

RESEARCH LETTER

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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

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Collapse and recovery of forage fish populations prior to commercial exploitation

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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 numerous, 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,

or from fishery-independent surveys because the approximate wavelength of long-period fluctuations in abundance is the same order (≈ 60 –100 years [Baumgartner *et al.*, 1992]) as our longest fishery-independent surveys (currently 67 years) or the fishery catch records (≈ 100 years). Record length for stock assessments using consistent and comparable methods is notably shorter. In addition, forage fishes are prone to boom and bust cycles [Soutar and Isaacs, 1969; Baumgartner *et al.*, 1992; Field *et al.*, 2009], producing highly skewed abundance records, containing many zeros when abundances collapse. Collapse, which is defined differently by various authors [Essington *et al.*, 2015; Pinsky and Byler, 2015], is generally considered undesirable for the sustainability of both the fishery and the resource.

We elaborate here on collapse as an intrinsic property of some forage fish populations that should be expected, just as droughts are expected in an arid climate. The fact that forage fish collapses occur naturally in the absence of commercial fishing can be planned for, and we offer new predictions of average persistence and return times to aid that planning process. Various estimates of persistence and return times for forage fishes have been published [Soutar and Isaacs, 1969, 1973; Baumgartner *et al.*, 1992], but we offer refined estimates derived from extreme value statistics. By fitting a generalized extreme value distribution to the distributions of scale deposition rates we are able to effectively interpolate and thereby obtain finer resolution, which provides better estimates of return times and persistence, along with confidence limits on these estimates.

The frequency distributions of abundance data from forage fishes is both strongly skewed and heavy tailed. That is to say that the tailing off of the right limb of the distribution occurs much more slowly than either a normal or an exponential distribution. 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 interacts 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 [Katz *et al.*, 2005]. Once a model is fit, the return times for extreme events can be obtained by inverting the percentiles of the fitted distribution. With appropriate data, such as the paleoceanographic fish scale record, obtaining the return times for forage fish boom and busts is analogous to predicting the 50 year flood event for a river, or how frequently extreme precipitation events will occur.

We use extreme value statistics to model the paleorecord time series and to estimate return times. This permits us to view current forage fish declines from the broader perspective of natural variation and to predict, on average, the recovery time of sardine and anchovy off California to levels likely to support a fishery again. To do this requires long time series with a reliable age model, which have recently become available through analysis of fish scales and proxies of environmental variability based on a new, robustly dated, large diameter core taken from the anoxic Santa Barbara Basin sediments [Skrivanek and Hendy, 2015; Barron *et al.*, 2015].

2. Methods

2.1. Paleoceanographic Sampling

Kasten core SPR0901-02KC (588 m water depth; $34^{\circ} 16.845'N$, $120^{\circ} 02.332'W$), a 17×17 cm core (with an area of 289 cm^2), was continuously sampled every 0.5 cm. This study examined samples between 125.5 and 75.5 cm below core top, corresponding to the time interval between 1000 and 1500 A.D. Samples were wet sieved with deionized water over a $125 \mu\text{m}$ screen with the coarse fraction ($250 \mu\text{m}$) collected for fish scale analysis. This is a significant improvement over the smaller (45 cm^2) cores, sampled at 1 cm by Baumgartner *et al.* [Baumgartner *et al.*, 1992] spanning the same time interval.

The sediments of Santa Barbara Basin provide well-preserved, continuous fish scale records of pelagic fish populations because unusually high sedimentation rates, low bottom water oxygen concentrations, and high pH (≈ 8) preserve scale and bone constituents such as inorganic carbonates and apatites [Field *et al.*, 2009; Soutar and Isaacs, 1969]. Fish scales were picked under a binocular dissecting microscope, and identification of northern anchovy, Pacific sardine, and Pacific hake were compared with a reference scales from the University of Michigan Exhibit Museum fish collection (Gerald Smith, personal communication, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109-1079) that were identified by scale shape, circuli appearance, and the presence of lateral field lines that is fully described in Skrivaneck and Hendy [2015]. Instantaneous sediment

deposition events (turbidites and flood deposits) that interrupt the annual sediment laminae are excluded from the scale counts [Skrivanek and Hendy, 2015]. There is a possibility that species-specific scale dissolution rates and/or scale shedding rates not related to population dynamics might contribute to bias or variability, but Skrivaneck and Hendy [2015] found no evidence that this is a problem.

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 [Baumgartner et al., 1992; Soutar and Isaacs, 1973]. Independent 14C dating of terrestrial organic material and marine carbonate from a companion kasten core SPR0901-06KC (34° 16.914'N, 120° 2.419'W [Hendy et al., 2013]) demonstrates the error in the varve chronology has been underestimated, increasing dramatically with depth by up to 30% per 100 years [Hendy et al., 2013]. This error impacts the validity of previous flux estimates in addition to preventing correlation between fish scale deposition rates and environmental forcing—especially prior to the arrival of Europeans in the region [Baumgartner et al., 1992; Soutar and Isaacs, 1973]. 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 [Hendy et al., 2013; Schimmelmann et al., 2013]. In this contribution, high-resolution 14C dating was employed to generate an age model. Terrestrial organic carbon 14C ages samples were calibrated using the terrestrial carbon calibration curve Intcal09, while planktonic foraminifera carbonate 14C ages were corrected for variable 14C reservoir ages (ΔR) and calibrated using the marine carbonate calibration curve Marine09 [Hendy et al., 2013; Reimer et al., 2009]. Additionally, instantaneous sedimentary deposits (0.5–5 cm in thickness) associated with flood events and downslope processes were removed from the fish scale deposition rates as these events could bias deposition rates toward the appearance of more frequent occurrence of collapsed fish populations. Instantaneous deposits were identified using 14C dating.

All ages in this publication refer to years A.D. Sedimentation rates were calculated using the new age model to calculate scale deposition rates or fluxes using the following equation:

$$SDR = 1000 NSR \tag{1}$$

where SDR = Scale Deposition Rate (1000 scales $\text{cm}^{-2} \text{yr}^{-1}$), N = fish scale count (scales cm^{-3}), and SR = Linear Sedimentation Rate (cm yr^{-1}).

2.2. Extreme Value Analysis and Return Times

The SDR paleorecord contains some irregular spaced time intervals. The last 100 years of the record has 11 year spacing which is approximately twice as long as the mean spacing for the first 400 years of data (5.6 ± 1.6 years, mean \pm SD). For this reason the autocorrelation, cross correlation, and the extreme value analysis of the paleorecord were limited to the first 400 years of the time series. The SDR time series are effectively binned annual data, because the time interval of each core sample contains more than 1 year, as described above. The generalized extreme value (GEV) distribution function is an appropriate family of models to fit binned data [Coles, 2001].

We fitted a GEV to the anchovy, sardine, and hake SDR time series using the extRemes package [Gilleland and Katz, 2011] in the R Statistical language [Ihaka and Gentleman, 1996]. The GEV can describe three families of distributions depending on whether the distribution is limited (Weibull family), or if not limited, on the decay rate for the extreme tail of the distribution, i.e., thin tailed (Gumbel) or fat tailed (Fréchet family):

$$G(x) = \exp \left\{ - \left[1 + \xi \left(\frac{x - \mu}{\sigma} \right) \right]^{-1/\xi} \right\} \tag{2}$$

where ξ = shape, μ = location, and σ = scale. The data determine which family is selected during the fitting process, and there is no prior selection of family [Coles, 2001]. Estimates of extreme quantiles are obtained by inverting equation (2).

$$z_p = \mu - \frac{\sigma}{\xi} \left[1 - \{-\log(1 - p)\}^{-\xi} \right] \quad \text{for } \xi \neq 0 \tag{3}$$

$$z_p = \mu - \sigma \log \{-\log(1 - p)\} \quad \text{for } \xi = 0 \tag{4}$$

where z_p is the return level associated with a return period $1/p$. z_p is expected to be exceeded on average every $1/p$ years. The return level of interest to us is not as much the booms and busts in the time series as

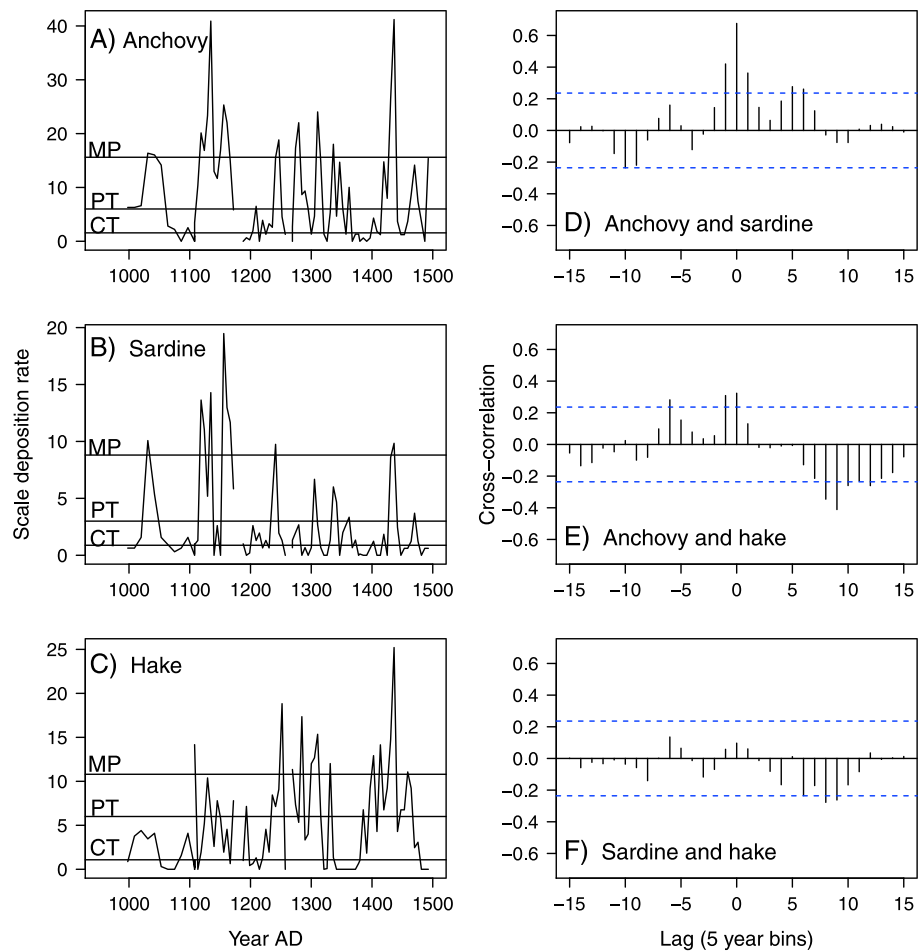


Figure 1. Time series of (a) anchovy, b sardine, and (c) hake scale deposition rate (SDR) from A.D. 1000–1500 derived from a sediment core from Santa Barbara Basin. Peaks were defined as values above a peak threshold (PT) and averaged to estimate mean peak (MP) height. An operationally defined “collapse threshold” (CT) was estimated as 10% of MP. (d–f) Cross correlation between pairs of forage species at different lags. Dotted lines are 95% confidence intervals (CI). Vertical lines extending beyond the CI are significant at the indicated lags. Each lag is 5 years.

the level at which a fishery might be viable. For the purpose here, we defined this return level as one third of mean peak height ($R0.33$). This is an operational definition based on the observation that the recent California sardine fishery was successfully operating during the period when biomass approached one million metric tonnes [Hill *et al.*, 2015] or approximately one third of the estimated sardine biomass during the heyday of the 1930s fishery. We calculated the 95% confidence intervals for $R0.33$ and associated return times using the extRemes package [Gilleland and Katz, 2011]. For reasons described above, return times were multiplied by 5.6 years due to the sample spacing.

Persistence was estimated using the extRemes package by declustering the SDR data for each species above a threshold equal to $R0.33$. 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 to 10 to determine that the number of clusters was stable and calculated the mean and standard deviation of cluster lengths to estimate mean persistence. Persistence was stable for run intervals 1–3 in the case of sardine but increased with run length for anchovy and hake. Persistence is reported for run length = 1 (5.6 years on average) for all three species.

3. Results

3.1. Recent Trends From a Paleoceanographic Perspective

Based on scale deposition rates (SDR, equation (1)), anchovy, hake, and sardine showed large fluctuations during the period A.D. 1000 to 1500, prior to any commercial fishing (Figure 1). All three forage species show

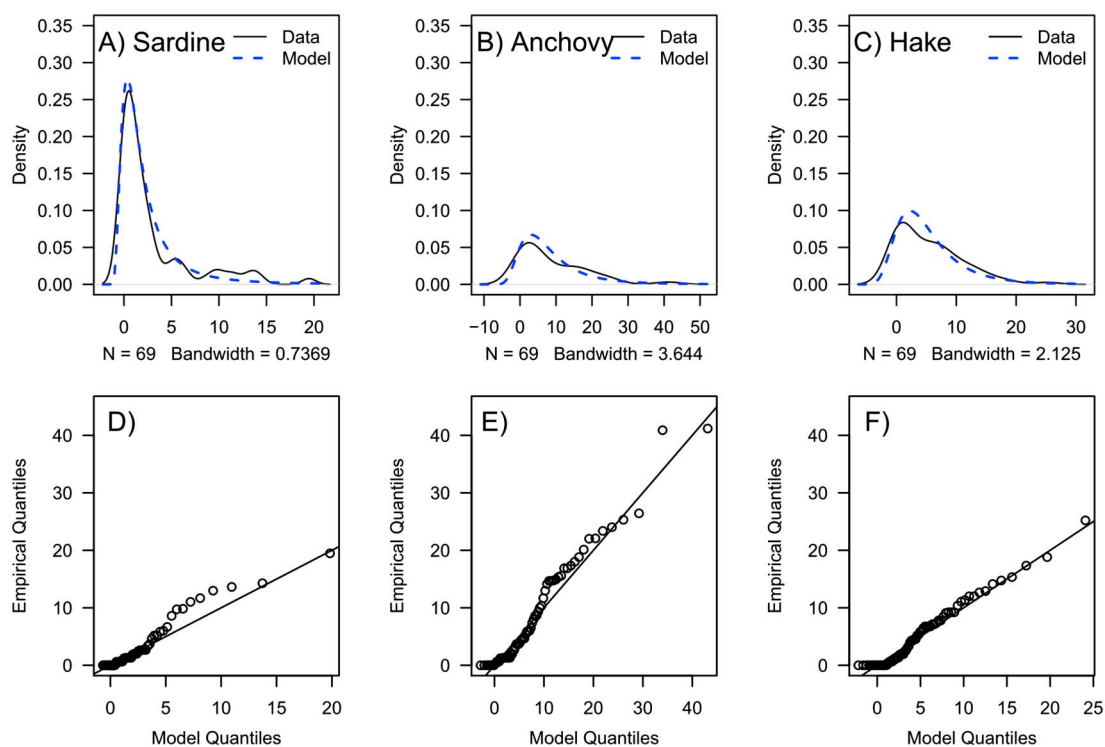


Figure 2. Density distribution of (a) anchovy, (b) sardine, and (c) hake scale deposition rate (SDR) using data from Figures 1a–1c. The fitted generalized extreme value (GEV) distribution model is overlaid on the density distributions. Quantile diagnostic plots showing the fit of the GEV model for (d) sardine, (e) anchovy, and (f) hake SDR.

repeated peaks followed by troughs in the paleorecord. Fish SDR, which can be used as a proxy for fish abundance [Field *et al.*, 2009], varied by a factor of 40 times for anchovy, compared to factors of 25 for hake and 20 for sardine (Figure 1). From the 500 year context provided by the paleorecord, a recent 72% decline of forage [Koslow *et al.*, 2015], which corresponds to abundance reduced to $\approx 1/4$, or a factor of 4 change over the last 25 years off Southern California does not appear exceptional. Current declines of forage off Southern California fall within the expected bounds of natural fluctuations for sardine, anchovy, and hake.

3.2. Synchrony of Forage Species

The calibrated paleorecord is sufficiently long to test for correlations between forage species [McClatchie, 2012]. Contrary to some previous work [Lluch-Belda *et al.*, 1989; Chavez *et al.*, 2003] based on data spanning only 50 years, we found that abundances of anchovy and sardine are significantly positively correlated around zero lags over 400 years in the 500 year paleorecord (see Methods, section 2.2) (Figure 1d). Anchovy and hake are significantly positively correlated at zero but negatively correlated at longer positive lags (Figure 1e). Sardine and hake are weakly correlated in the paleorecord (Figure 1f). Our results indicate that previously reported inverse correlation between anchovy and sardine based on shorter time series was true for one realization of these strongly fluctuating populations but lacks generality when tested with longer time series [see also Field *et al.*, 2009]. Our finding supports those earlier analyses of long-term scale records that also detected positive correlations between anchovy and sardine [Soutar and Isaacs, 1973; Baumgartner *et al.*, 1992].

3.3. Extreme Value Analysis and Return Times

We used the SDR time series (Figure 1) to estimate the proportion of time that forage populations were at very low densities (i.e. collapsed) prior to commercial fishing (A.D. 1000–1400, see Methods, section 2.2). For the purposes of this study, we define a collapse threshold (CT) as $<10\%$ of the mean peak (MP) height (Figures 1a–1c). Pinsky and Byler [2015] used a different definition of collapse based on maximum sustainable yield (B_{MSY}), but in populations that fluctuate strongly, B_{MSY} is hard to determine. Consequently, we prefer to use a simpler definition based on a fraction of observed mean peak abundances. Based on this criterion, anchovy were collapsed 29% of the time between A.D. 1000 and 1500, while sardine were collapsed 40% of the

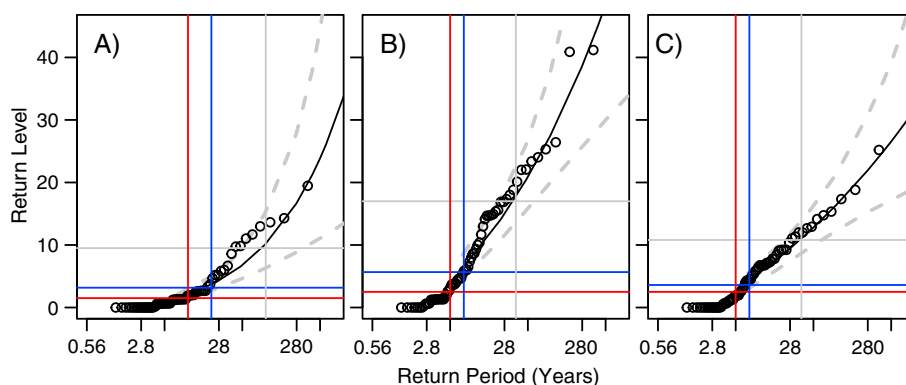


Figure 3. Return rates for (a) sardine, (b) anchovy, and (c) hake based on the generalized extreme value (GEV) model. Return times (units are 5 year intervals) estimated using data from Figures 1a–1c. Gray lines show return times for return level = mean peak size (MP, Figure 1). Blue lines are return times for return level = 0.33 MP. Red lines are return times for the collapse threshold (CT=0.1 MP, Figure 1). Dashed lines are confidence intervals for the GEV model.

time, and hake were collapsed 30% of the time (Figure 1). Collapse is a common state for these populations, even in the absence of commercial fishery exploitation.

SDR distributions for sardine, anchovy, and hake were characterized by fat tails that could be fitted with a generalized extreme value (GEV) model of the Fréchet family (equation (2), Figures 2a–2c). Diagnostic plots of model and empirical quantiles suggest that the model fit is reasonable (Figures 2a–2c), although the fit is better for anchovy and hake than for sardine (Figures 2d–2f). Using the GEV models for sardine, anchovy, and hake (Figures 3a–3c), we calculated return periods for levels corresponding to one third of mean peak biomass ($R0.33$) (see Figure 1 for an illustration of mean peak biomass, MP). $R0.33$ for sardine was 22.4 years (Figure 3a), compared to 8.4 years for both anchovy and hake (Figures 3b and 3c). The 95% confidence intervals (CI) for $R0.33$ corresponding to these return periods are tight compared to CIs around estimated peaks, as shown by the rapid widening of CIs in Figure 3. This indicates that average return times for peaks cannot be estimated well, but that $R0.33$ or return times for collapses can be much more reliably estimated. The 95% CIs expressed relative to mean peak biomass for sardine gives 24–44% MP with mean return times of ≈ 22 years. For anchovy, the 95% CI is 21–48% and for hake it is 21–47% MP, both with a mean return time of ≈ 8 years. Mean persistence of $R0.33$ was 12 ± 7 years for sardine, 19 ± 18 years for anchovy, and 15 ± 17 years for hake. Variability of persistence was lower for sardine (CV = 0.58) than for anchovy (CV = 0.95) and highest for hake (CV = 1.13).

4. Discussion

Our analyses make the untested assumption that there is some degree of stationarity in the time series and that conditions during different 500 year time periods are comparable. While we cannot currently test this assumption, we expect a new 2000 year long time series to be available in the near future. When the longer series is available we will be able to explicitly test the assumption of stationarity.

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]. Soutar [1967] used four short cores from the Santa Barbara Basin to demonstrate that sedimented fish scales could be used to characterize long-term fluctuations in hake, sardine, and anchovy abundance. Soutar and Isaacs [1969] used a single, longer core to develop an 1800 year time series with 10 year intervals for the Santa Barbara Basin. They concluded that sardine occurrences were interspersed by absences, but that anchovy were always abundant. Hake were the most abundant in the scale record and exhibited long-term periodicity. The summed abundance of all three species was relatively constant. Soutar and Isaacs [1969] used scale width to develop a size structure for anchovy, which they applied to estimate mortality rates and the population biomass. Assumptions notwithstanding, these population estimates indicated that the abundance of anchovy was considerably higher than sardine, but that a factor of 5 decrease in anchovy numbers occurred in the last 1500 years [Soutar and Isaacs, 1969]. They also estimated

that there were 12 peaks in sardine abundance in the past 1800 years, that the average time between peaks was 80 years (range = 20–200 years), and that the average duration of sardine occurrences was 20–150 years.

Soutar and Isaacs [1973] developed a shorter time series (160 years, from 1810 to 1970 A.D.) with 5 year intervals, using a larger sample derived from four box cores. They compared biomass estimates derived from the later part of this scale time series with sardine population estimates from 1930 to 1959. The size distribution of the sardine scales indicated they were from 1 to 2 year old fish, and *Soutar and Isaacs* [*Soutar and Isaacs*, 1973] obtained a tight linear relationship between sardine scale deposition rates and the numbers of 2 year old fish for these years. In rather lyrical prose, *Soutar and Isaacs* [*Soutar and Isaacs*, 1973] concluded

“The historical decline of the sardine, seen in perspective, appears as a subdued finale to a movement that had begun in 1890, thirty years before the inception of the fishery, and this movement in turn belongs to a theme extending into the millennia (*Soutar and Isaacs*, 1969) ... Even higher levels of success suggested by the sedimentary record between 1855 and 1865 afforded insufficient reserve against a precipitous and natural decline. Nor can the virtual absence of the sardine from the waters off Alta California be considered an unnatural circumstance.”

These authors also noted that there was a “less than significant” positive correlation between the abundance of sardine and anchovy in the scale time series. *Baumgartner et al.* [1992] extended the data sets developed by *Soutar and Isaacs* [1973] to produce a scale deposition record of 1700 years (270–1970 A.D.). After filtering out high-frequency noise, they used spectral analysis to show peaks of variability at 57 and 76 years for sardine, and at 57, 72, and 99 years for anchovy. *Baumgartner et al.* [1992] considered that the weak positive correlation between sardine and anchovy reported by *Soutar and Isaacs* [1973] was due to low-frequency variability and that there was virtually no correlation at shorter time scales. They estimated that sardine recoveries take 10–70 years (mean = 36 years), and collapse took 20–50 years. We note that improved techniques applied in our study reduced estimates of recovery and persistence times, although it is difficult to directly compare studies since the definitions of recovery and collapse differ. We estimated that mean (\pm SD) persistence of one third mean peak biomass from the paleorecord were 19 ± 18 , 15 ± 17 , and 12 ± 7 years for anchovy, hake, and sardine. Mean return times to the same biomass were 8 years for anchovy, but 22 years for sardine and hake. This is consistent with *Baumgartner's* assessment that most recoveries of sardine are followed relatively quickly by collapses.

4.1. Collapse of Forage Populations Is Inevitable and Common

Earlier studies on the paleorecord showed repeated collapses and recoveries of both sardine and anchovy over 1700 years [*Baumgartner et al.*, 1992] despite some problems with accurately dating these time series. The new paleorecord [*Skrivernek 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. 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, raising questions about sustainability of these fisheries.

Sardine exploitation in the United States is tightly regulated, and exploitation is nominally capped at 15% of total biomass. In addition, harvest drops to 5% if environmental conditions are unfavorable for recruitment, and a fishing moratorium is instituted if population estimates fall below a reserve threshold biomass [*McClatchie*, 2013]. Sardine biomass in 2015 and 2016 has been below the reserve threshold biomass and is considered “collapsed” despite low fishing mortality [*Zwolinski and Demer*, 2012; *MacCall et al.*, 2012]. Similarly, the anchovy fishery has been small off California during the past three decades, but biomass collapsed after 2005 [*MacCall et al.*, 2016]. However, analysis of the paleorecord indicates that forage populations can collapse frequently in the absence of fishing, and a reserve threshold cannot prevent collapses. Given that evidence, debate about the appropriate magnitude of a forage reserve threshold is critical to maximize recovery from collapses.

4.2. Sardine and Anchovy Are Positively Correlated Over 400 Years

The alternation of sardine and anchovy associated with alternation of warm and cool phases of the Pacific Decadal Oscillation has been promoted as a conceptual model in small pelagic fisheries literature [*Chavez et al.*, 2003; *Zwolinski and Demer*, 2012], although this idea has been vigorously challenged based on the paleorecord [*Baumgartner et al.*, 1992; *Field et al.*, 2009; *Finney et al.*, 2010]. We provide a quantitative analysis, based on a well-resolved age model [*Hendy et al.*, 2013; *Schimmelmann et al.*, 2013] showing that negative

correlations between sardine and anchovy are an artifact of short (50-year) time scale. While it is clear that for shorter time series, correlations between sardine and anchovy can be negative, longer time series show this is illusory, and over 400 years, correlations between these species are positive. The implications of this finding for the ecosystem are serious because coincident collapse of both abundant forage species exaggerates food limitation of predators, as is currently the case in the California Current System [McClatchie et al., 2016].

4.3. Collapse and Recovery Cycle Is Fitted to Pulsed Exploitation Strategy

Mean persistence and return times for $R0.33$, and the inevitability of collapse of forage fish populations make forage fish well suited to varied exploitation rates. One possible strategy is to fish them during periods of abundance while recognizing that mean persistence of fishable populations is one to two decades, and that switching to other target species will become a necessity. A pulsed exploitation strategy where periods of high fishing mortality alternate with periods of much reduced or no fishing mortality might fit the natural fluctuations of these populations.

The inevitability of collapse means that periods of famine will occur for predators that cannot move to more productive areas or switch to alternate prey. The mean return times that we calculated from the paleorecord of one to two decades are of the same order as mean persistence of $R0.33$. These return times are also similar to the depreciation times for small pelagic fishing vessels, indicating that return times are on average too long for the industry to simply wait out the return of the forage fish. The paleorecord shows that forage populations are resilient on 500 year time scales, but that crashes and prolonged periods of scarcity will be experienced by both human and other predators. Sustainability depends upon the time scale observed. There may be long periods when little harvest or no harvest at all can be sustained due to natural population dynamics. It would be undesirable to drive the populations so low that the genetic stock is compromised and the stock cannot rebuild. Well-designed reserve thresholds and varied exploitation rates will serve to protect the forage, the fishery, and the nonhuman predators. However, reserve thresholds only protect the seed stock for recovery and cannot prevent collapses from occurring. When the stocks are abundant considerable fishery take may be sustainable, while recognizing that collapse will inevitably follow a period of abundance. Given that small pelagic fishes in other boundary current systems also exhibit boom and bust cycles, the results of our study are likely to be relevant worldwide.

Acknowledgments

S.McC. conceived the study, performed analyses, and wrote the paper. I.L.H. provided collected core samples, made the paleoceanographic data available and contributed to writing. A.R.T. contributed to analyses, graphics, and writing. W.W. identified the fish larvae samples and contributed to writing. The authors declare no competing financial interests. Funding was provided by the National Oceanic and Atmospheric Administration (NOAA) to the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program, the NOAA Fisheries And The Environment (FATE) program to S.McC., and by NSF grant OCE-0752093 to I.L.H. We are grateful to Kevin Hill, Bill Sydeman, and Sarah Shoffler for a presubmission reviews, and to the crew of the R/V *Robert Gordon Sproul* for assistance in collecting core material. CalCOFI data used are publicly available through NOAA ERDDAP <http://upwell.pfeg.noaa.gov/erddap/index.html> in the CalCOFI program data tables.

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