

Response of Japanese anchovy (*Engraulis japonicus*) to the Pacific Decadal Oscillation in the Yellow Sea over the past 400 a

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Abstract

Quantitative identification of long-term changes in the abundance of Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea is particularly important for understanding evolutionary processes of the Yellow Sea ecosystem. Unfortunately, the driving mechanisms of climate variability on the anchovy are still unclear due to the lack of long-term observational data. In this study, we used the fish scale deposition rate in the central Yellow Sea to reconstruct the time series of the anchovy stock over the past 400 a. On this basis, we further explored the impacts of the Pacific Decadal Oscillation (PDO) on the anchovy. Our results show that the anchovy stock is positively correlated with the PDO on a decadal time scale. In addition, anchovy abundance was relatively high during 1620–1860 AD (the Little Ice Age, LIA), though in a state of constant fluctuation; anchovy abundance maintained at a relatively low level after ~1860 AD. In particular, followed by overfishing since the 1980s, the anchovy stock has declined sharply. Based on these findings, we infer that fluctuations of the anchovy stock may be regulated by basin-scale “atmosphere–ocean” interactions. Nevertheless, the role of overfishing should not be ignored.

Key words: Japanese anchovy, scale deposition rate, population fluctuation, Pacific Decadal Oscillation, Yellow Sea

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1 Introduction

Knowledge of fish population dynamics is particularly important for our understanding of marine ecosystems and exploited populations. In particular, small pelagic fishes such as anchovies, sardines, and herrings have an r-type life history strategy that causes their populations to be highly sensitive to environmental stress (Stenseth et al., 2002; Alheit et al., 2012). In addition, such fishes are ideal target species for indicating the changes in marine ecosystems due to their great plasticity in growth, survival, and other life history characteristics (Alheit et al., 2012). Meanwhile, they are playing an increasingly important role in many marine ecosystems, both ecologically and economically. In the past few decades, small pelagic fish populations have shown frequent large fluctuations in abundance. Well-known examples include sardine (*Sardinops sagax*) in the California Current (Kawasaki, 2002), the Peruvian anchovy (*Engraulis ringens*) in the Humboldt Current (Alheit and Niquen, 2004), the sardine (*Sardinops sagax*) in the Benguela Current (Cury and Shannon, 2004), and the Japanese sardine (*Sardinops melanostictus*) in the Kuroshio and Oyashio Currents (Yasuda et al., 1999). Overall, small pelagic fishes directly and indirectly contribute approximately 16.9 billion dollar to the global fishery economy each year, accounting for 20% of the global marine fishery economy (Pikitch et al., 2014). Therefore, identifying driving mechanisms behind anchovy stock fluctuations will help us to better understand dynamic characteristics of the marine food web.

Data employed in previous studies of fish population dynamics have generally come from fishery records. Due to the short

time scale, results of such studies may be biased to varying degrees. Fortunately, marine sediment records as precious archives can be used to help us understand the long-term relationship between fish populations and their environment, meaning that a bridge could be built between fish dynamics and the evolution of marine ecosystems. In the late 1960s, Soutar and Isaacs (1969) pioneered the idea of reconstructing fish abundance in historical periods, based on the fish scale deposition rate (SDR) for the Pacific sardine (*Sardinops caerulea*), northern anchovy (*Engraulis mordax*), and the Pacific hake (*Merluccius productus*) in anaerobic sediments off the California coast. Subsequently, to reconstruct long-term changes in small pelagic fish abundance, the SDR was carried out in several regions worldwide, for example the west coast of Canada (Patterson et al., 2005), northern Mexico (Holmgren-Urba and Baumgartner, 1993), central Peru (Gutiérrez et al., 2009), northern Chile (Valdés et al., 2008), and the southwest coast of Japan (Kuwae et al., 2017). All such studies have shown that fish population fluctuations are closely related to climate variability, which provide scientific basis for future fisheries management in a warming world.

China has also conducted similar work in the Yellow Sea (YS) and obtained some preliminary results. Specifically, Jia et al. (2008) extracted and identified the well-preserved scales for major fish species in the YS and East China Sea (ECS) in the sediments, such as anchovy (*Engraulis japonicus*), small yellow croaker (*Pseudosciaena polyactis*), Pacific herring (*Clupea pallasii*), half-fin anchovy (*Setipinna taty*), white croaker (*Argyrosomus argentatus*), and firefly fish (*Acropoma japonicum*). Fur-

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ther, Huang et al. (2014) discussed the necessary conditions of preservation and spatial distribution of fish scales in the YS and ECS, and confirmed the reliability of using SDR to reconstruct the abundance of fish populations in historical periods. Moreover, Huang et al. (2016) analyzed the fluctuation characteristics of anchovy in the past 150 a and compared it with anchovy SDR in other regions around the Pacific, suggesting that the Pacific Decadal Oscillation (PDO) may be the principal driver for the simultaneous fluctuations of anchovy populations on a basin scale. The above-mentioned studies showed that before industrial fishing, fish populations were in constant fluctuation between high and low densities. In particular, the PDO was considered one of the most significant climate signals in the North Pacific (Newman et al., 2016), and it is well documented and largely associated with changes in fish populations (Ma et al., 2019). In reality, there are numerous papers on the relationships between the PDO and fish populations, and though some of the links between the two have been identified (Mantua et al., 1997; Mantua and Hare, 2002; Chavez et al., 2003; Salvatelli et al., 2018; Litzow et al., 2020; Li et al., 2020), no solid conclusion has been reached. Besides, Zhou et al. (2015) showed that the PDO may indirectly affect the anchovy fluctuations in the YS through changes in sea surface temperature (SST). In other words, the positive phase of the PDO (cold SST) corresponds to high anchovy abundance, while the negative phase of the PDO (warm SST) corresponds to low anchovy abundance. Hence, the PDO could be used to reveal the reasons behind anchovy fluctuations to some degree.

A large amount of evidence suggests that both climate variability and human activities are two major driving forces that affect fish population fluctuations (Tang et al., 2016; Lindegren et al., 2013; Ma et al., 2019). There are many reports on the dynamics of fish populations, especially concerning small pelagic fishes and climate variability (Checkley et al., 2017; Lindegren et al., 2018; Salvatelli et al., 2018). However, due to limited data availability, relevant research progress has been relatively slow. We do not yet have a complete understanding of the reasons behind fish population fluctuations, though some important findings have been made during this period. In this study, we further explore the relationship between the PDO and the anchovy in the YS on a larger spatial and longer temporal scale than previous research. We added an additional sampling site to the original sites used by Zhou et al. (2015), and we also greatly extended the length of the time series (i.e., from 1860–2005 AD to 1620–2005 AD). The results will contribute to further understand the history of anchovy and facilitate future predictions, thereby providing guidance for sustainable development and utilization of the anchovy in the YS.

2 Materials and methods

2.1 Study area and sample collection

Located between the Korean Peninsula and mainland China, the YS is a semi-closed shelf shallow sea in the western North Pacific. The average water depth is about 44 m with a maximum of 140 m, and the total area is about 400 000 km². The east side is affected by the Kuroshio Current (KC) and the Yellow Sea Warm Current (YSWC), a branch of the Tsushima Warm Current (TSWC); the west side is mainly affected by the Yellow Sea Coastal Current (YSCC) (Fig. 1). Generally, the SST in winter is lower than in other seasons, together with the stronger East Asian Winter Monsoon (EAWM), and hence both the YSWC and the YSCC are strengthened. Therefore, the YSWC and the YSCC have the greatest impacts on the YS in winter. For the past few dec-

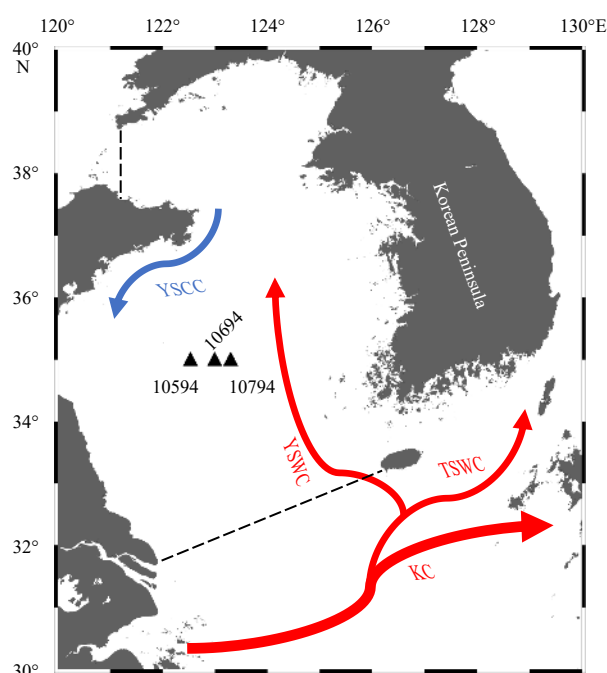


Fig. 1. The map of the study area in the Yellow Sea. Arrows with solid lines represent the ocean currents; warm currents (red) include Kuroshio Current (KC), Tsushima Warm Current (TSWC), and Yellow Sea Warm Current (YSWC); cold current (blue) is Yellow Sea Coastal Current (YSCC). Black triangles show the sampling Sites 10594, 10694 and 10794. Black dashed lines show boundaries between seas.

ades, the YS has become one of the most active fishing grounds in the world, with distinctive topography, hydrology, and productivity (Jin et al., 2010; Tang et al., 2016). The anchovy in the YS was a bycatch fishery prior to the 1980s (Zhao, 2006). The development of an industrial fishery soon after led to peak landings in the mid-to-late 1990s, and the subsequent increase in fishing effort resulted in the anchovy resources almost collapsing at the beginning of the 21st century (Zhao, 2006).

Jia et al. (2008) found that the central YS, as the main wintering ground for the anchovy, corresponds to the largest SDR. Additionally, Huang et al. (2014) showed that the wintering anchovy in the central YS can well represent the entire anchovy size in the YS. The sampling sites are shown in Fig. 1: these are designated as Sites 10594 (34°59.9'N, 122°29.9'E, water depth: 64 m), 10694 (35°0.0'N, 123°0.0'E, water depth: 70 m), and 10794 (35°0.1'N, 123°18.2'E, water depth: 76 m). The sedimentary samples consist of two periods: (1) 1860–2005 AD: obtained by a non-disturbance box sampler (30 cm×30 cm×100 cm) during the summer cruise of R/V *Beidou* in August 2005, with core lengths for samples at Sites 10594, 10694, and 10794 being 50 cm, 30 cm, and 31 cm, respectively (Huang, 2015); (2) 1620–1860 AD: obtained by a gravity corer (11 cm in diameter) during the summer cruise of R/V *Beidou* in August 2018, where the core lengths of samples at Sites 10594, 10694, and 10794 were 136 cm, 132 cm, and 128 cm, respectively. The sampling process was detailed in Huang et al. (2014). Overall, the three cores were gray-black, while the color intensity significantly changes with the increase in depth (above ~20 cm for light gray-black; below ~20 cm in dark gray-black) and were mainly composed of silty clay. In addition, the water content of the sediment decreases with the increase in the depth of the cores.

2.2 Extraction and identification of the fish scales

Cores were sub-sampled at 1-cm intervals for the top 30 cm, and at 2-cm intervals below 30 cm. Pre-treatment method for sub-samples was conducted as described by Holmgren (2001). In order to obtain enough scales to reconstruct a reliable time series, the amount of sediment used is an important criterion that must be considered. Unlike Salvatelli et al. (2019), who used less sediment, we used relatively large amount (the larger diameter of 11 cm of the gravity sampler used in this study) to avoid the low density of fish scales affecting the counting. In short, approximately 100–150 g of wet sub-sample was incubated with H₂O₂ solution (5%) for 3–5 h, then passed through a 250- μ m mesh sieve gently. Fish scales were identified using a light microscope by comparing fossil scales with modern scales from fresh fishes captured in the same area.

2.3 Chronology

In this study, the three cores ages were determined by ²¹⁰Pb dating during 1860–2005 AD (Yang et al., 2012; Huang et al., 2014). The sedimentation rates (SRs) of Sites 10594, 10694, and 10794 were estimated as 0.35 cm/a, 0.14 cm/a, and 0.10 cm/a, respectively. This was basically consistent with the results of Qiao et al. (2017), with the SR in the central YS estimated as 0.1–0.5 cm/a. Additionally, Kim et al. (1998) showed that the sea level of the YS has been relatively high for the past 7 000 a, and hence experienced a low SR with a relatively stable sedimentary environment. Therefore, we assumed that the SR in the central YS was relatively constant during the study period. The chronological time series required for this study was obtained by extrapolation (Liu et al., 2013).

2.4 Reconstruction of the anchovy stock

In order to avoid the interference of excessive counting of anchovy scale fragments, only one anchovy scale can be counted when an intact focus is found (Patterson et al., 2005). We adopted the method proposed by McClatchie et al. (2017) to calculate the SDR. That is, SDR was calculated using the following equation:

$$\text{SDR} = 1\,000 \times N \times \text{SR}, \quad (1)$$

where SDR is the scale deposition rate (1 000 cm⁻²·a⁻¹, according to the number of scales); N is the fish scale count in per unit volume (cm⁻³, according to the number of scales); and SR is the linear sedimentation rate in yearly (cm/a). Because the SR of Site 10794 was 0.10 cm/a, the SDR in all cores was interpolated to 10-a intervals. Then, we followed the method of Zhou et al. (2015) to reconstruct the anchovy stock. Specially, we first averaged the size of wintering anchovy by acoustic estimation (Jin et al., 2001; Zhao, 2006) and our SDR from 1985 to 2005 at 5-a intervals, and then to fit a regression model, which could be used to reconstruct longer time series of anchovy. Here, the SDR was based on the composition of two time periods (i.e., 1620–1860 AD and 1860–2005 AD) to greatly extend the length of the time series for the anchovy.

2.5 Analysis with the Ensemble Empirical Mode Decomposition (EEMD)

The anchovy stock fluctuation cycles of 50–70 a on a decadal time scale (Zhou et al., 2015) will inevitably induce some misunderstandings if the original PDO is used directly. To find multiscale consistency between anchovy stock, climatic indices,

and the oceanic variable, we used an EEMD approach (Wu and Huang, 2009). EEMD analysis is applicable to extracting meaningful signals from noisy, nonlinear, and nonstationary data. The data are decomposed by a filtering process into several limited Intrinsic Mode Functions (IMFs) with different timescales. The results of the EEMD are detailed in the supplementary materials (Figs S2–S7). We then conducted Pearson's correlation to explore the relationship between the anchovy and the PDO (with corresponding IMFs). Likewise, Pearson's correlations were conducted between the anchovy and other climate variables (with corresponding IMFs) and biogeochemical proxies.

3 Results

3.1 Fish debris composition in the cores

Similar to the results of Jia et al. (2008), the fish debris in the sediments were mainly composed of fish scales, and most of them were relatively complete in morphology, which helps confirm their species; only a very small amount of other fish debris has been found (i.e., bones, tooth, and vertebrae). We also identified these scales such as small yellow croaker, Pacific herring, half-fin anchovy, white croaker, and firefly fish, except for the most abundant anchovy scales. Here, considering the topic of this study, we do not discuss further fish scales for other species.

3.2 Fluctuation characteristics of the anchovy SDR

In general, the SDR has seven peak intervals for the past ~400 a: 1620–1650 AD, 1680–1700 AD, 1740–1760 AD, 1800–1820 AD, 1850–1870 AD, 1910–1930 AD, and 1970–1990 AD (Fig. 2).

Specifically, the SDR between cores was relatively high during the period 1620–1860 AD (the Little Ice Age, LIA); after the end of the LIA, the SDR between cores was maintained at a low level. Additionally, in the LIA, the mean SDR of Sites 10594, 10694, and 10794 showed decreasing trends in order eastward; after the LIA, the mean SDR of the three cores basically stayed the same (Fig. 3). Compared with LIA, the mean SDR after LIA is smaller.

In addition, due to the SDR between cores having zero values with a non-Gaussian distribution, this excludes the use of most parametric methods. Therefore, we conducted a non-parametric Spearman correlation analysis to confirm the relationship between the SDR from the three cores. The results showed that the SDR between cores had a significant positive correlation (Table 1).

3.3 Time series of the anchovy stock

According to results of the fitted linear regression equation, we found that there was a significant positive correlation between the SDR and the wintering anchovy size by acoustic estimation for the period from 1985 to 2005 (Fig. 4). Hence, this relationship enables us to effectively estimate the anchovy size in historical periods. We then used the regression equation to reconstruct the time series of the anchovy stock in the YS for the past 400 a (1620–2005 AD) (Table S1).

As shown in Fig. 5, the anchovy stock size fluctuated between $(0.13 \pm 0.57) \times 10^6$ t and $(6.10 \pm 1.28) \times 10^6$ t and continually alternated between high and low abundances. In general, the anchovy abundance was relatively high during the period 1620–1860 AD (LIA), and maintained at a lower level after ~1860 AD. Moreover, our sedimentary records show that anchovy stock has continued to decline since the late 1980s and collapsed by the early 2000s. This result is more consistent with previous reports based on anchovy landings.

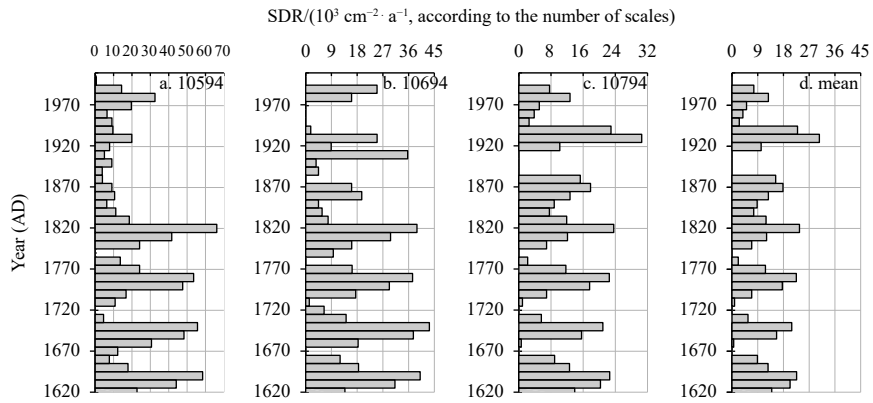


Fig. 2. Distribution of fish scale deposition rate (SDR) along the sediment cores and the mean for three cores in the Yellow Sea during the period 1620–2005 AD.

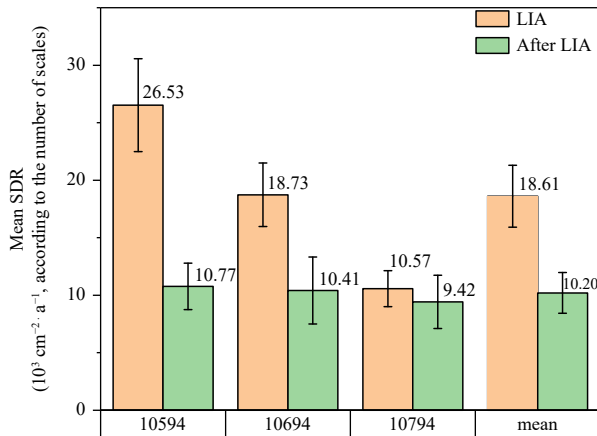


Fig. 3. The difference between three cores in the mean fish scale deposition rate (SDR) with standard error in the Yellow Sea during the period 1620–2005 AD. LIA is the abbreviation of the Little Ice Age (1620–1860 AD).

Table 1. Spearman’s correlation coefficients in scale deposition rate between sites of the Yellow Sea from 1620 AD to 2005 AD ($n=39$)

Site	10694	10794
10594	0.66****	0.63****
10694		0.58***

Note: Statistically significant correlations are indicated: ***, $p < 0.001$; ****, $p < 0.0001$.

4 Discussion

4.1 Preservation of anchovy scales in the sediments

Whether fish scales can be well-preserved in the sediments is the primary concern that needs to be considered when using the SDR to trace the dynamics of fish populations in historical periods. Previously, fish scales have been demonstrated to be well-preserved in the sediments for the past ~150 a (Jia et al., 2008; Huang et al., 2014). We also examined this point based on the scale integrity index (SII) proposed by Salvattecchi et al. (2012) (i.e., the ratio of whole relative to fragmentary scales for each sample). In fact, most of the fish debris in the sediments were composed of intact anchovy scales, as shown in the Section 3.1. Therefore, we did not strictly rate for the anchovy scales as described by Salvat-

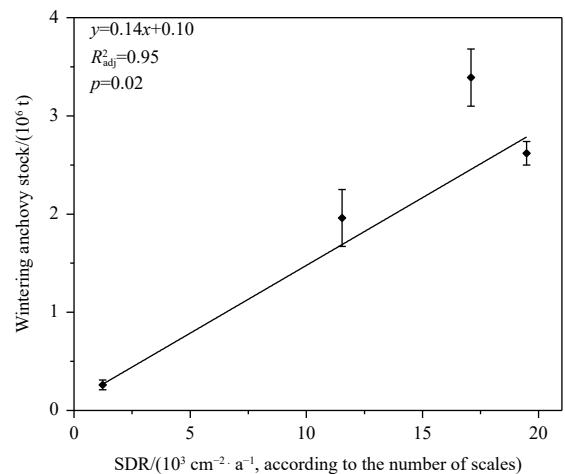


Fig. 4. The relationship between the wintering anchovy stock estimated from acoustic investigations (Jin et al., 2001; Zhao, 2006) and fish scale deposition rate (SDR) in sediment cores in the Yellow Sea from 1985 AD to 2005 AD. The straight line is the fitted linear regression between the wintering anchovy stock and the SDR and was used to reconstruct the historical anchovy stock.

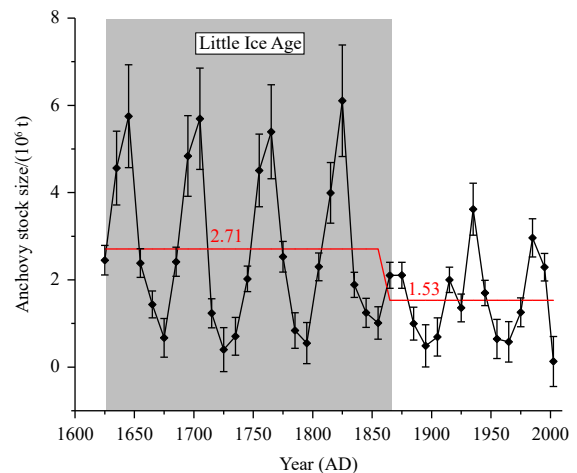


Fig. 5. The reconstructed anchovy stock in the Yellow Sea from 1620 AD to 2005 AD. The red line indicates the mean values.

teci et al. (2012). Here, we improved on the SII based on Salvateci et al. (2012). That is, we used the average values in the SII of all samples in each core to evaluate the effect of degradation. These ratios were 84% for Core 10594, 81% for Core 10694, and 78% for Core 10794, indicating that the scales were well preserved with less degradation. Moreover, the degradation rate of fish scales would likely increase with depth. However, the accumulation rate of the SDR on average for three cores was significantly positively correlated with age (Fig. S1), indicating that the degradation of scales may be weak.

4.2 Relationship between the anchovy stock and the PDO

During the period 1620–2005 AD, there was a weak positive correlation between the reconstructed anchovy and the PDO (Fig. 6). Although the specific causes for this difference are unclear, we speculate that the following two factors may be involved. First, the results of Shen et al. (2006) suggested that the PDO mainly oscillated in a quasi-centennial period (75–115 a) before 1850 AD, and in a pentadecadal (50–70 a) period after 1850. In this study, the average period of the PDO (the fifth component, IMF 5) selected by EEMD was about 76 a, in line with the quasi-centennial pattern. Second, the impact of the LIA on the anchovy may significantly exceed the PDO, masking the signal of the PDO.

In order to better determine the role of the LIA, we made a comparison to explore the impacts of the LIA and after the LIA on anchovy. In the LIA, anchovy had no correlation with the PDO, while a strong positive correlation existed with PDO after the LIA (Fig. 7), which is consistent with the research of Zhou et al. (2015). This suggests that the LIA may have a significant impact on the PDO, with large regime shifts resulting in the anchovy fluctuations. However, more evidence is needed to support this argument. As a consequence, we suggest that the positive correlation between the anchovy and the PDO is reliable, though there are noises to varying degrees.

It is generally accepted that the PDO is negatively correlated with SST in the central-western North Pacific, i.e., the SST is below average during the positive phase of the PDO, and vice versa in the eastern North Pacific (Mantua and Hare, 2002; Newman et al., 2016). As a wintering ground for the anchovy, the central YS is located at the intersection of the YSWC and the YSCC. During the positive phase of the PDO followed by colder periods, both the

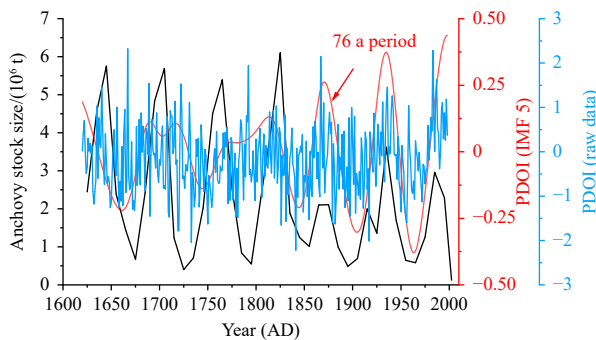


Fig. 6. Relationship of the reconstructed anchovy stock in the Yellow Sea with the Pacific Decadal Oscillation index (PDOI) (data were obtained from Shen et al. (2006)). The fifth Intrinsic Mode Function (IMF 5) with 76 a period by Ensemble Empirical Mode Decomposition during the 1620–1998 AD (red vertical axis) was used ($r=0.29$, $p=0.07$, $n=38$). The raw data of PDOI during 1620–1998 AD were adopted.

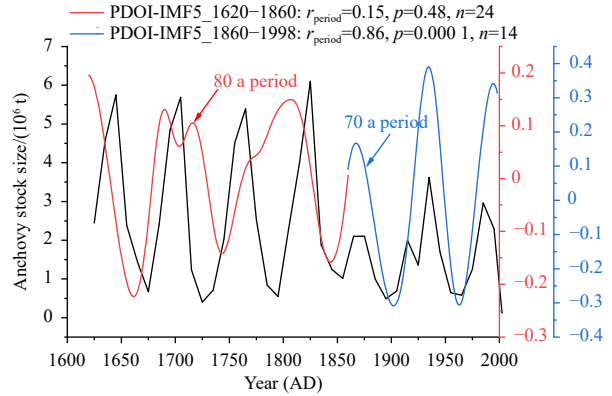


Fig. 7. Relationship of the reconstructed anchovy stock in the Yellow Sea with the Pacific Decadal Oscillation index (PDOI) (data were obtained from Shen et al. (2006)). The fifth Intrinsic Mode Function (IMF 5) with 80 a and 70 a period by Ensemble Empirical Mode Decomposition during the Little Ice Age (LIA) (1620–1860 AD) and after the LIA (1860–1998 AD) was used, respectively.

YSWC and the YSCC are strengthened (Yuan and Hsueh, 2010), and nutrients are enriched in the central YS, providing favorable conditions for wintering anchovy.

Based on the landings, Izquierdo-Peña et al. (2019) and Oozeki et al. (2019) found that the anchovy populations in the Humboldt and Kuroshio Currents have fluctuated in-phase over the past few decades. They suggest that this mode may be controlled by large-scale climate variability. In particular, the Peruvian anchovy was greatly reduced during the LIA in the Humboldt Current (Gutiérrez et al., 2009), which is opposite to the anchovy in the YS (Fig. 5). In the meantime, the Peruvian anchovy showed signs of migrating southward during the LIA (Gutiérrez et al., 2009), which may also explain our results to some degree. In other words, the intensified EAWM led to the strong YSWC (Hu et al., 2012; Zhang et al., 2019), with a relatively high SST during the LIA (Li et al., 2020), and the anchovy stock around the seas of Japan (lower SST) may have migrated southward to the central YS for overwintering, as described by Zhou et al. (2015). Therefore, anchovy abundance in the YS was relatively high during the LIA. Moreover, temperature change has important effects on the reproduction, growth, and migration for the anchovy. Taken together, our suggestion is that the responses of the anchovy to the PDO have both indirect effects on food availability and direct effects on physiological behavior.

4.3 Fishing effects on the anchovy stock

In general, anchovy was maintained at relatively high density before the 1980s (with moderate fishing pressure), though some fluctuations in abundance were inevitable. The traditional viewpoint was that overfishing was the fundamental reason for the rapid decline of the anchovy in the YS (Zhao, 2006). However, the long-term changes in reconstructed anchovy stock in our results show that there were continuous fluctuations before the 1980s, when fishing pressure was approximately zero (Fig. 5). Furthermore, research in other Pacific locations also indicated natural fluctuations for the anchovy populations based on the SDR with little or no fishing pressure (Baumgartner et al., 1992; Valdés et al., 2008; Guíñez et al., 2014; McClatchie et al., 2017; Kuwae et al., 2017). Therefore, the reason behind the anchovy depletion was possibly different from the traditional view, and that it may be the

result of natural fluctuations. Nevertheless, this does not suggest that the decline in anchovy abundance has nothing to do with overfishing.

In brief, fishing may lead to an age truncation effect (Hsieh et al., 2006; Deyle et al., 2013) and changes in life history traits (Kuparinen et al., 2016; Britten et al., 2016; Pinsky and Byler, 2015). Both of these can magnify the sensitivity of fish populations to climate variability (Planque et al., 2010), thus leading to stock fluctuations that are greater than just climate impact alone. This may increase variability of the exploited populations, reducing the capacity of populations to buffer climate events, and hence increased risks of collapse. Particularly, with the increase in the number of fishing vessels with greater horsepower, combined with the updating of fishing gears and methods (Tang et al., 2016), the anchovy resources in the YS drastically declined from the mid-to-late 1990s to the early 2000s (Zhao, 2006). This combination of overfishing and unfavorable climate conditions likely led to the decline that the YS anchovy stock is currently experiencing.

4.4 Potential mechanism under anchovy fluctuations

Understanding the mechanism driving fish population dynamics is essential to accurately predicting changes under climate variability and overexploitation. To date, several hypotheses (e.g., bottom-up and top-down control) have been proposed to explain the fluctuations in fish populations. There is evidence that in the absence of fishing, many large and highly productive marine ecosystems such as those in the North Pacific and North Atlantic are subject to bottom-up processes that are also widely recognized as a response to climate variability (Chavez et al., 2003; Ware and Thomson, 2005; Greene and Pershing, 2007; Pitois et al., 2012; Salvatelli et al., 2018; Capuzzo et al., 2018). In contrast, other studies have shown that bottom-up processes would switch to top-down control and potentially lead to trophic cascading effects on food webs in marine ecosystems (Worm and Myers, 2003; Frank et al., 2005; Möllmann et al., 2008). In fact, these hypotheses are not mutually exclusive, making it more difficult to elucidate fish population fluctuations. However, with the accumulation of evidence, some oceanographers are gradually inclined to accept the view of multi-factor control (Tang et al., 2016; Mcowen et al., 2015), though most do not deny the possibility of a single dominant factor. Undoubtedly, this provides a new way for us to understand fish population fluctuations from a novel perspective.

Extensive studies have shown that global warming results in a deeper thermocline and enhanced water column stratification with a shallow mixed layer, thereby reducing the supply of nutrients to the euphotic zone and thus lowering fish productivity (Roemmich and McGowan, 1995; Behrenfeld et al., 2006; Doney

et al., 2012; Rykaczewski and Dunne, 2010). On the one hand, though the YS lacks coastal upwelling, the EAWM has a significant impact on this area that may provide a function similar to coastal upwelling. In the western North Pacific, the winter monsoon may affect the biological productivity by controlling the mixed layer depth. That is, the strong winter monsoon brings greater nutrient input into the euphotic zone and ultimately increases ecosystem productivity and hence fish productivity. On the other hand, the overall shoaling in the mixing layer due to intensified upper-ocean stratification caused by surface warming affects phytoplankton dynamics through controlling the availability of nutrients and hence biological productivity (Jang et al., 2011; Jacox et al., 2015) and ultimately fish abundance. Moreover, in order to identify the reasons behind the anchovy fluctuations in the YS, we explored the relationship between the anchovy and environmental proxies from 1860 AD to 2005 AD. During the period 1860–1950 AD, the anchovy and proxies for primary and secondary productivity were in good agreement (Table 2).

Since the People's Republic of China was founded in 1949, Chinese marine fisheries entered a new era (Shen and Heino, 2014). From 1950, especially since the end of the 1980s, the above-mentioned consistency has been almost completely absent due to the intensive fishing (Fig. 8). Consequently, we suggested that anchovy fluctuations are regulated by bottom-up effects via climate variability under moderate fishing pressure. In other words, climate variability seems to indirectly influence the anchovy stock through bottom-up control via a cascading effect from the changes in the PDO. The impacts of these changes on the hydrodynamic features of the YS in turn influence the productivity of plankton prey for the anchovy.

Here, taking the anchovy in the YS as a case, we attempted to make a reasonable explanation of anchovy fluctuations based on our findings and perspectives (Fig. 8; Table 2). Overall, a physical-biological mechanism of fluctuations in anchovy abundance could be constructed based on a bottom-up control hypothesis under lessened (or absent) fishing pressure (Fig. 9). That is, when the PDO is in a positive phase, the Aleutian Low Pressure is intensified, followed by strong EAWM results in low SST, which drives weaker stratification of the upper water column. This enhances mixing in some parts of the ocean with more nutrient availability, increasing biological productivity with more food availability and thus high anchovy abundance.

However, it is important to emphasize that the PDO itself does not directly affect anchovy–sardine fluctuations. For example, Lindegren et al. (2013) suggested that fluctuations of anchovy–sardine in the California Current System are explained by interacting density-dependent processes (i.e., through species-

Table 2. Pearson's correlation coefficients between anchovy stock, climate variables and biogeochemical proxies from 1860 AD to 1950 AD ($n=10$)

	PDOI (IMF 5)	ALPI (IMF 5)	EAWMI (IMF 6)	SSTA (IMF 6)	Detrended lgBra	Detrended lgCho
Anchovy stock	0.81**	0.68	0.52	-0.29	0.18	0.47
PDOI (IMF 5)		0.98**	0.57	-0.26	0.20	0.46
ALPI (IMF 5)			0.65	0.11	0.26	0.82
EAWMI (IMF 6)				-0.90**	-0.49	-0.44
SSTA (IMF 6)					0.41	0.63
Detrended lgBra						0.75*

Note: PDOI is abbreviation of Pacific Decadal Oscillation index; ALPI, Aleutian Low Pressure index; EAWMI, East Asian Winter Monsoon index; SSTA, sea surface temperature anomaly. *Bra* represents brassicasterol content; *Cho*, cholesterol content. IMF n , n th Intrinsic Mode Function by Ensemble Empirical Mode Decomposition. Statistically significant correlations are indicated: *, $p<0.05$; **, $p<0.01$.

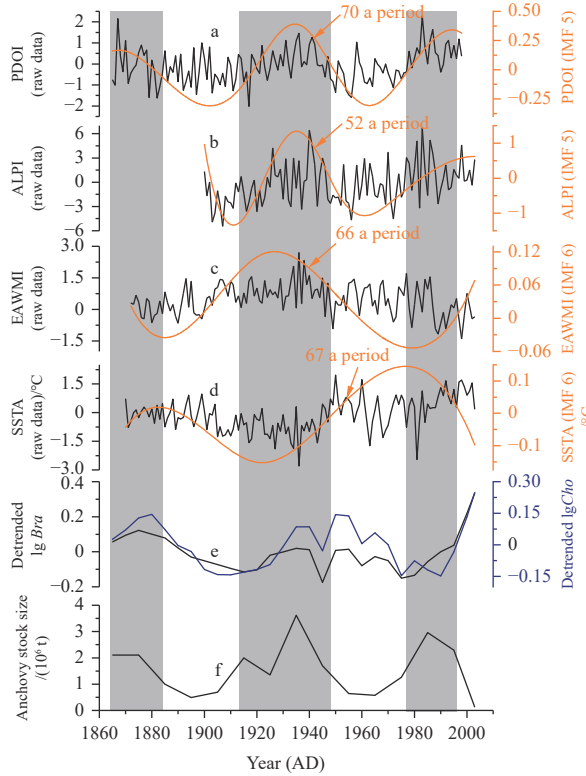


Fig. 8. Comparison of the reconstructed anchovy stock with environmental variables in the Yellow Sea. a. The data of Pacific Decadal Oscillation index (PDOI) were obtained from Shen et al. (2006); b. the Aleutian Low Pressure index (ALPI) from Surry and King (2015); c. the East Asian Winter Monsoon index (EAWMI) from Zhang et al. (2013); d. the winter (average in January–March) sea surface temperature anomaly (SSTA) with a resolution of $1^{\circ} \times 1^{\circ}$ (latitude \times longitude) for the range 32° – 37° N, 120° – 125° E from Rayner et al. (2006); e. the data of biomarkers in the Core 10694 from Xing et al. (2009). The orange lines indicate the selected Intrinsic Mode Functions (IMFs) with different periods by Ensemble Empirical Mode Decomposition. The brassicasterol content (*Bra*) could be used to represent diatom productivity (primary productivity), and the cholesterol content (*Cho*) for zooplankton abundance (secondary productivity). The gray rectangles represent periods when the anchovy stock dominated.

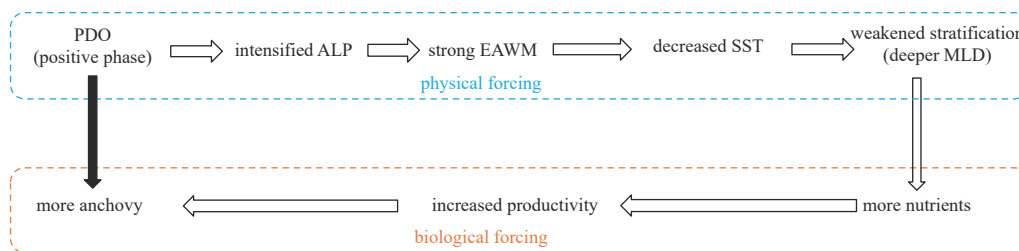


Fig. 9. Schematic illustrating the potential “atmosphere–ocean” pattern based on a bottom-up hypothesis for anchovy stock in the Yellow Sea. Closed and open arrows indicate direct and indirect effects, respectively. PDO is the abbreviation of Pacific Decadal Oscillation; ALP, Aleutian Low Pressure; EAWM, East Asian Winter Monsoon; SST, sea surface temperature; MLD, mixed layer depth.

specific life-history traits) and climate forcing. In the Humboldt Current system, changes in the 3D habitat driven by large-scale climate forcing and regional processes were the main drivers of anchovy–sardine fluctuations (Salvatteci et al., 2018). These studies suggest that the mechanism behind small pelagic fish fluctuations are more complicated than previously stated in other studies (Chavez et al., 2003). Hence, this present study is still a preliminary result and needs more supporting evidence in the near future.

5 Conclusions

We reconstructed the time series of the anchovy stock in the YS over the past 400 a. Like many small pelagic fishes, the an-

chovy has frequently experienced historic “boom and bust” cycles between very high and very low abundance. We first proposed a conceptual framework of potential driving forces. We suggest that the PDO may be the principal driving force for the long-term changes in the anchovy stock under moderate fishing pressure. However, we should also realize that under the combined pressures of climate variability and overfishing, the decline of the anchovy abundance is not simply attributed to either of them. Therefore, a comprehensive consideration of the relative effects of climate and fishing on the dynamics of the anchovy could ultimately achieve the goal of scientific management and sustainable utilization. Particularly, climate variability should be integrated into the development of adaptive management

strategies of anchovy. In the future, we plan to collect data for other biogeochemical proxies as well as observational data, and to conduct integrated studies to further verify the reliability of the mechanism proposed by the present study.

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Supplementary information:

Fig. S1. Variation in accumulation of anchovy scale deposition rate (SDR) in the Yellow Sea.

Fig. S2. Results of Pacific Decadal Oscillation index (PDOI) by Ensemble Empirical Mode Decomposition (EEMD) during 1620–1998 AD.

Fig. S3. Results of Pacific Decadal Oscillation index (PDOI) by Ensemble Empirical Mode Decomposition (EEMD) during 1620–1860 AD.

Fig. S4. Results of Pacific Decadal Oscillation index (PDOI) by Ensemble Empirical Mode Decomposition (EEMD) during 1860–1998 AD.

Fig. S5. Results of Aleutian Low Pressure index (ALPI) by Ensemble Empirical Mode Decomposition (EEMD) during 1900–2003 AD.

Fig. S6. Results of East Asian Winter Monsoon index (EAWMI) by Ensemble Empirical Mode Decomposition (EEMD) during 1872–2003 AD

Fig. S7. Results of sea surface temperature anomaly (SSTA) by Ensemble Empirical Mode Decomposition (EEMD) during 1870–2003 AD.

Table S1. The reconstructed anchovy stock in the Yellow Sea from 1620 to 2005 AD.

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