Collapse and recovery of forage fish populations prior to commercial fishing

Sam McClatchie¹, Andrew Thompson¹ Ingrid Hendy² & William Watson¹

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¹NOAA Fisheries, Southwest Fisheries Science Center, Fisheries Resources Division

² Department of Earth and Environmental Sciences, University of Michigan





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Key Points:

- The paleorecord shows that "collapse" is a normal state repeatedly experienced by northern anchovy, Pacific hake, and Pacific sardine
- Mean return times to "fishable" biomass was 8 years for anchovy, but 22 years for sardine and hake, and persistence was of the same order
- Sardine and anchovy are positively correlated over 400 years, consistent with coherent declines of both species off California

Correspondence to:

S. McClatchie, Sam.McClatchie@noaa.gov

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Collapse and recovery of forage fish populations prior to commercial exploitation

S. McClatchie¹, I. L. Hendy², A. R. Thompson¹, and W. Watson¹

¹ Fisheries Resources Division, NOAA Fisheries Service, Southwest Fisheries Science Center, La Jolla, California, USA, ² Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, USA

Abstract We use a new, well-calibrated 500 year paleorecord off southern California to determine collapse frequency, cross correlation, persistence, and return times of exploited forage fish populations. The paleorecord shows that "collapse" (defined as <10% of the mean peak biomass) is a normal state repeatedly experienced by northern anchovy, Pacific hake, and Pacific sardine which were collapsed 29–40% of the time, prior to commercial fishing exploitation. Mean (\pm SD) persistence of "fishable biomass" (defined as one third mean peak biomass from the paleorecord) was 19 ± 18 , 15 ± 17 , and 12 ± 7 years for anchovy, hake, and sardine. Mean return times to the same biomass was 8 years for anchovy but 22 years for sardine and hake. Further, we find that sardine and anchovy are positively correlated over 400 years, consistent with coherent declines of both species off California. Persistence and return times combined with positive sardine-anchovy correlation indicate that on average 1–2 decades of fishable biomass will be followed by 1–2 decades of low forage. Forage populations are resilient on the 500 year time scale, but their collapse and recovery cycle (based on the paleorecord) are suited to alternating periods of high fishing mortality and periods of little or no fishing.

1. Introduction

Elucidating causes of fish population fluctuation has been a fundamental focus of fisheries science for the past century [*Hjort*, 1913, 1926; *Houde*, 2008]. While it is now clear that large, long-lived, site-attached fish populations are directly, negatively affected by commercial fishing [*Love et al.*, 1998; *DeMartini et al.*, 2008; *Sandin et al.*, 2008], the role of harvest on small, pelagic fishes that undergo extended periods of dramatic booms and busts is still not fully settled [*Beddington and May*, 1977; *Hutchings and Reynolds*, 2004; *Essington et al.*, 2015; *Pinsky and Byler*, 2015]. One factor that hampers our capacity to directly evaluate the role of fishing on population dynamics of small pelagic fishes is a paucity of population data prior to the onset of large-scale commercial fishing.

Fishery catches off Southern California are dominated in terms of biomass by pelagic rather than demersal fishes [McClatchie, 2013]. Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) have, at different times, represented the largest tonnages removed from the California Current System (CCS) by humans [Van Voorhees and Lowther, 2012]. Although commercial catches of Pacific hake (Merluccius productus) are higher to the north, hake spawning is centered off Southern California [Lo, 2007], and hake larvae are often the most abundant commercial species collected there by fishery-independent ichthyoplankton surveys [Hsieh et al., 2005]. Collectively, anchovy, sardine, and hake comprise the most numerous forage species in the southern CCS, constituting a resource that is exploited not only by fisheries but also by pinnipeds (most numerously, sea lions) [Lowry et al., 1990; Melin et al., 2012], sea birds (including brown pelicans) [Szoboszlai et al., 2015], and by some cetaceans (such as humpback whales and short-beaked common dolphins) [Barlow et al., 2008]. In this paper we refer to hake as a forage species but recognize that with increasing size, hake become an important piscivorous predator of forage fishes like sardine and anchovy.

Understanding forces driving fluctuations in the abundance and variability of forage fish is relevant to the regulation of sardine, anchovy, and hake fisheries, to achieving their sustainable management, to ensuring an adequate forage reserve for birds and mammals, and to maintaining a productive and resilient ecosystem. Forage fishes are known to fluctuate widely in abundance even in the absence of commercial fishing, and this variability is usually attributed to climate-related drivers [Soutar and Isaacs, 1969; Baumgartner et al., 1992; Field et al., 2009]. Population variability is challenging to assess from fishery catches, stock assessments,

Published 2017. This article is a U.S. Government work and is in the public domain in the USA. Our results build on a wealth of studies of fish scales from the sediments of the Santa Barbara Basin as well as the Gulf of California:

[Soutar, 1967; Soutar and Isaacs, 1969, 1973; Baumgartner et al., 1992; Holmgren-Urba and Baumgartner, 1993; Field et al., 2009].

Earlier studies on the paleorecord showed repeated collapses and recoveries of both sardine and anchovy over 1,700 years [Baumgartner et al., 1992] despite some problems with accurately dating these time series.

A new paleorecord [Skrivanek and Hendy, 2015] allowed us to calculate persistence and return times for exploited forage populations in the absence of commercial fishing more accurately than earlier work [Baumgartner et al., 1992], due to a well-resolved age model and larger sample sizes.

We use a new, well-calibrated, 500-year paleorecord of fish scale deposition rates from the Santa Barbara Basin to determine collapse frequency, cross-correlation, and return times following collapse of forage fish populations.

Questions addressed were:

Is "collapse" a normal state repeatedly experienced by anchovy, hake and sardine?

Are sardine and anchovy fluctuations correlated on the 500-year time scale?

How long, on average, did it take forage fish biomass to recover in this paleo-record?

Are there any implications for management of forage fish?

What is special about this fish scale time series?

Reconstructing paleoceanographic change at a time step resolution similar to historic records requires an extremely well resolved age model.

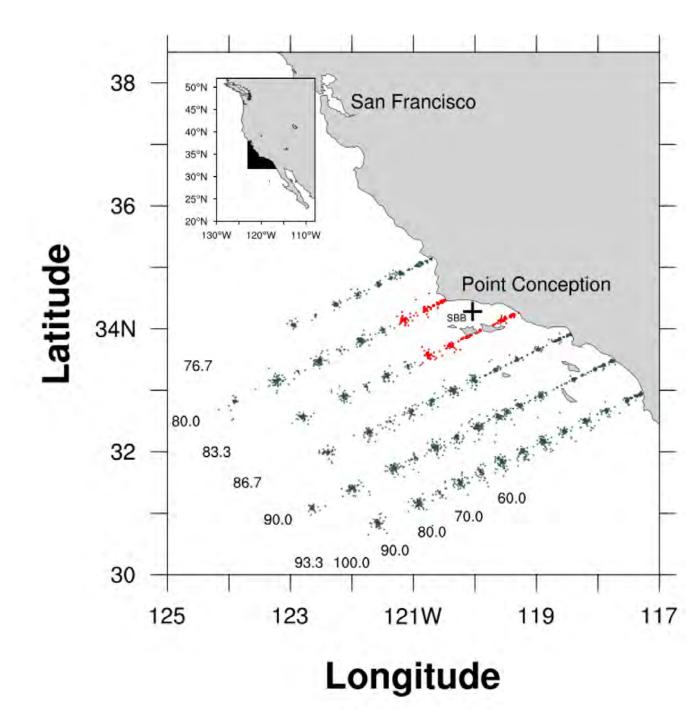
Previous California fish population reconstructions utilized the well-preserved annual sediment laminae as a varve chronology to generate fish scale fluxes.

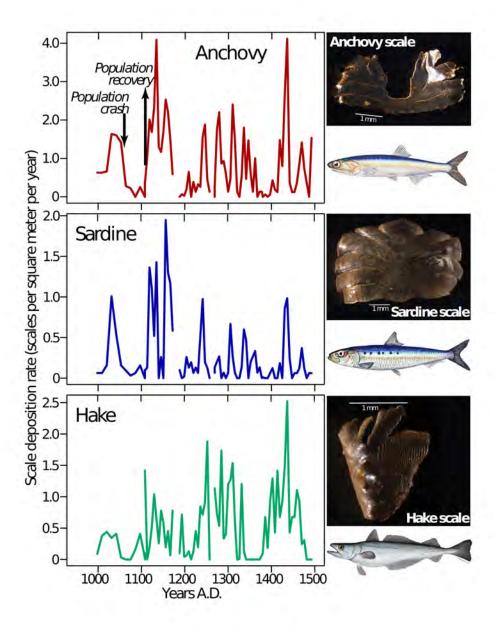
Independent 14C dating of terrestrial organic material and marine carbonate demonstrates the error in the varve chronology has been underestimated, increasing dramatically with depth by up to 30% per 100 years.

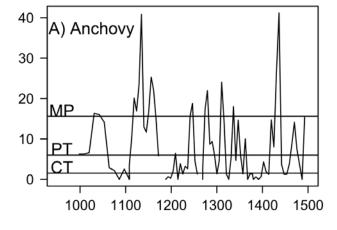
Errors due to undercounting of varves result from: discontinuous sedimentation during drought years, bioturbation, and/or erosion of laminae by intermittent turbidite or flood deposits.

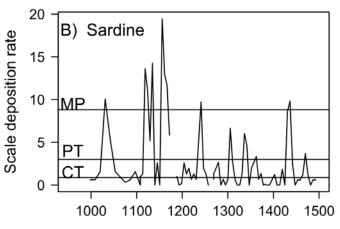
In this contribution, high resolution 14C dating was employed to generate an age model, calibrated against terrestrial and marine calibration curves.

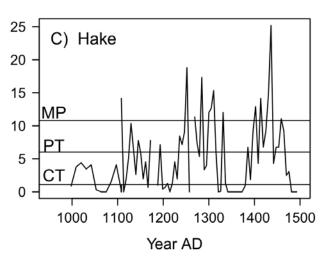
Instantaneous sedimentary deposits associated with flood events and downslope processes were removed from the fish scale deposition rates.











Time series of (A) anchovy, (B) sardine, and (C) hake scale deposition rate (SDR) from AD 1000 – 1500 derived from the new sediment core from Santa Barbara Basin. Peaks were defined as values above a peak threshold (PT) and averaged to estimate mean peak height (MP). An operationally defined "collapse threshold" (CT) was estimated as 10% of MP.

Sardine, anchovy and hake showed large fluctuations in the period AD 1000-1500, prior to commercial fishing.

Scale Deposition Rate varied by a factor of 40 X for anchovy, 25 X for hake and 20 X for sardine.

Based on the collapse threshold (CT) anchovy were collapsed 29% of the time, sardine 40% of the time and hake 30% of the time in the period AD 1000-1500.

Collapse is a frequent occurrence that persists for some time, even in the absence of commercial fishing, before recovery occurs.

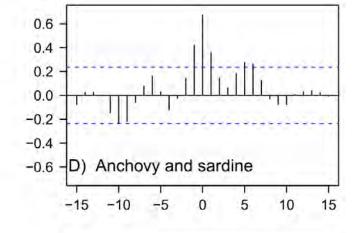
This shows cross-correlation between pairs of forge species at different lags. Dotted lines are 95% confidence intervals. Vertical lines extending beyond the CI are significant at the indicated lags. Each lag is 5 years.

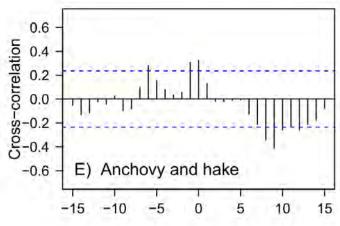
Anchovy & sardine are positively correlated around zero lags in the 500 year paleorecord.

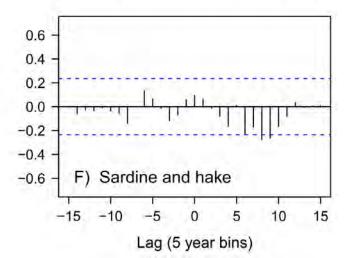
Previously reported inverse correlations between sardine and anchovy in modern times is likely an artefact of short time series.

Previously published paleo studies reported positive, negative or no correlation between sardine and anchovy time series.

Our results using a better calibrated age model for scale deposition rates support those previous paleo studies reporting positive correlation between sardine & anchovy.







The frequency distributions of abundance data from forage fishes is both strongly skewed and heavy tailed.

Heavy tailed distributions are common for data where extreme events occur, such as precipitation data containing storm deluges, river flow data containing floods, or seed production data for trees that produce mast years.

In the case of forage fishes that undergo cycles of boom and bust, the booms are years where a combination of successful recruitment and cohort structure interact with favorable environmental conditions to produce a remarkable abundance.

Providing there are sufficient data, these heavy-tailed distributions can be modeled with a family of extreme value distributions to predict, on average, how frequently extreme events will occur.

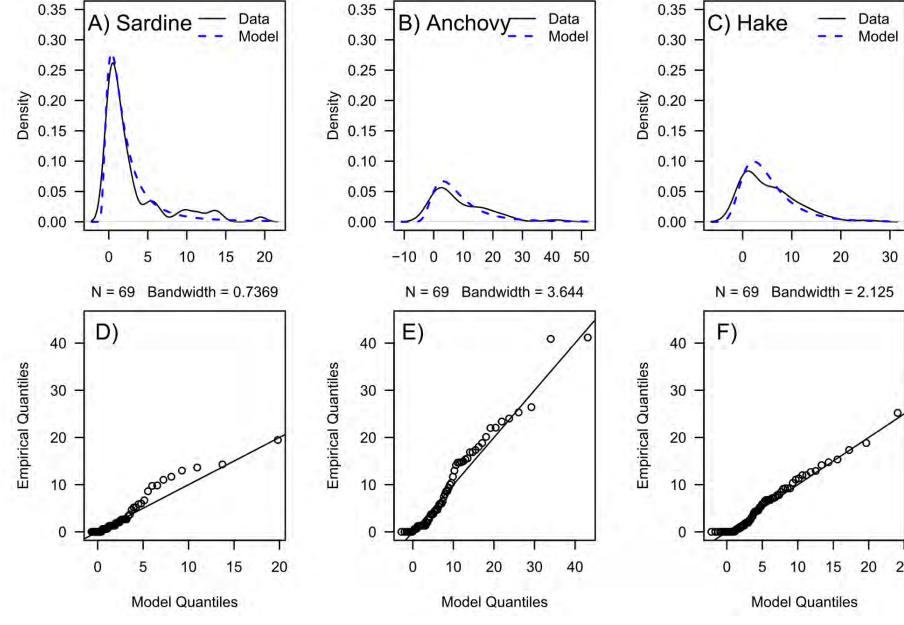
Once a model is fit, the return times for extreme events can be obtained by inverting the percentiles of the fitted distribution.

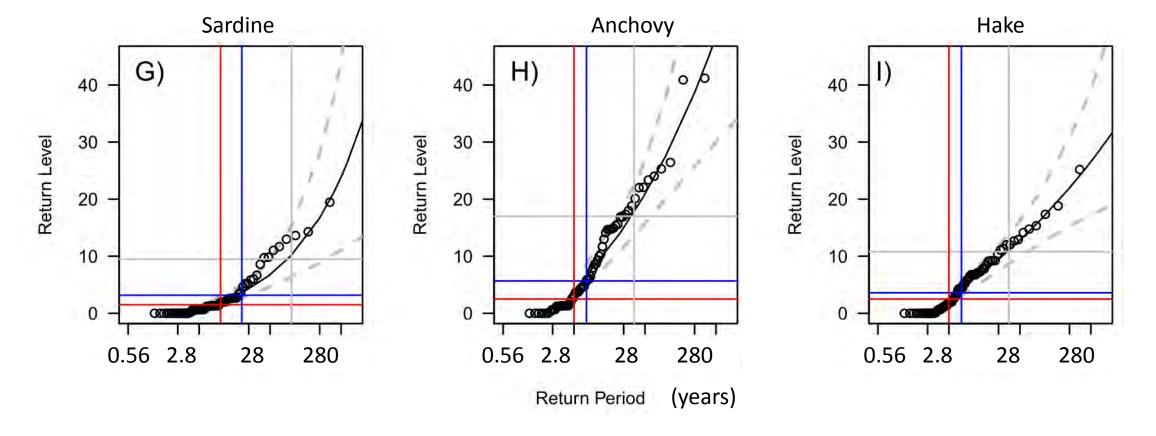
Obtaining the return times for forage fish boom and busts is analogous to pedicting the 50-year flood event for a river, or how frequently extreme precipitation events will occur.

A, B & C: Density distribution of sardine, anchovy and hake scale deposition rates The fitted generalized extreme value (GEV) distribution is overlaid on the density distributions.

D, E & F: Quantile diagnostic plots showing the fit of the GEV model to sardine (D), anchovy (E), and hake (F) scale deposition rate distributions.

The scale distributions approximate "heavy tailed" extreme value distributions quite well, as shown by the quantile plots, and consequently can be modeled with an Generalized Extreme Value (GEV) model.





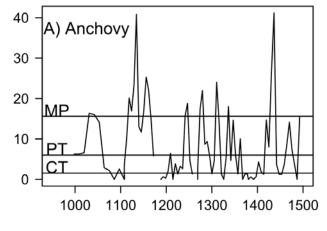
Return rates for based on the GEV model.

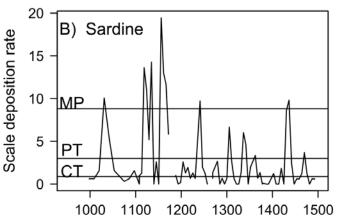
Gray lines show return times for return level = mean peak size (MP).

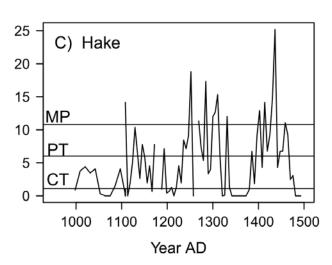
Blue lines are return times for return level = 0.33MP.

Red lines are return times for the collapse threshold (CT = 0.1MP).

Dashed lines are confidence intervals for the GEV model.







Persistence was estimated by declustering the SDR data for each species above a threshold equal to R 0.33.

Cluster duration can be affected by the selection of run length, which is the number of below-threshold points that separates clusters. We tested run lengths from 1-10 to determine that the number of clusters was stable, and calculated the mean and standard deviation of cluster lengths to estimate mean persistence.

Mean persistence of R 0.33 was 12 ± 7 years for sardine, 19 ± 18 years for anchovy and 15 ± 17 years for hake.

Conclusions

The paleorecord shows that "collapse" is a normal state repeatedly experienced by anchovy, hake and sardine in the absence of commercial fishing.

Sardine and anchovy are positively correlated on the 500-year time scale.

Mean return time to 1/3 of peak biomass was 22 years for sardine, but 8 years for anchovy and hake.

Persistence and return times, combined with positive sardine-anchovy correlation indicates that on average 1-2 decades of fishable biomass will be followed by 1-2 decades of low forage.

Implications for management of forage:

- Setting a high reserve threshold below which there is no fishing may not prevent forage fish populations from collapsing.
- Predators dependent on forage fishes are likely to experience repeated periods of forage scarcity.