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Reconsidering Trans-Pacific “synchrony” in population fluctuations of sardines

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The causes of Trans-Pacific synchrony and asynchrony in sardine populations were evaluated by examining commercial catch, fishing mortality, spawning stock biomass, and productivity, defined as *ln*-transformed recruitment residuals (*LNRR*). Anomalies of basin-scale and regional sea-surface temperatures (SSTs) are key environmental drivers of population dynamics of some stocks of sardines. Key results were: 1) productivity was synchronized between the Humboldt sardine (*Sardinops sagax sagax*) and the Japanese sardine (*S. melanostictus*) (Pacific stock) during the period for which data were available (1970–99), 2) sudden recoveries in recruitment and productivity of the Humboldt and Japanese sardines during the early 1970s were associated with favorable regional SST anomalies that were enhanced under the favorable PDO regime that followed after 1977, 3) recruitment failures coincided with a climate regime shift in 1988/89 (Humboldt and Japanese sardines and probably California sardine (*S. sagax caeruleus)* in the Gulf of California) and negative anomalies of PDO and CalCOFI SST during 2008–12 (the northern subpopulation of California sardine) caused natural stock declines, and 4) high fishing mortalities coupled with generally unfavorable regional SST anomalies during the 1990s and 2000s prevented recoveries of the Humboldt and Japanese sardines, under a generally favorable PDO regime for sardines. Finally, implications for fisheries management, such as long-term management coping with mismatch between economic and ecological scales of variability, were discussed.

Key words: California sardine, Humboldt sardine, Japanese sardine, PDO, regime shifts, sea-surface temperatures, fisheries management

Introduction

Trans-Pacific synchrony in catch trajectories of the California sardine (*Sardinops sagax caeruleus)*, Humboldt sardine (*S. sagax sagax*) and Japanese sardine (*S. melanostictus*) led to a concept of regime shift (Kawasaki, 1983, 2013). World-wide synchrony of the sardine cycle was linked to global or basin-scale climatic regime shifts (e.g., Chavez et al., 2003; Kawasaki, 2013). Sardines flourish during periods of warmer than average global air temperatures and positive phases of the Pacific Decadal Oscillation (PDO) index (Mantua et al., 1997). A fascinating aspect of the synchrony of sardine catch and biomass in the Pacific is that a favorable temperature for sardine is cool in the western North Pacific and warm in the eastern North Pacific because of the spatial sea-surface temperature (SST) anomaly pattern that is associated with the PDO. Centennial scale variations in sardine abundance have occurred off California, Chile, and Japan since the 13th century and they correspond to low frequency variation of a reconstructed PDO index (Kuwae et al., 2012). Furthermore, age-structured population dynamic models of sardine off California with reconstructed PDO index, Lindegren et al. (2013) recreated sardine fluctuations since the 17th century, with dominant periodicities of approximately 80 years.

During the 1990s, however, when the PDO was generally positive and supposedly favorable for sardines, the Humboldt and Japanese sardine stocks declined while the California sardine had a swift increase (Figs. 1 and 2). Catches increased smoothly along the West coast of the USA as well as Canada and Mexico, however, catches in the Gulf of California (Mexico) were variable but without any specific trend (Fig. 1). During the 2010s, catches of the northern subpopulation of California sardine began to decrease while those of the Japanese sardine were increasing (Fig. 1).

There are two standard hypotheses for collapses of small pelagic fishes (MacCall, 2009); overfishing and natural environmental fluctuations. As they are not mutually exclusive, catch trajectories do not always represent natural stock fluctuations. In the present study, we have examined

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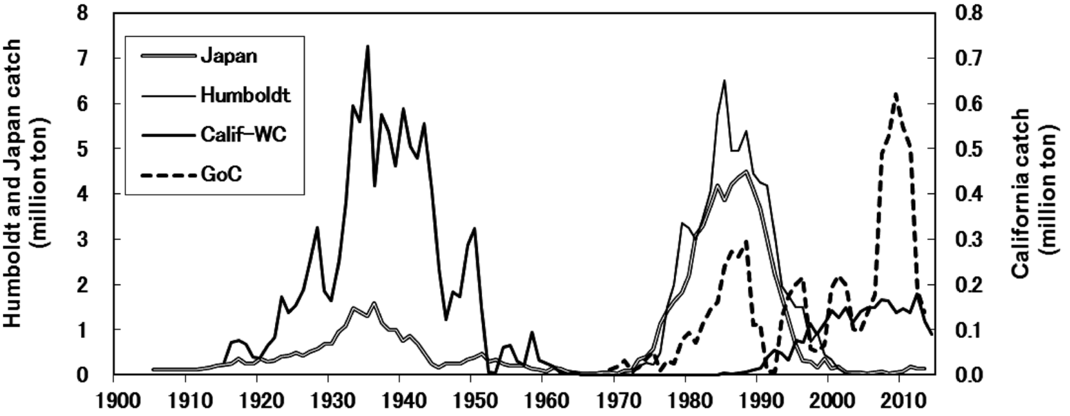

Figure 1. Catch trajectories of the California, Humboldt and Japanese sardines. N.B. Catch of Humboldt and Japanese sardines and sardines in California west coast (Calif-WC) include all stocks/subpopulations except for Gulf of California (GoC), and fishery moratorium in California's west coast during 1967–85.

long-term trajectories of fishing mortality, biomass, and productivity of the California, Humboldt, and Japanese sardines, in relation to the PDO index in winter and regional SST anomalies that are known as their key environmental drivers. Schwartzlose et al. (1999), Alheit et al. (2009) and Barange et al. (2009) should be referred to for historical details of the fisheries and key physical and biological events for the three sardine species/subspecies.

Data and Methods

We used long-term data of annual commercial catch, fishing mortality coefficient (*F*), spawning stock biomass (*SSB*), and reproductive success on the primary target stocks (Tables 1–2, Figs. 1, 3–5; N.B. data missing periods including US fishery moratorium during 1967–85). Commercial catch data was obtained from Yatsu et al. (2008), Kawabata et al. (2014) and Ohshimo et al. (2014) for the Japanese sardine, FAO statistics "FishStatJ" (South American pilchard in the Pacific Southeast) for the Humboldt sardine, and Hill et al. (2011, 2015) for the California sardine in the California west coast, and the Mexican catch statistics for the California sardine in the Gulf of California[1] until 2008, and those of California west coast subtracted from California pilchard total catch (FishStatJ) after 2008. In general, the population dynamics of sardine, in relation to environmental drivers, have been intensively studied, allowing us to make reasonable assumptions about basic parameters. Natural mortality (*M*) was assumed to be in a range of 0.3–0.4 (Table 2). Fishing mortality (*F*) was defined arbitrarily as high (F>0.4), moderate (0.2–0.4) and low (<0.2). In reality, a sustainable *F* depends on variable biological traits such as somatic growth, maturation, and survival rates of the target stock, particularly during early life stages. *F* was estimated by different assessment methods for each stock (Table 2) therefore they may not be directly comparable.

Recruit per spawner (*RPS*) analysis is used generally to explore how density-independent factors (environmental) and density-dependent factor (*SSB*) affect the productivity of a stock. To remove the influence of *SSB* on *RPS*, productivity was calculated as *ln*-transformed recruitment residuals (*LNRR*) from a Ricker model (see Appendix 1, Fig. 5). Statistical significance of correlation coefficients among productivity time series was calculated according to the method of Pyper and Peterman (1998). Phase shifts in productivity were detected as statistically significant shifts in mean values (Regime Shift index) using Sequential Regime Shift Detection software (version 3.4) developed by Rodionov (2004) (http://www.climatelogic.com/documentation/shifts-in-variance, 30 September 2016). Model parameters were set as follows: Target significance level (*P*)=0.1, cutoff length=7 by considering the shortest period of SST regime (see Fig. 2), Huber's weight=5, and red-noise estimations=none. In order to evaluate effects of high *F*, we simulated *SSB* and catch under reduced *F* during 1976–78 and since 1992 for the Pacific stock of the Japanese sardine by using a forward-type virtual population analysis (VPA) (Appendix 2).

As ocean temperature features prominently in the dynamics of sardine populations, we examined temperature variation at both basin-scale (PDO in winter[2]) and regional scales (SST anomalies): CalCOFI,[3] Scripps pier,[4] Niño in-

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[1] http://www.inapesca.gob.mx/portal/documentos/publicaciones/Anexo1_InfTec_CaptEsfuerzoFlota_PMGC.pdf, 29 January 2015

[2] January–March mean index (http://www.data.jma.go.jp/kaiyou/data/db/climate/pdo/pdo_month.html, 20 May 2017)

dex,[5] and Kuroshio Extension South area (KESA)[6] (Fig. 2) that are considered to be principal environmental drivers of recruitment or *RPS* variability of the target stocks of California and Japanese sardines (Yatsu et al., 2005, 2008; Jacobson and McClatchie, 2013; Lindegren et al., 2013; Lindegren and Checkley, 2013) or overall biomass of the Humboldt sardine (Alheit et al., 2009), although potential drivers are diverse and interdependent (Yatsu et al., 2008, 2013; Lindergen et al., 2013).

PDO index in winter is linked to winter activity of the Aleutian Low, which enhanced or reduced the subarctic circulation and brought about anomalies of regional SST, mixed layer depth (MLD), upwelling, and productivity of lower trophic ecosystems, and probability of encountering predators of sardines, such as skipjack tuna (*Katsuwonus pelamis*) (Yatsu et al., 2008, 2013; Di Lorenzo et al., 2013). Hypothetical linkages between a positive PDO, regional SST anomalies and MLD, and optimum environmental windows for sardine stocks have been reported (Table 3), although in California, there is a debate on which indicator best represents local environmental variability. The regular CalCOFI area covers a large part of the southern California Bight and the main spawning area of sardine, whereas the Scripps pier is a single coastal point affected by warm and more saline waters of tropical origin (McClatchie et al., 2010).

Since temperatures in the spawning grounds primarily influence survival rates of eggs and growth rates and physiological conditions of larvae after hatching (Takasuka et al., 2008), and winter KESA SST is regarded as a proxy of winter MLD and SST near the axis of Kuroshio and Kuroshio Extension (nursery grounds) of the Pacific stock of Japanese sardine (Nishikawa et al., 2011), selected regional SST anomalies potentially affect recruitment and *RPS*. Since long-term stock assessment results and environmental drivers for recruitment or biomass of the Gulf of California were unavailable, we treated the Gulf of California subpopulation as a secondary target.

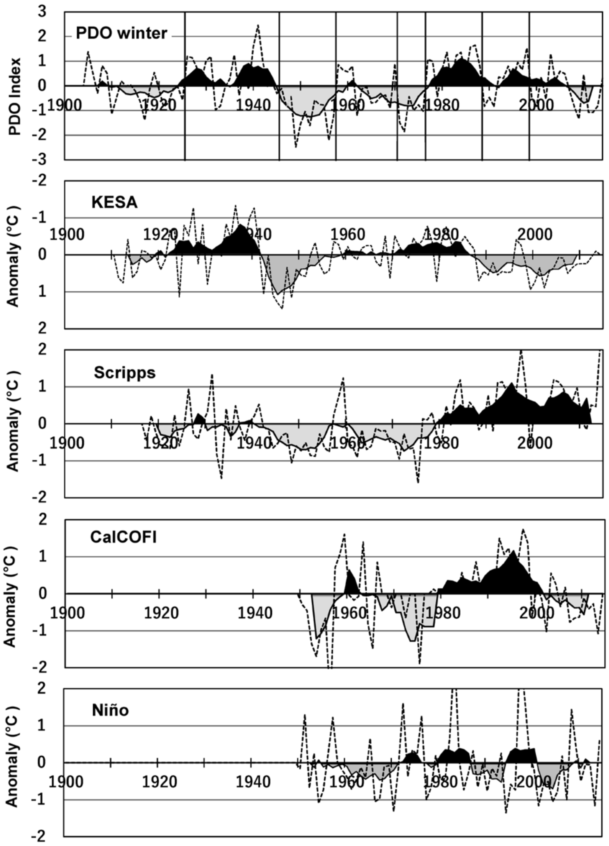

Figure 2. Trajectories of the Pacific Decadal Oscillation (PDO) in winter and sea-surface temperature (SST) anomalies (dotted lines) and their 7-year running means (shaded areas) of the Kuroshio Extension South Area (KESA, vertical-axis reversed), the Scripps Institution of Oceanography pier, the regular CalCOFI area, and the Humboldt Current area (Niño). Black and grey colored periods are considered favorable and unfavorable for each sardine, respectively. Vertical lines indicate years of SST regime shifts (Yasunaka and Hanawa, 2002; Yatsu et al., 2008).

Results and Discussion

"Synchrony" during 1920s–80s

An increase of Japanese sardine catch during 1924–33 (N.B. the 1925/26 SST regime shift; Yasunaka and Hanawa, 2002) was primarily caused by population growth and development of the fisheries, while the major cause of population declines in the 1940s was attributed to recruitment failures during 1938–41 (N.B. prior to the 1944/45 SST regime shift), associated with abiotic environmental conditions such as the Kuroshio path (Nakai, 1962). A decline in productivity of California sardine started in 1941 and was negative in the mid 1940s (Fig. 5). Barnes et al. (1992) concluded that effects of both fishing and SST were responsible for the persistent low biomass and catch of California sardine during 1941–65: exploitation rates generally exceeded 30% and SST was generally unfavorable. The collapse of the California sardine during the 1950s, however, was inevitable due to poor recruitments regard-

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[3] January–December mean 5–15 m depth temperatures from the regular CalCOFI area (https://sio-calcofi.ucsd.edu/, 8 September 2015)

[4] January–December mean SST anomaly at the Scripps Institution of Oceanography pier (ftp://ftp.iod.ucsd.edu/shore/active_data/lajolla_sio/temperature/, 12 May 2015)

[5] July–September mean SST anomaly of Niño 4 region were subtracted from those of Niño 1 and 2 regions (http://www.cpc.ncep.noaa.gov/data/indices/ersst3b.nino.mth.81–10.ascii, 29 January 2015)

[6] February SST averaged over KESA (30–35°N, 145–180°E) according to Yatsu et al. (2008) and Nishida et al. (2012)

Table 1. Biological characteristics of California, Humboldt and Japanese sardine stocks examined for population dynamics in relation to environmental recruitment/biomass drivers. Footnotes indicate data sources.

Species/region	California	Humboldt*		Japanese*,†
Stock or subpopulation	Northern subpopulation*, ** (California west coast***)	North–Central Peru stock	South Peru–North Chile stock	Pacific stock (Kuroshio/Oyashio)
Age at recruitment	0 (6–12 months)	n.a.	1	0
Age at first maturation	1 (1982–2014)–2 (1935–63)	3–4	5	1
Max. age	15	8	11	7
Max. body length (cm)	41	39	40	23

*Barange et al. (2009). **Hill et al. (2015). ***Jacobson and MacCall (1995). †Kawabata et al. (2014).

Table 2. Available data period and methods of stock assessments in California, Humboldt and Japanese sardine stocks. Footnotes indicate data sources. *M*: natural mortality coefficient.

Species/region	California	Humboldt		Japanese
Stock or subpopulation	Northern subpopulation (California west coast)	North–Central Peru stock	South Peru–North Chile stock	Pacific stock (Kuroshio/Oyashio)
Spawning stock biomass and recruitment	1935–63*, 1986–90*, 1993–2014**	1970–99***	1974–92***	1951–75††, 1976–2012†††
Fishing mortality coefficient (*F*)	1950–63***, 1986–2005***, 1994–2014†	1963–2003***	1974–96***	1976–2012†††
Stock assessment method	1935–63 (VPA), 1986–90 (CANSAR), 1993–2014 (Stock Synthesis Ver. 3.24s)	Acoustic survey (biomass of juveniles and adults)	VPA	1951–75 (A forward-simulation approach fitted to egg production data), 1976–2012 (VPA)
Assumed M (yr^{-1})	0.4	n.a.	0.3	0.4

*Jacobson and MacCall (1995). **Hill et al. (2015). ***Barange et al. (2009).
†Estimated from Table 12a of Hill et al. (2015). ††Wada and Jacobson (1998). †††Kawabata et al. (2014).

less of exploitation levels (Lindegren et al., 2013).

The trajectories of productivity of the California and Japanese sardines can be compared from 1951 to 1963. At the start of this period, productivity of the California sardine was lowest in its history while productivity of the Japanese sardine was at or slightly above average (Fig. 5). During this period, they shared a sudden increase from 1957 to 1958 followed by a swift decline in the early 1960s. However, year to year covariation was not statistically significant from 1951 to 1963 ($R^2=0.4849$, $p>0.1$, Fig. 6). Also, a positive but statistically insignificant shift in productivity of the California and Japanese sardines coincided with the 1957/58 SST regime shift (Fig. 5). Nevertheless, in both time series, regime shift analysis indicated that their years of significant negative shifts (1960—Japan and 1961—California) occurred within 1 year (Fig. 5).

The 1970s through the 1980s was a puzzling period, made more so by a lack of productivity data from California. The Humboldt and Japanese sardine catch and *SSB* began to increase in the early 1970s, owing to strong year-classes (Figs. 1 and 4, Yatsu et al., 2008; Alheit et al., 2009; Barange et al., 2009). A positive correlation of productivity between the Japanese sardine and either of the two Humboldt sardine stocks was statistically significant ($p<0.05$) (Fig. 6). These positive phases for sardine were associated with favorable SST anomalies off the coast of South America and in the KESA that were enhanced under the favorable PDO regime that followed after 1977 (Fig. 2). Later, significant negative shifts in productivity of the Humboldt and Japanese stocks occurred following the 1988/89 regime shift (Fig. 5) indicating synchrony in productivity of these sardine stocks during the 1970s–90s. Since the US sardine fishery was closed during 1967–85, effects of the 1970/71 and 1976/77 regime shifts on the northern subpopulation are uncertain. There is some evidence to suggest an increase of abundance of the northern subpopulation from the late 1970s to early 1980s (Barnes et al., 1992; Hill et al., 2006). Sardine recruitment in the Gulf of California in-

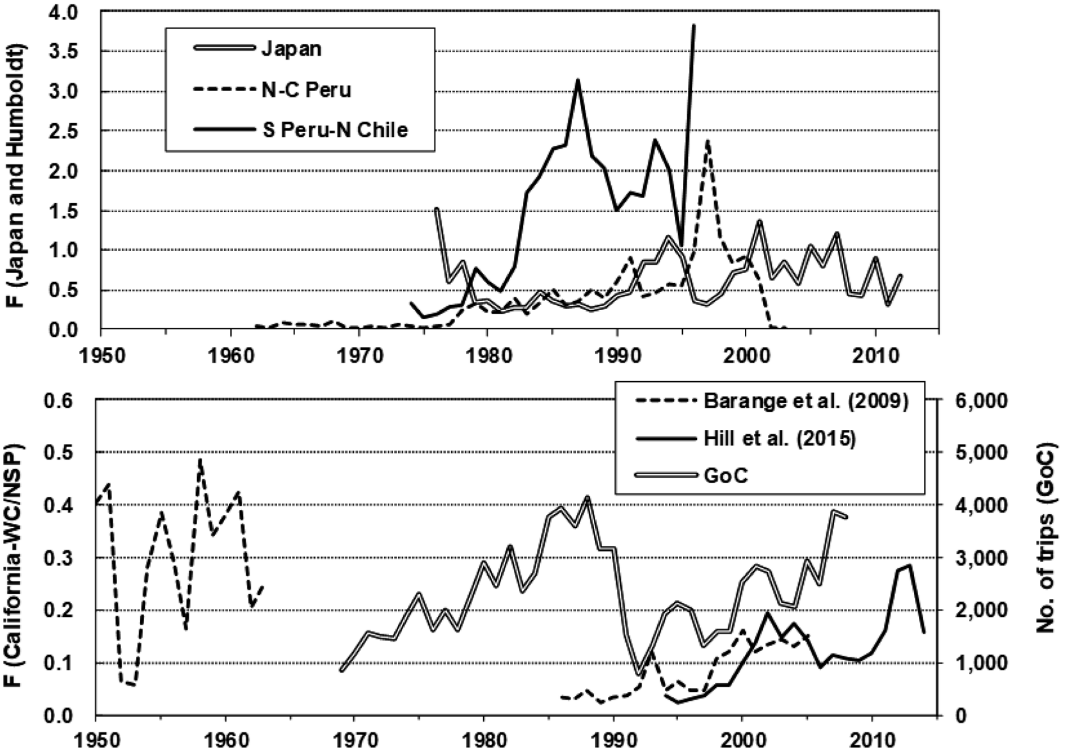

Figure 3. Trajectories of fishing mortality coefficient (*F*) of the California sardine in California's west coast (WC, 1950–63, 1985–93) and northern subpopulation (NSP, 1994–2014), the Pacific stock of Japanese sardine, and the North–Central Peru and South Peru–North Chile stocks of Humboldt sardine, and number of fishing trips, as a proxy of *F*, in the Gulf of California (Anonymous, 2011).

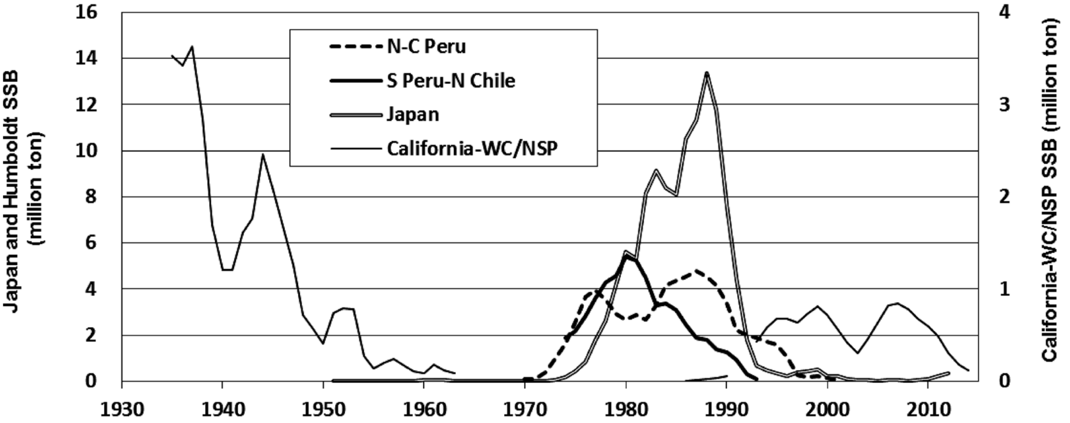

Figure 4. Trajectories of spawning stock biomass (*SSB*) of the California sardine in California's west coast (WC, 1935–63, 1985–90) and northern subpopulation (NSP, 1993–2014), the Pacific stock of Japanese sardine, and the North–Central Peru and South Peru–North Chile stocks of Humboldt sardine.

creased during 1975–85 before falling dramatically (Schwartzlose et al., 1999). From the late 1970s to late 1980s, favorable PDO and regional SST anomalies and a period of high catch generally coincided among the three sardine species but most of the California catch was derived from the Gulf of California (Figs. 1 and 2).

During the 1970–80s, *F* was moderate in the Pacific stock of Japanese sardine (except for 1976–78 when *F* was high) and in the North–Central Peru stock of Humboldt sardine, whereas *F* increased from approximately 0.2 to

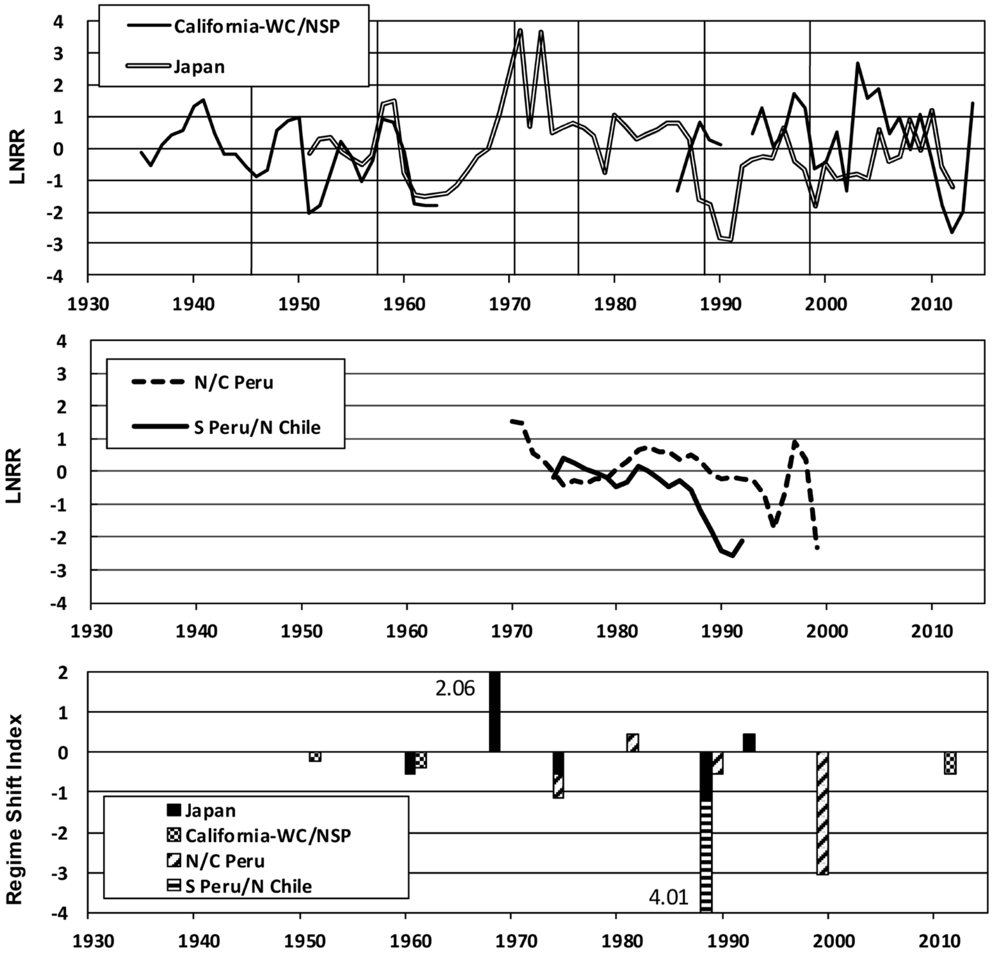

Figure 5. Trajectories of productivity (*LNRR*) of the California sardine in California's west coast (WC, 1935–63, 1985–90) and northern subpopulation (NSP, 1993–2014), the Pacific stock of Japanese sardine, and the North–Central Peru and South Peru–North Chile stocks of Humboldt sardine, and years of statistically significant Regime Shift index for productivity trajectories (bottom panel). Vertical lines indicate years of SST regime shifts (Yasunaka and Hanawa, 2002; Yatsu et al., 2008).

above 1.0 in the South Peru–North Chile stock of Humboldt sardine (Fig. 3). *F* was low in the California west coast during this period (Fig. 3). For the Pacific stock of Japanese sardine, fishing effort increased during the 1980s through construction of large-scale transport ships (the 330 gross tons type) (Makino and Mitani, 2010). In spite of this elevated fishing effort, fishing mortalities from the early 1970s to the 1988/89 SST regime shift, including high *F* during 1976–78 in the Japanese sardine, were considered sustainable since *SSB* had steadily increased (Fig. 4). The effects of high *F* during 1976–78 in the Japanese sardine were studied by simulation with reduced *F* (Appendix 2), and results indicated a swift increase in *SSB*. On the other hand, high *F* and generally negative productivity since the end of 1970s in the South Peru-North Chile stock of Humboldt sardine resulted in a decline of *SSB* throughout the 1980s (Figs. 3–5).

The 1988/89 regime shift led to SST anomalies that were not favorable for sardines, which lasted only 3 years (PDO) or longer (Niño and KESA), but those of Scripps and CalCOFI changed little (Fig. 2). Years when negative shifts occurred in productivity of the Humboldt and Japanese sardines were coherent with the 1988/89 regime shift (Fig. 5). Recruitment failures of the Pacific stock of Japanese sardine during 1988–91 were attributed to the 1988/89 regime shift (Yatsu et al., 2008) and neither growth overfishing nor recruitment overfishing was responsible for the stock decline during this period (Watanabe et al., 1995). The North-Central Peru stock of Humboldt sardine also declined with slightly negative productivity in the late 1980s (Figs. 4 and 5). The South Peru–North Chile stock of Humboldt sardine and the California sardine in the Gulf of California swiftly declined from the late 1980s to early 1990s due to extremely negative productivity during 1988–92 and poor recruit-

Table 3. Characteristics of selected region/index, reported linkages between positive PDO and anomalies of regional SST and mixed layer depth (MLD), and optimum environmental windows of California, Humboldt and Japanese sardine stocks. Footnotes indicate information sources. For their mechanistic linkages, see text.

Species/region	California	Humboldt	Japanese
Regional SST	CalCOFI, Scripps pier	Niño index	Kuroshio Extension South area (KESA)
Characteristics of region/index	CalCOFI area covers main spawning grounds[*] Scripps pier is affected by warm poleward flows[**]	Niño index represents approach or retreat of warm subtropical waters towards the coasts of Peru and Chile[†††]	KESA SST is considered as a proxy of MLD and SST in nursery grounds[##]
Regional SST will become	Warmer[***]	Warmer[***]	Cooler[***]
MLD will became	Shallower[***, †]	Shallower[***, †††]	Deeper[***]
Optimum spawning SST relative to sympatric anchovy	Warmer[††] (13–25°C with a peak at 23–25°C)	Not available, but an optimum upwelling window for recruitment[#]	Cooler[††] (13–20°C with a peak at 16–17°C)

[*] Lindegren and Checkley (2013). [**] McClatchie et al. (2010). [***] Chavez et al. (2003). [†] MacCall (2009).
[††] Takasuka et al. (2008). [†††] Alheit et al. (2009). [#] Serra et al. (1998). [##] Nishikawa et al. (2011).

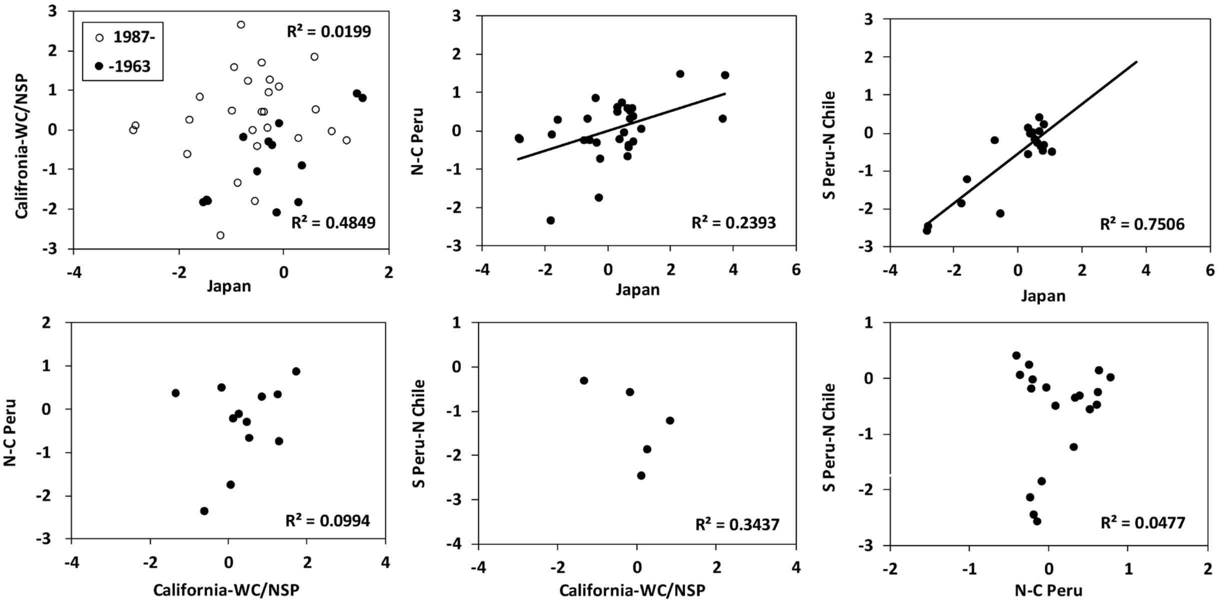

Figure 6. Pairwise correlations of productivity (*LNRR*) among the California sardine (California west coast (WC, –1990), northern subpopulation (NSP, 1993–)), the Pacific stock of Japanese sardine, and the North–Central Peru and South Peru–North Chile stocks of Humboldt sardine. Statistical significance of correlation coefficients in pair-wise comparisons of productivity among the four sardine stocks were adjusted to account for autocorrelation and length of time series according to the method of Pyper and Peterman (1998). Statistically significant ($0.01<p<0.05$) correlations were indicated by solid regression lines.

ment, respectively (Figs. 1, 4, 5, Schwartzlose et al., 1999; Alheit et al., 2009; Barange et al., 2009). Productivity of the northern subpopulation of California sardine was slightly positive during 1988–90 (Fig. 5), which was consistent with SST anomalies of Scripps and CalCOFI.

“Asynchrony” during 1990s–2000s

SSB and catch of the northern subpopulation of California sardine were relatively high under favorable PDO and regional SST anomalies, and low *F* (Figs. 1–4). In contrast, the biomass of Humboldt and Japanese sardine continued to decline and was depleted by the early 2000s, under generally unfavorable regional SST and high *F*, confirming MacCall et al. (2012), who stated that unregulated fisheries were unable to tolerate even a brief decline in reproductive rate. Higher *F* can arise from a higher catchability coefficient (*q*) and/or greater fishing effort. MacCall (1976) detected an inverse relation between *q* and population abundance of the California sardine during 1937–44. Higher *q* is plausible for the Peru, Chile, and Japanese fisheries in the early 1990s, since *SSB* declined sharply from the end of 1980s (Fig. 4). The elevated fishing effort for the Pacific stock of Japanese sardine during the 1980s caused excessive capitalization after the 1988/89 regime shift, when productivity was reduced dramatically (Makino and Mitani, 2010, Fig. 5).

Among the Pacific stock of Japanese sardine and the two stocks of Humboldt sardine, whose productivity were generally negative during the 1990s (Fig. 5), the South Peru–North Chile stock, which had much higher *F* (>1.0) since the end of the 1970s, was depleted in the mid 1990s. The Japanese sardine and the North–Central Peru stock, where *F* generally ranged from 0.5 to 1.4, were depleted in the early 2000s (Figs. 3 and 4). While effects of these different levels of *F* on *SSB* during this period can be hypothesized as the cause of the different periods until depletions, the data are inconclusive because of the generally negative, but stock-specific, productivity trajectories since the 1988/89 regime shift (Fig. 5), and because of different methods of estimating *F* in each stock.

These results, together with our simulation studies on the Japanese sardine (Appendix 2) suggest that the asynchrony in the *SSB* and catch trajectories among the three sardine species during the 1990s and 2000s was caused by differences in the regional SST anomalies and magnitudes of *F*, which were supposedly elevated in the Humboldt and Japanese sardines owing to recruitment failures associated with the 1988/89 regime shift, and for the Japanese sardine, increased fishing effort since the 1980s.

Recent events on California and Japanese sardines

Zwolinski and Demer (2012) predicted that a cold regime in the California Current and high exploitation rates would cause a collapse of the California sardine. Surprisingly, in spite of a generally warm Scripps SST regime since the 1980s, biomass of the northern subpopulation of California sardine declined during the 2010s under generally low harvest rates, with extremely low recruitments from 2010 to 2013 (Hilborn, 2015; Hill et al., 2015). The projected biomass for 2015–16 was so low that no catch was recommended for 2015–16 (Hill et al., 2015). The 2010 to 2013 year-classes were some of the weakest in recent history, following a series of years where recruitments had been overestimated (Hill et al., 2015). The exploitation rate of the northern subpopulation ranged 9–17% during 2000–11, but in 2012 and 2013 it suddenly increased to 27% (Hill et al., 2015, also see *F* values in Fig. 3) which exceeded the overfishing limit (ca. 15% during 2012–13) (http://usa.oceana.org/predators-prey/modern-day-pacific-sardine-collapse-how-stop-overfishing-and-prevent-future-crisis, 4 June 2015). Hilborn (2015) argued the high exploitation rates in 2012 and 2013 were a result of a natural decline of recruitment. If so, the recent decline of this subpopulation was associated with strong negative anomalies of PDO and CalCOFI SST during 2008–12 (Fig. 2).

The negative anomalies of PDO during 2008–12 were associated with positive anomalies of KESA SST, as expected. However, productivity of the Pacific stock of Japanese sardine became recurrently positive in the second half of the 2000s (Figs. 2 and 5). The cause(s) of the positive anomalies of productivity are unknown. This positive productivity coupled with reduced *F* since 2008 brought about a slight recovery of *SSB* and catch of the Japanese sardine (Figs. 1, 3, 5). Thus, another period of asynchrony may be emerging.

Implications for fisheries management

Overfishing of the Pacific stock of Japanese sardine during the 1990s was caused by a mismatch between economic and ecological scales of variability. The ecosystem effects of the 1988/89 regime shift (poor productivity regime involving a shallow MLD and northward retreat of the Oyashio) occurred abruptly, but the investments in new high capacity fishing fleets during the 1980s continued fishing for two decades (Yatsu et al., 2008; Makino and Mitani, 2010). Heavy fishing may also induce high-frequency stochastic variability of populations (Lindegren et al., 2013) that would increase year-to-year variability in catch. Since sustainable exploitation rates are regime-dependent and stock productivity-dependent, there is a need for more mechanistic studies of sardine population dynamics and their association with environmental variation. New studies would benefit from continuous monitoring of key environmental drivers and year-class strength, improvements of accuracy and precision of stock assessments, long-term management strategies that would match investment cycles with regime shifts. Given the variability that has occurred on both the ecological and economical dimensions, a precautionary approach is needed for a rational fisheries management. The recent overestimation of year-class strength of the California sardine suggests that monitoring targets and methods must be continuously reviewed and improved whenever necessary.

Conclusions

Based on our results and available information, we conclude that: 1) productivity of two stocks of the Humboldt and the Japanese Pacific stock was synchronized during the period for which data were available (1970–99), 2) abrupt recoveries in recruitment and productivity of the Humboldt and Japanese sardines occurred during the early 1970s and were associated with favorable regional SST anomalies, and their abundances increased further under the subsequent favorable PDO and regional SST regime after 1977, 3) recruitment failures followed regime shifts in 1988/89 (Humboldt and Japanese sardines and probably California sardine in the Gulf of California) and negative anomalies of PDO and CalCOFI SST during 2008–12 (the northern subpopulation of California sardine) caused natural stock declines, and 4) high fishing mortalities coupled with generally unfavorable regional SST anomalies during the 1990s–2000s prevented stock recoveries of the Humboldt and Japanese sardines, despite the PDO being generally favorable. On the other hand, neither the PDO, regional SST anomalies, nor SST regime shifts seemed consistently associated with the observed productivity variability. This inconsistency is potentially derived from regional differences in various physical/biological mechanisms in spawning and recruitment processes, such as changes in primary productivity and its phenology associated with upwelling and MLD, biological changes in sardines, and reorganizations of pelagic ecosystems with some time-lag from SST regime shifts (Yatsu et al., 2008; Alheit et al., 2009; MacCall, 2009). Although there is no generally accepted theory at present, comparative studies among regions, using multi-trophic level ecosystem models for distribution, migration and population dynamics of sardine stocks incorporating various environmental variability (e.g., Okunishi et al., 2012; Di Lorenzo et al., 2013; Lindegren et al., 2013) may provide new insights into regional similarities/differences in mechanisms in spawning and recruitment processes of sardine stocks.

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太平洋東西におけるマイワシ資源変動の「同期性」に関する再検討

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東西太平洋のマイワシ資源変動の同期性を検討するため，漁獲量，漁獲死亡係数，親魚量及び生産力（加入量の対数残差：*LNRR*）を検討した結果，以下の結論を得た：1) フンボルト海域のマイワシ(*Sardinops sagax sagax*)と日本のマイワシ(*S. melanostictus*) 太平洋系群の生産力は1970–99年に同期した，2) 1970年代初期のフンボルト海域と日本のマイワシの加入量と生産力の増加は各海域の表面水温の好適な偏差と関連し，1977年以降の好適レジームにより水温偏差は更に増加した，3) フンボルト海域，日本および恐らくカリフォルニア湾のマイワシ(*S. sagax caeruleus)*で1988/89年に生じた加入の失敗は気候レジームシフト年と一致した自然現象，2008–12年に生じたカリフォルニア北部系群マイワシの加入の失敗はこの間のPDOとCalCOFI海域の表面水温の負偏差と一致した自然現象である，4) 1990–2000年代はPDOが一般的にマイワシに好適と見なされるレジームであったが，フンボルト海域と日本のマイワシへの高い漁獲圧と各海域の不適な表面水温偏差により資源回復が妨げられた．漁業管理への意義についても考察した．

キーワード：カリフォルニア・マイワシ，フンボルト・マイワシ，日本・マイワシ，PDO, レジームシフト，表面水温，漁業管理

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Appendix 1: Density-dependence of reproductive success rates

Reproductive success rates or *RPS* are generally used to explore density-independent (environmental) and density-dependent (*SSB*) effects. In the California and Japanese sardines, both effects were detected and the Ricker-type model (equation A1) with environmental covariates was suggested (Jacobson and MacCall, 1995; Yatsu et al., 2005; Lindegren and Checkley, 2013). Low-frequency fluctuations in *SSB* trajectories were observed, although *SSB* data was unavailable for some periods (Fig. 4). In order to reduce the influence of density-dependent effects, we examined trajectories of *ln*-transformed recruitment residuals from the Ricker-type *SSB-R* model (*LNRR*, equation A2), which are considered to represent process-errors in *RPS* caused by environmental variability (Jacobson and MacCall, 1995). Positive and negative *LNRR* imply recruitments above and below the assumed *SSB-R* model, respectively.

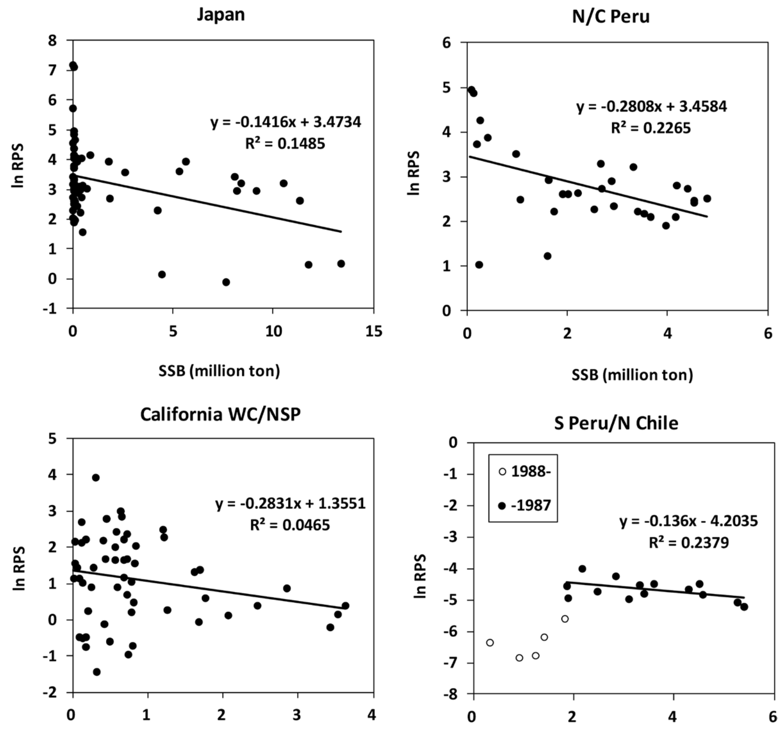
$$\ln RPS(y) = a - bSSB(y) + \varepsilon \qquad \text{(A1)}$$

$$LNRR(y) = \ln(RPSobserved(y)/RPSmodel(y)) \qquad \text{(A2)}$$

where *a* is intercept parameter, *b* is parameter for density dependence, *ε* is error term, and *y* is year.

The relationship between *SSB* and *ln*-transformed *RPS* for each stock (Appendix Fig. 1) suggested density-dependent effects, where the South Peru–North Chile stock of Humboldt sardine, five years (1988–92) were excluded from our parameter estimation, since they deviated considerably from the pattern of the other years and a negative effect of the 1988/89 regime shift was suspected (Fig. 5).

Estimated parameters for the equation 1 appear in Appendix Fig. 1. They were statistically significant ($p<0.01$), except for parameter *b* of the California sardine and the Southern Peru–Northern Chile stock of Humboldt sardine. Given the Ricker-type density-dependence in California and Japanese sardines described above, we applied equation 2 to all stocks for the sake of consistency in the present analysis, although the Beverton–Holt model was used in the most recent assessment of California sardine (Hill et al., 2015).



Appendix Figure 1. Relationships between spawning stock biomass (*SSB*) and *ln*-transformed reproductive success rate (*RPS*) and fitted regression lines in the California sardine in California's west coast (WC, 1935–90) and northern subpopulation (NSP, 1993–2014), the Pacific stock of Japanese sardine, and the North–Central Peru and South Peru–North Chile stocks of Humboldt sardine.

Appendix 2: Simulations of population dynamics of the Pacific stock of Japanese sardine during 1976–78 and 1992–2012

F was high from 1976 to 1978 and after 1992 following a period of extremely low productivity and a sharp decline of *SSB* during 1988–91 (Figs. 4–5). To ascertain the role of high *F*, we simulated population dynamics with a forward-type VPA (Haddon, 2001) with a 50% reduction of *F* for each age and year. In the simulations, we assumed density-dependent maturation, growth and *RPS*, where year-specific environmental effects were also considered.

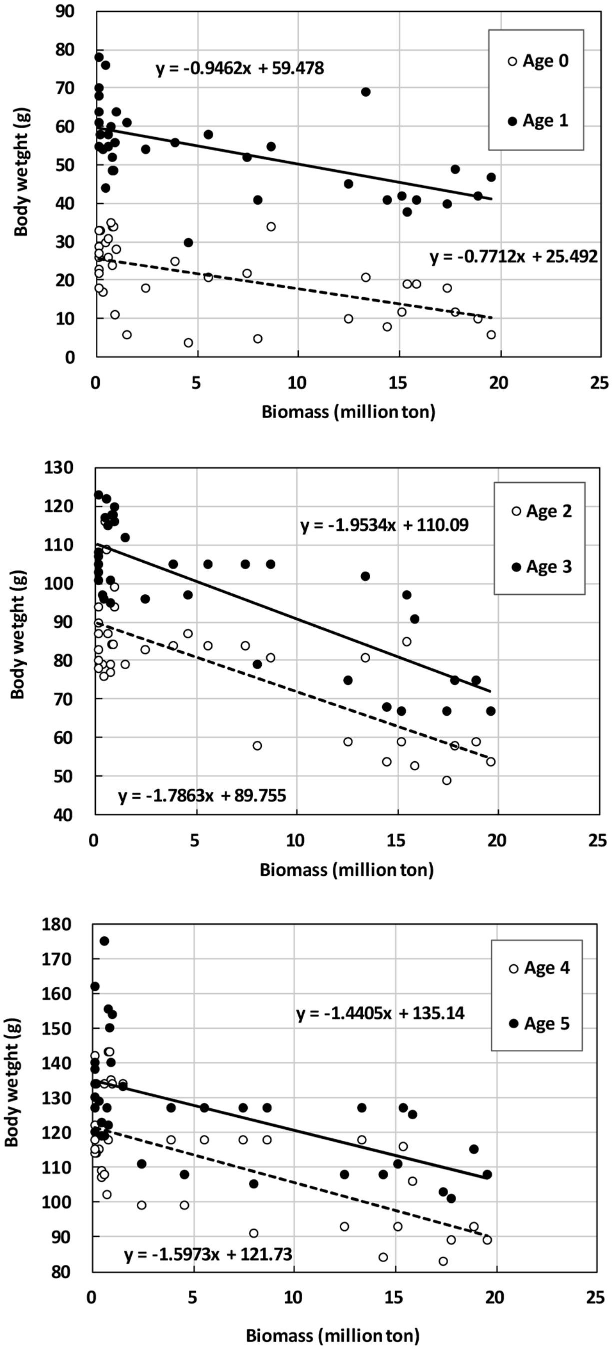
Age- (0–5; age 5 is a plus group) and year- (1976–2012) specific abundance in number of individuals (*N*), *F*, mean body weight (*BW* in g), and maturation rate (*MR*) were adopted from the Japanese stock assessment results (Kawabata et al., 2014), where *M* was assumed constant (0.4) over the ages and years. All age 0 fish and age 2 and older fish were assumed immature and mature, respectively, while *MR* of age 1 fish was assumed variable depending on age-aggregated biomass (*B*): 0.1 (*B*>one million ton), 0.2 (one million ton >=*B*>800,000 ton), 0.5 (*B*=<800,000 ton). Relationships between *B* and *BW* of age 0–5 fish are shown in Appendix Fig. 2. Recruitments (*N* at age 0) were derived from equations (A3) and (A4).

$$N(0,y) = \exp(LNRR(y))(3.4734 - 0.1416 SSBsimulation(y)) \tag{A3}$$

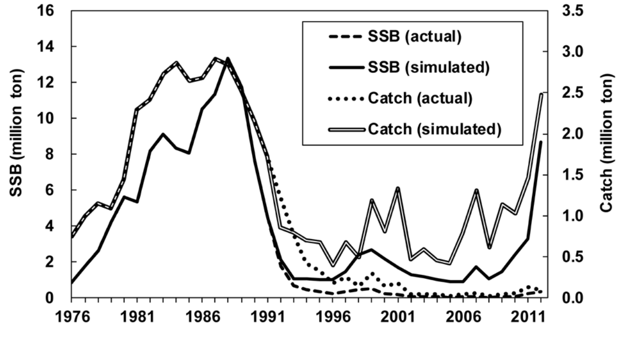
$$SSBsimulation(y) = \Sigma_{a=0}^{a=5} N(a,y)BW(a,y-1)MR(a,y-1) \tag{A4}$$

where *a* is age, and *y* is year.

In these simulations, *SSB* increased more swiftly than observed during the late 1970s (figure not shown), and *SSB* and catch slightly recovered in the late 1990s and further recovered since the late 2000s (Appendix Fig. 3), although the magnitudes of catch recovery were less than those of the California sardine during the 1990s and 2000s (Fig. 1).



Appendix Figure 2. Relationships between age-aggregated biomass and body weight for age 0–5 fish of the Pacific stock of Japanese sardine during 1976–2012, with solid and broken regression lines for solid and open circles, respectively.



Appendix Figure 3. Actual and simulated *SSB* and catch trajectories of the Pacific stock of Japanese sardine. In this simulation, annual *F* were reduced by half of the actual value since 1992.