

Modeling sardine and anchovy low-frequency variability

Salvador E. Lluch-Cota¹

Fisheries Ecology Program, Northwest Biological Research Center, La Paz, 23096, Mexico

The group of small pelagics (sardines, anchovies, herrings, etc.) is the largest source of wild marine protein worldwide, providing annually between 21% and 43% of the total marine capture production during at least the last 60 y (1). Even when large-scale fisheries have been operating for decades to centuries, their assessment and management remains difficult and highly uncertain (2). Such challenges are mainly because these species do not conform to the traditional assumptions of population dynamic models, such as a steady level of unexploited stock (carrying capacity), or that the influence of climate on the population is negligible when compared to fishing mortality. In other words, it has been clear for decades that the traditional toolbox of fisheries management is clearly unsuitable to these massive resources. The paper by Lindegren et al. (3) in PNAS provides an alternative framework to study and ultimately to develop management-supporting knowledge for these types of resources.

The modern era of small pelagic fishes research began exactly three decades ago, when the major sardine and anchovy fisheries catch series from remote systems in the western (Humboldt and California) and eastern (Japan) Pacific were presented together, and synchrony between them was first suggested (4). The sardine-anchovy puzzle was further complicated when alternation between sardine and anchovy stocks within each system and empirical linkages with climate were proposed, conforming to what was called The Regime Problem (5, 6). During these last 30 y, very valuable research has been conducted to document abundance fluctuations, synchrony between regions, and alternation between species observed during the 20th century, and many hypotheses have been proposed to explain the underlying mechanisms (7) or question the existence of such patterns (8). A comprehensive review of the history of scientific research on small pelagic fishes and their variability (9) crudely recognizes that the 20th century ended without a generally

accepted theory to explain the nature and mechanisms governing small pelagic fishes fluctuations, but optimistically claims that the science of fisheries oceanography seems to be close to achieving the breakthrough. The paper by Lindegren et al. (3) is a solid step forward because, just as happens when new technical tools and models become available, their framework brings new opportunities to test already existing hypotheses and formulate new ones.

Surprisingly, the model by Lindegren et al. (3) was able to hindcast the fluctuations of the California sardine and anchovy populations at two time scales, using independent experiments. On one hand, the model captured the major features of the sardine and anchovy population trends during the last \sim 80 y, including the sardine collapse in the 1940s-1950s, its recovery during the 1980s-1990s, and even the most recent population decrease during the last decade. On the other hand, the model properly reproduces mutidecadal fluctuations (before the industrial fishery) that have also been observed in the rates of sardine and anchovy scales sedimentation in anaerobic sediments (paleoreconstruction using abundance proxys).

These robust results provide an exciting opportunity to explore the major paradigms of The Regime Problem: the large fluctuations pattern occurring at the major sardineanchovy systems, the apparent synchrony between them, and the alternation of species within each of them (Fig. 1). An effort toward exporting the model to all major systems may allow testing whether (i) the same basic climate forcing is operating in all systems [i.e., sea surface temperature (SST)], (ii) similar fluctuations occur due to other environmental forcing, such as winds and mesoscale ocean dynamics (10) or oxygen limitations (11), and (iii) they can be synchronized at the global scale.

Based on the long-term variability experiments, Lindegren et al. (3) were able to detect 50–100 y dominant periodicities in the simulated fluctuations of sardines and anchovies, which grossly agrees with the observed fre-



Fig. 1. Sardine and anchovy catch series from the main fishing regions of the world: California (USA and Mexico, including the Gulf of California), Humboldt (Chile and Peru), Japan (Japan, Korea, China, Russia/USSR), and Benguela (Namibia and South Africa). Data sources include the SCORWG98 (6) covering from 1920 to 1997, and FAO fisheries statistics for the 1950–2011 period (1). Dots indicate catch values reported by SCORWG98 (blue/red) and FAO (green/yellow). Curves are 11–y moving averages for sardine (blue) and anchovy (red) time series. Shaded areas represent periods where sardine (light blue) and anchovy (light red) dominated in most of the Pacific basin fisheries. The SCORWG98 California catch series do not include the Gulf of California.

quencies from the scales-based paleorecords (7), as well as the dominant frequencies detected in the fisheries period (12). Interestingly, they detect differences in the dominant periods between sardines (80 y) and anchovies (60 y), which in the long term translates to nonsynchronic alternation between species (a perfect alternation would only occur under equal dominant periods). It has already been

Author contributions: S.E.L.-C. wrote the paper.

The author declares no conflict of interest.

See companion article on page 13672.

¹E-mail: slluch@cibnor.mx.

recognized that paleorecords suggest that the species alternation pattern observed during the 20th century may have resulted from chance (13). Clearly, as stated by Lindegren et al. (3), these explorations must be accompanied by new modeling approaches (14, 15) and meta-analytical techniques.

The model by Lindegren et al. (3) allows for a combination of stock recruitment and age structured models to be forced by fishing and climate, the latter represented by sea surface temperature or the Pacific decadal oscillation (PDO), a basin-scale proxy of temperature variability. In this context, the model settings also open the possibility to explore whether the observed fluctuation patterns of small pelagic fishes thus far will remain similar in the future, given that temperature is changing rapidly and is expected to change further in the near future.

It should be considered, for example, that over the last half century, the global ocean surface has been warming at a rate close to 0.1 °C/decade (16), which would add 0.8 °C in 80 y (the dominant periodicity of sardine multidecadal fluctuations). Such an increase lies within the range of temperature affecting the probability of stock collapse (see figure 2A of Lindegren et al.). The temperature is inversely related to the probability of collapse, such that the SST conditions at which the sardine collapse probability is currently very high at any fixed level of catch ration, would potentially become very low in less than the time needed for one sardine cycle. The modeling framework should allow the use of regional-scale general circulation modelsbased SST projections to explore probable future fluctuations of these resources in the California Current system and eventually export the capacity to other major small pelagic fisheries.

Another major opportunity brought by Lindegren et al. (3) is the potential value for fisheries administration. The California sardine fishery management system is still the only one that explicitly recognizes the effects of SST on the abundance of sardine stocks. Today, both the harvest control and the stock recruitment function of the stock assessment model incorporate the SST time series from the Scripps Institution of Oceanography Pier in San Diego (17). The panacea of a climatefisheries model for the small pelagic fisheries stakeholders (fishers, managers, scientists)

Surprisingly, the model by Lindegren et al. was able to hindcast the fluctuations of the California sardine and anchovy populations at two time scales, using independent experiments.

would be the ability to forecast, or at least to have the capacity to make an opportune detection of, large stock fluctuations (i.e., collapses and recoveries).

In one of their simulation exercises, Lindegren et al. (3) investigate whether the sardine stock collapse in the early 1950s could have been avoided through proper

3 Lindegren M, Checkley DM, Jr., Rouyer T, MacCall AD, Stenseth NChr (2013) Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc Natl Acad Sci USA* 110:13672–13677.

4 Kawasaki T (1983) Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuations from their viewpoint of evolutionary ecology. *FAO Fish Rep* 291(3): 1065–1080.

5 Lluch-Belda D, et al. (1989) World-wide fluctuations of sardine and anchovy stocks: The regime problem. S Afr J Mar Sci 8(1):195–205.
6 Schwartzlose RA, et al. (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. S Afr J Mar Sci 21(1):289–347.
7 Checkley D, Alheit J, Oozeki Y, Roy C (2009) Climate change and small pelagic fish (Cambridge Univ Press, Cambridge, UK).
8 Fréon P, Mullon C, Voisin B (2003) Investigating remote synchronous patterns in fisheries. *Fish Oceanogr* 12(4-5):443–457.
9 MacCall AD (2009) A short scientific history of the fisheries. *Climate change and small pelagic fish, current trends in the assessment and management of stocks*, eds Checkley D, Alheit J, Oozeki Y, Roy C (Cambridge Univ Press, Cambridge, UK), pp 6–11.
10 Rykaczewski RR, Checkley DM, Jr. (2008) Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc Natl Acad Sci USA* 105(6):1965–1970.

management. They estimated a probability of collapse at different combinations of SST and exploitation, together with the rate of decline and recovery time after the collapse. Results showed that the collapse was unavoidable, independently of the exploitation level, but that at high catch ratios, such as those occurring just before the early 1950s collapse, the rate of decline accelerates and recovery is retarded. In short, the model was able to hindcast the collapse by simultaneously incorporating climate and fishing impacts. The recent (last decade) trends in the California sardine abundance have propelled an ongoing debate on whether the California sardine is currently collapsing again or not (18-20), based on the related rates of change of the stocks and the associated causes (climate, fishing, or combined effect). This situation represents a historical, timely, and relevant opportunity for the Lindegren et al. (3) model to prove practical value and to potentially become a major information source for California sardine fishery management.

11 Bertrand A, et al. (2011) Oxygen: A fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. *PLoS ONE* 6(12):e29558.

12 Chavez FP, Ryan J, Lluch-Cota SE, Niquen C M (2003) From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299(5604):217–221.

13 Finney BJ, et al. (2010) Paleoecological studies on variability in marine fish populations: A long-term perspective on the impacts of climatic change on marine ecosystems. *J Mar Syst* 79(3-4): 316–326.

14 Di Lorenzo E, Ohman MD (2013) A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proc Natl Acad Sci USA* 110(7):2496–2499.

15 Deyle ER, et al. (2013) Predicting climate effects on Pacific sardine. *Proc Natl Acad Sci USA* 110(16):6430–6435.

16 Solomon S, et al. (2007) Climate change 2007: The physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ Press, Cambridge, UK).

17 Hill KT, et al. (1999) Stock assessment of the Pacific sardine for 1998 with management recommendations for 1999 (California Department of Fish and Game, La Jolla, CA).
18 Zwolinski JP, Demer DA (2012) A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proc Natl Acad Sci USA* 109(11): 4175–4180.

19 MacCall AD, Hill KT, Crone P, Emmett R (2012) Weak evidence for sardine collapse. *Proc Natl Acad Sci USA* 109(19):E1131.
20 Demer DA, Zowlinski JP (2012) Reply to MacCall et al.: Acoustic trawl survey results provide unique insight to sardine stock decline. *Proc Natl Acad Sci USA* 109(19): E132–E133.

FAO Fisheries and Aquaculture Department Statistics and Information Service (2011) FishStatl: Universal Software for Fishery Statistical Time Series. (Food and Agriculture Organization, Rome).
 Barange M, et al. (2009) Current trends in the assessment and management of stocks. Climate change and small pelagic fish, current trends in the assessment and management of stocks, eds Checkley D, Alheit J, Oozeki Y, Roy C (Cambridge Univ Press, Cambridge, UK), pp 191–255.