic study model comparison**

Table A.1: Bayes factor and DIC results for synthetic data. The true model is M_{pro} with correlated process noise. Variations on prior choice: default with uniform priors on process and observation noise, broad prior with twice standard deviation for normal priors of other static parameters, and default choice but with a half-Cauchy prior on process noise standard deviations.

		M_{ind}	M_{pro}	M_{com}	M_{obs}	DIC
Uniform	M_{ind}	0	-1.5	1.8	-1.1	283.9
	M_{pro}	1.5	0	3.3	0.4	276.1
	M_{com}	-1.8	-3.3	0	-2.9	288.3
	M_{obs}	1.1	-0.4	2.9	0	278.3
Broad	M_{ind}	0	-1.5	2.4	-1.1	284.5
	M_{pro}	1.5	0	3.9	0.4	276.6
	M_{com}	-2.4	-3.9	0	-3.5	288.9
	M_{obs}	1.1	-0.4	3.5	0	278.8
Half-Cauchy	M_{ind}	0	-1.4	1.5	-1.3	285.9
	M_{pro}	1.4	0	3	0.2	277.3
	M_{com}	-1.5	-3	0	-2.8	291.2
	M_{obs}	1.3	-0.2	2.8	0	279.6

841 **Appendix B. Posterior means and 95% CI's of model parameters**
842 **for the real data analyses.**

Table B.1: Posterior means and 95% credible intervals of the model parameters.

Model	Parameter	California	Peru	South Africa	Japan (Pacific)	Japan (Combined)
M_{ind}	$x_0^{(a)}$	2.29 [0.23, 4.23]	2.07 [-0.85, 4.61]	1.38 [-0.63, 2.83]	1.03 [0.42, 1.65]	-1.27 [-1.74, -0.82]
	$x_0^{(s)}$	-3.71 [-4.96, -2.35]	-2.87 [-4.54, -1.17]	3.16 [1.95, 4.45]	-0.98 [-2.24, 0.25]	0.15 [-0.68, 0.99]
	$h^{(a)}$	0.02 [-0.35, 0.42]	0.98 [0.11, 1.96]	1.3 [0.47, 2.19]	0.2 [0.02, 0.4]	0.05 [0.01, 0.1]
	$h^{(s)}$	0.34 [0.14, 0.51]	-0.02 [-0.29, 0.26]	0.38 [-0.07, 0.93]	0.02 [-0.14, 0.2]	0.03 [-0.07, 0.14]
	$G^{(a,a)}$	0.82 [0.52, 1.07]	0.7 [0.43, 0.96]	0.58 [0.29, 0.85]	0.8 [0.6, 0.98]	0.95 [0.89, 1]
	$G^{(s,s)}$	0.89 [0.79, 0.99]	0.98 [0.88, 1.07]	0.82 [0.57, 1.04]	0.96 [0.88, 1.04]	0.97 [0.91, 1.02]
	$\sigma_\epsilon^{(a)}$	0.72 [0.35, 1.1]	0.97 [0.61, 1.17]	0.38 [0.26, 0.5]	0.22 [0.16, 0.29]	0.2 [0.15, 0.24]
	$\sigma_\epsilon^{(s)}$	0.32 [0.08, 0.73]	0.84 [0.66, 1.06]	0.41 [0.23, 0.6]	0.61 [0.49, 0.76]	0.4 [0.34, 0.46]
	$\sigma_\omega^{(a)}$	0.43 [0.1, 0.86]	0.66 [0.19, 1.09]	0.17 [0.06, 0.34]	0.11 [0.05, 0.18]	0.09 [0.05, 0.14]
	$\sigma_\omega^{(s)}$	0.42 [0.2, 0.67]	0.2 [0.06, 0.43]	0.26 [0.08, 0.44]	0.16 [0.06, 0.32]	0.09 [0.05, 0.16]
M_{pro}	$x_0^{(a)}$	2.09 [-0.08, 4.11]	1.85 [-1.17, 4.42]	1.49 [-0.42, 2.87]	1 [0.35, 1.61]	-1.3 [-1.75, -0.84]
	$x_0^{(s)}$	-3.65 [-4.86, -2.29]	-2.76 [-4.42, -1.05]	3.2 [2.06, 4.44]	-0.99 [-2.28, 0.3]	0.13 [-0.71, 0.95]
	$h^{(a)}$	0.05 [-0.32, 0.46]	1.08 [0.21, 2.06]	1.27 [0.47, 2.12]	0.19 [0.01, 0.38]	0.06 [0.01, 0.1]
	$h^{(s)}$	0.35 [0.17, 0.52]	0 [-0.28, 0.27]	0.38 [-0.06, 0.9]	0.03 [-0.15, 0.2]	0.04 [-0.06, 0.14]
	$G^{(a,a)}$	0.78 [0.47, 1.04]	0.68 [0.4, 0.93]	0.59 [0.31, 0.85]	0.81 [0.62, 0.99]	0.94 [0.89, 0.99]
	$G^{(s,s)}$	0.87 [0.76, 0.96]	0.96 [0.86, 1.06]	0.82 [0.58, 1.03]	0.94 [0.86, 1.03]	0.96 [0.91, 1.02]
	$\sigma_\epsilon^{(a)}$	0.76 [0.38, 1.11]	0.96 [0.6, 1.17]	0.38 [0.26, 0.51]	0.22 [0.15, 0.3]	0.19 [0.14, 0.24]
	$\sigma_\epsilon^{(s)}$	0.33 [0.09, 0.72]	0.85 [0.67, 1.08]	0.41 [0.24, 0.6]	0.62 [0.5, 0.78]	0.4 [0.34, 0.46]
	ρ_ϵ	-0.6 [-0.99, 0.36]	-0.3 [-0.65, 0.07]	-0.36 [-0.72, 0.08]	-0.19 [-0.51, 0.17]	-0.24 [-0.46, -0.02]
	$\sigma_\omega^{(a)}$	0.43 [0.1, 0.88]	0.7 [0.22, 1.1]	0.17 [0.06, 0.34]	0.11 [0.05, 0.19]	0.09 [0.05, 0.15]
$\sigma_\omega^{(s)}$	0.41 [0.22, 0.64]	0.21 [0.06, 0.45]	0.26 [0.08, 0.44]	0.16 [0.06, 0.32]	0.09 [0.05, 0.16]	
M_{com}	$x_0^{(a)}$	1.1 [-3.21, 4.74]	1.7 [-1.82, 4.69]	1.15 [-1.57, 2.83]	0.84 [-0.16, 1.71]	-1.3 [-1.77, -0.82]
	$x_0^{(s)}$	-3.22 [-5.39, 0.33]	-3.24 [-5.09, -1.32]	2.71 [0.21, 4.34]	-0.89 [-2.09, 0.33]	0.02 [-0.86, 0.91]
	$h^{(a)}$	0.63 [-0.14, 1.42]	1.43 [0.08, 2.69]	1.54 [0.18, 2.94]	0.48 [0.22, 0.76]	0.07 [0, 0.13]
	$h^{(s)}$	0.49 [-0.49, 1.75]	0.61 [-0.48, 2.04]	0.96 [-0.66, 2.91]	-0.41 [-1.11, 0.29]	0.07 [-0.06, 0.2]
	$G^{(a,a)}$	0.24 [-0.47, 0.92]	0.6 [0.25, 0.97]	0.54 [0.19, 0.87]	0.54 [0.27, 0.78]	0.94 [0.88, 1]
	$G^{(s,a)}$	-0.41 [-0.84, 0.02]	-0.1 [-0.26, 0.05]	-0.05 [-0.3, 0.19]	-0.06 [-0.1, -0.02]	-0.01 [-0.04, 0.02]
	$G^{(s,s)}$	-0.15 [-1.44, 0.78]	-0.18 [-0.59, 0.11]	-0.15 [-0.62, 0.25]	0.42 [-0.24, 1.1]	-0.06 [-0.18, 0.05]
	$G^{(s,s)}$	0.81 [0.09, 1.33]	0.93 [0.79, 1.05]	0.76 [0.42, 1.03]	1.01 [0.89, 1.11]	0.96 [0.9, 1.02]
	$\sigma_\epsilon^{(a)}$	0.5 [0.1, 0.97]	0.96 [0.52, 1.17]	0.37 [0.23, 0.51]	0.21 [0.14, 0.27]	0.2 [0.15, 0.24]
	$\sigma_\epsilon^{(s)}$	0.33 [0.08, 0.72]	0.81 [0.59, 1.05]	0.42 [0.24, 0.62]	0.6 [0.47, 0.75]	0.39 [0.34, 0.46]
$\sigma_\omega^{(a)}$	0.6 [0.15, 1.02]	0.69 [0.19, 1.13]	0.19 [0.06, 0.41]	0.11 [0.05, 0.2]	0.09 [0.05, 0.14]	
$\sigma_\omega^{(s)}$	0.41 [0.15, 0.68]	0.21 [0.06, 0.45]	0.26 [0.08, 0.46]	0.17 [0.06, 0.33]	0.09 [0.05, 0.16]	
M_{obs}	$x_0^{(a)}$	2.29 [0.18, 4.21]	2.06 [-0.85, 4.56]	1.43 [-0.64, 2.84]	1.03 [0.4, 1.66]	-1.27 [-1.72, -0.81]
	$x_0^{(s)}$	-3.72 [-4.92, -2.32]	-2.88 [-4.52, -1.21]	3.13 [2.03, 4.34]	-0.99 [-2.27, 0.28]	0.16 [-0.64, 0.95]
	$h^{(a)}$	0.02 [-0.33, 0.43]	0.99 [0.14, 1.94]	1.29 [0.44, 2.19]	0.2 [0.01, 0.4]	0.05 [0, 0.1]
	$h^{(s)}$	0.34 [0.15, 0.51]	-0.01 [-0.29, 0.26]	0.36 [-0.08, 0.89]	0.02 [-0.15, 0.19]	0.03 [-0.08, 0.14]
	$G^{(a,a)}$	0.8 [0.5, 1.07]	0.7 [0.43, 0.95]	0.59 [0.29, 0.86]	0.8 [0.61, 0.98]	0.95 [0.89, 1]
	$G^{(s,s)}$	0.89 [0.79, 0.98]	0.98 [0.88, 1.08]	0.83 [0.58, 1.04]	0.96 [0.88, 1.04]	0.97 [0.92, 1.02]
	$\sigma_\epsilon^{(a)}$	0.73 [0.34, 1.1]	0.98 [0.63, 1.17]	0.37 [0.25, 0.5]	0.22 [0.16, 0.29]	0.2 [0.15, 0.24]
	$\sigma_\epsilon^{(s)}$	0.32 [0.07, 0.75]	0.84 [0.67, 1.06]	0.39 [0.23, 0.58]	0.61 [0.49, 0.76]	0.4 [0.34, 0.46]
	$\sigma_\omega^{(a)}$	0.43 [0.1, 0.88]	0.65 [0.19, 1.08]	0.18 [0.06, 0.35]	0.11 [0.05, 0.19]	0.09 [0.05, 0.14]
	$\sigma_\omega^{(s)}$	0.44 [0.19, 0.7]	0.2 [0.06, 0.43]	0.28 [0.09, 0.45]	0.16 [0.06, 0.32]	0.09 [0.05, 0.16]
	ρ_ω	-0.28 [-0.94, 0.71]	-0.17 [-0.96, 0.9]	-0.51 [-0.98, 0.56]	-0.36 [-0.98, 0.79]	-0.4 [-0.97, 0.67]

843 **Appendix C. Analysis of abbreviated Japan (combined) time se-**
844 **ries**

Table C.1: Bayes factor and DIC results for the analysis of the Japan (combined) data series abbreviated to years of overlap with the Japan (Pacific) series under default prior choice with uniform priors on process and observation noise standard deviations.

	M_{ind}	M_{pro}	M_{com}	M_{obs}	DIC
M_{ind}	0	-0.5	0.7	-0.1	82.2
M_{pro}	0.5	0	1.2	0.5	79.2
M_{com}	-0.7	-1.2	0	-0.8	80.5
M_{obs}	0.1	-0.5	0.8	0	81.7

845 **Appendix D. Model comparison under alternative priors**

846 This appendix provides Bayes factors and posterior means of the param-
 847 eter estimates under two alternative prior formulations.

Table D.1: Bayes factor and DIC results. Broad priors.

		M_{ind}	M_{pro}	M_{com}	M_{obs}	DIC
California	M_{ind}	0	-0.6	0.4	0.1	94.0
	M_{pro}	0.6	0	1	0.7	90.2
	M_{com}	-0.4	-1	0	-0.4	90.4
	M_{obs}	-0.1	-0.7	0.4	0	94.5
Peru	M_{ind}	0	-0.2	1.6	0	261.6
	M_{pro}	0.2	0	1.8	0.2	260.5
	M_{com}	-1.6	-1.8	0	-1.6	261.3
	M_{obs}	0	-0.2	1.6	0	261.3
South Africa	M_{ind}	0	-0.4	2.2	-0.2	112.9
	M_{pro}	0.4	0	2.6	0.2	110.7
	M_{com}	-2.2	-2.6	0	-2.4	118.3
	M_{obs}	0.2	-0.2	2.4	0	111.4
Japan (Pacific)	M_{ind}	0	0.2	0.4	-0.1	114.8
	M_{pro}	-0.2	0	0.3	-0.2	115.1
	M_{com}	-0.4	-0.3	0	-0.5	108.7
	M_{obs}	0.1	0.2	0.5	0	114.7
Japan (Combined)	M_{ind}	0	-0.3	3.3	0	97.0
	M_{pro}	0.3	0	3.6	0.3	94.2
	M_{com}	-3.3	-3.6	0	-3.4	99.2
	M_{obs}	0	-0.3	3.4	0	96.7

Table D.2: Bayes factor and DIC results with Half-Cauchy prior for the standard deviation of the process noise.

		M_{ind}	M_{pro}	M_{com}	M_{obs}	DIC
California	M_{ind}	0	-0.3	-0.6	0.1	166.2
	M_{pro}	0.3	0	-0.4	0.4	162.8
	M_{com}	0.6	0.4	0	0.8	62.7
	M_{obs}	-0.1	-0.4	-0.8	0	164.9
Peru	M_{ind}	0	-0.2	0.9	0	262.2
	M_{pro}	0.2	0	1.1	0.2	261.4
	M_{com}	-0.9	-1.1	0	-0.9	256.8
	M_{obs}	0	-0.2	0.9	0	261.9
South Africa	M_{ind}	0	-0.4	1.5	-0.3	112.6
	M_{pro}	0.4	0	1.9	0.1	110.5
	M_{com}	-1.5	-1.9	0	-1.8	118.7
	M_{obs}	0.3	-0.1	1.8	0	111.0
Japan (Pacific)	M_{ind}	0	0.2	-0.2	0	114.7
	M_{pro}	-0.2	0	-0.3	-0.2	115.0
	M_{com}	0.2	0.3	0	0.1	108.7
	M_{obs}	0	0.2	-0.1	0	114.2
Japan (Combined)	M_{ind}	0	-0.4	2.7	-0.1	97.2
	M_{pro}	0.4	0	3.1	0.3	95.0
	M_{com}	-2.7	-3.1	0	-2.8	99.2
	M_{obs}	0.1	-0.3	2.8	0	96.7