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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'ile d'Yeu, BP 21105, 44311 Nantes cedex 3, France

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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.

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; Takahashi et al., 2009; Takasuka et al., 2008) or indirect impacts through phytoplankton or zooplankton (e.g., Cury and Shannon, 2004; van der Lingen et al., 2006b; Yatsu et al., 2005) have been proposed to explain the negative temporal 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 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:

> H_{ind}: *Independence hypothesis* — Under this hypothesis, apparent negative temporal dependence between the two species is spurious. Indeed, both species have been simultaneously abundant in the 1980s in the Humboldt Current (Gutiérrez et al., 2007) and in the early 2000s in the southern Benguela (Barange et al., 2009a); both were low around Japan in the early 20th century (Lluch-Belda et al., 1989). Paleoecological fish scale data from the South Atlantic and the Pacific suggest that fluctuations of anchovy and sardine may sometimes exhibit independence or weak positive dependence (Baumgartner et al., 1992; Finney et al., 2010; Soutar and Isaacs, 1974).

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* Corresponding author.
E-mail address: geoff.hosack@csiro.au (G.R. Hosack).

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

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

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

H_{obs}: *Observation error dependence hypothesis* — In the process dependence hypothesis, changes in the exploitation rate that result from environmental conditions, effective effort, or catchability affect stock abundance. In Section 3.1, we show that such factors can also impact how catch functions as a proxy index for the stocks. Such factors that covary can thus introduce dependence into the observation error.

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

2. Sardine and anchovy landings data

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

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

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

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

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

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

3. State space models (SSMs) of sardine and anchovy landings

3.1. Motivation and model formulation

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

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

where $B_t^{(i)}$ is the biomass of species i in year t, $l^{(i)}$ controls density independent growth and natural mortality, $G^{(i,i)}$ controls intraspecific density dependence, $G^{(i,j)}$ controls interspecific density dependence, and