



Contrasting spawning temperature optima: Why are anchovy and sardine regime shifts synchronous across the North Pacific?

Akinori Takasuka^{a,*}, Yoshioki Oozeki^a, Hiroshi Kubota^a, Salvador E. Lluch-Cota^b

^aNational Research Institute of Fisheries Science, Fisheries Research Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan

^bFisheries Ecology Program, Centro de Investigaciones Biológicas del Noroeste, P.O. Box 128, La Paz, Baja California Sur, 23000, Mexico

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ABSTRACT

Anchovy and sardine are both abundant small pelagic fish that have exhibited out-of-phase population oscillations in both the western boundary current region off Japan and the eastern boundary current upwelling region off California. These species alternations could indicate approximately synchronous patterns (with some variations in timing between ecosystems) despite the reversed temperature regimes for certain periods across the North Pacific, at least until recently. Here we suggest a contrasting pattern of temperature optima for anchovy and sardine spawnings between the opposite sides of the North Pacific as a possible mechanism of the synchronous phases of species alternations. Spawning temperature optima were examined for Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*), based on occurrence of eggs and larvae in relation to sea surface temperature. The analyses were based on an updated long-term data set of egg and larval surveys from 1978 to 2004 (102,660 net tows) in the western North Pacific. The ratio of relative frequencies of plankton net samples that are positive for eggs or larvae versus all samples was calculated for temperature intervals of 0.1 °C for both species. This spawning temperature index exceeded 1.0 (baseline for optimum) from ca. 15 to 28 °C with a mid-point at 22 °C for anchovy and ca. 13–20 °C with a marked peak at 16–17 °C for sardine. Patterns of spawning temperature clearly show “warm” and “eurhythmic” Japanese anchovy and “cool” and “stenothermal” Japanese sardine in the western North Pacific. This relationship between anchovy and sardine showed a marked contrast to earlier published reports on the spawning temperature optima of northern anchovy (*E. mordax*) and California sardine (*S. sagax*) in the California Current system. The spawning temperature optimum appears to be species-specific rather than genus-specific. The reversed species-specific temperature optima of anchovy and sardine under the reversed temperature regimes could provide a possible theoretical solution to the synchronous anchovy and sardine regime shifts across the North Pacific.

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1. Introduction

Species-specific responses to environmental factors could provide a key to explain variations of population dynamics among different species in the field of comparative ecology. Here, we suggest a contrasting pattern of temperature optima for anchovy and sardine spawnings between the opposite sides of the North Pacific as a possible biological mechanism of the synchronous anchovy and sardine alternations for certain periods across the North Pacific at multi-decadal scales.

Anchovy and sardine are small pelagic fish that have displayed mysterious alternations in population abundances. Rarely are both species simultaneously abundant or rare simultaneously within a single ecosystem. When sardine become abundant, anchovy be-

come scarce; however, after a few decades, the dominant species starts to alternate (Fig. 1). Such patterns have been pointed out to be approximately synchronous (but with some variation in timing among ecosystems; see below) over the last century across the Pacific—off Japan, California, Peru, and Chile, at least until recently (Kawasaki, 1983; Lluch-Belda et al., 1989, 1992; Schwartzlose et al., 1999; Chavez et al., 2003; Alheit and Niquen, 2004). Past studies confirmed climate impacts on marine ecosystems (McGowan et al., 1998; Yasuda et al., 1999; Attrill and Power, 2002; McFarlane et al., 2002; Chavez et al., 2003; Roessig et al., 2004; Alheit et al., 2005). In the western North Pacific, Japanese sardine (*Sardinops melanostictus*) stock has virtually collapsed, while Japanese anchovy (*Engraulis japonicus*) stock has flourished since the late 1980s (Schwartzlose et al., 1999; Yatsu et al., 2003). These species alternations have also corresponded to the climate-induced ocean regime shifts, as revealed by climate indices such as the Pacific Decadal Oscillation (PDO) index (Mantua et al., 1997; Mantua

* Corresponding author. Tel./fax: +81 45 788 7636.

E-mail address: takasuka@affrc.go.jp (A. Takasuka).

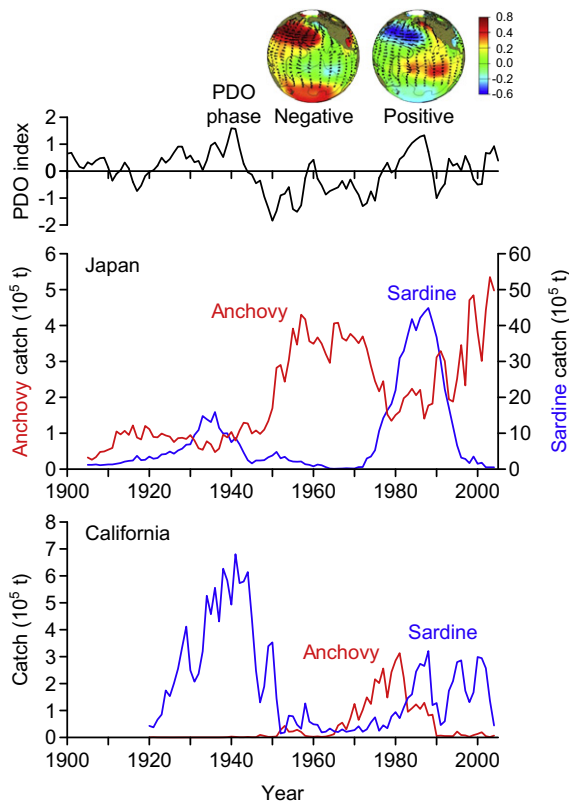


Fig. 1. Anchovy and sardine species alternations in the western and eastern North Pacific, recorded in catch histories of Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) off Japan and northern anchovy (*Engraulis mordax*) and California sardine (*Sardinops sagax*) off California in relation to the Pacific Decadal Oscillation (PDO) index. Catch data from the Gulf of California are included since the late 1970s. The PDO index is defined as the leading principal component of monthly SST anomalies in the North Pacific, poleward of 20°N (the monthly mean global average SST anomalies were removed) (Mantua et al., 1997; Mantua and Hare, 2002). Typical anomaly patterns of wintertime sea surface temperature (colors), sea level pressure (contours), and surface wind stress (arrows) are indicated for the positive and negative phases of the PDO index.

and Hare, 2002; Fig. 1). Such patterns of alternations might be called anchovy and sardine regime shifts. The term “anchovy/sardine regime” may seem sometimes confusing, in light of their different maximum biomass levels, possible time lags of biological responses to ocean regime shifts, etc. However, the “anchovy/sardine regime” here focuses on peaks observed in the long-term catch history and simply refers to a few decades when the anchovy/sardine population level is higher than before and after that period and the counterpart species population level is the reverse. For example, a “sardine regime” extended from the mid-1970s to the mid-1990s, when sardine populations flourished and anchovy populations collapsed simultaneously (Fig. 1). In this view, the western North Pacific has historically experienced sardine regimes when the PDO index is positive and the sea surface is relatively cool off Japan, and anchovy regimes when the PDO index is negative and the sea surface is relatively warm off Japan. That is, the warm anchovy regime has shifted to the cool sardine regime and back. However, the biological processes and dominant factors linking climate changes to alternating species dominance are not well identified. Various hypotheses have been developed to address single species dynamics; in particular, food-based scenarios that focus on bottom-up control seem most prevalent at present for various ecosystems, and this holds true for studies on Japanese sardine (Kawasaki, 1995; Noto and Yasuda, 1999; Yatsu et al., 2005). Yet, most theories have failed to explain several key issues for multi-

species dynamics, for example, why anchovy flourish and sardine collapse or vice versa under the same ocean regime.

The “optimal growth temperature” hypothesis (Takasuka et al., 2007) focuses on the differential optimal temperatures for growth rates during early life stages of Japanese anchovy and Japanese sardine, which were detected to be 22.0 and 16.2 °C, respectively, in the western North Pacific. This hypothesis posits that subtle environmental temperature shifts between these species-specific optimal growth temperatures can lead to dramatic shifts between “warm” anchovy and “cool” sardine regimes in the western North Pacific.

This temperature-based idea has been extended here to address the “East–West paradox” of species alternations: Why are anchovy and sardine regime shifts synchronous despite the reversed temperature regimes for certain phases between the western and eastern sides of the Pacific? In the western North Pacific (the western boundary current region off Japan), Japanese anchovy experienced their high-biomass phases and simultaneously Japanese sardine experienced their low-biomass phases before the mid-1920s, between the mid-1940s and the mid-1970s, and after the mid-1990s (Fig. 1). These anchovy regimes approximately correspond to negative PDO periods. In turn, the sardine regimes were identified between the mid-1920s and the mid-1940s and between the mid-1970s and the mid-1990s with a marked peak around the late 1980s, corresponding approximately to positive PDO periods. In the eastern Pacific (the eastern boundary current upwelling region off California), northern anchovy (*Engraulis mordax*) populations started to increase around the mid-1960s and decrease around the early 1980s, while California sardine (*Sardinops sagax*) populations were abundant between the early 1920s and the late 1940s. The California sardine populations started to increase again around the late 1970s and have been abundant in recent years, although this sardine regime was mainly due to the increase of the populations in the Gulf of California. Thus, the anchovy and sardine regimes in the eastern North Pacific tend to be observed mainly during the positive and negative PDO periods, respectively, although the recent trends off California is out of these trends. Of note is that during the same period, temperature regimes were roughly reversed between the opposite sides of the Pacific (Mantua et al., 1997; Chavez et al., 2003; Fig. 1). In the eastern North Pacific, the local SST anomalies tend to be warmer during positive PDO periods and cooler during negative PDO periods, in contrast to the pattern in the western North Pacific. These mean that for certain periods, both anchovy species experienced their high-biomass phases mainly during negative PDO periods, and that both sardine species did the same mainly during positive PDO periods despite the reversed temperature regimes, although some time lags were observed in the peaks of population abundance between these two ecosystems. In the present paper, we regard these phenomena that occurred for certain periods as “synchronous anchovy and sardine regime shifts” between the opposite sides of the North Pacific, although the patterns have not consistently been synchronous for the entire period (esp. the most recent two decades). The background is still under debate for the synchronous alternations, which has been regarded as a paradox in relation to the opposed temperatures (McFarlane et al., 2002; Bakun and Broad, 2003; Chavez et al., 2003).

Lluch-Belda et al. (1991) compared preferred temperatures for spawning between northern anchovy (*E. mordax*) and California sardine (*S. sagax*) in the California Current system, based on the 39-year data set of the egg and larval surveys by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). They revealed substantial spawning temperature differences between northern anchovy and California sardine. Temperatures in the spawning grounds primarily influence survival rates of eggs and growth rates and physiological conditions of larvae after hatching

(Blaxter, 1992; Meekan et al., 2003; Takasuka and Aoki, 2006). Species-specific spawning temperatures should be determined for better understanding of population dynamics of pelagic fish. Despite such a common recognition, past studies often assumed that temperature effects operated on the fish through changes in the type or amount of food (plankton) available to the fish—e.g. through a bottom-up trophodynamic process. This assumption may have been made because if environmental spawning temperature were the dominant (and direct) factor responsible for the alternation of anchovy and sardine in one region, and the near synchrony across regions, it would require that similar anchovy and sardine species would respond differently to temperature changes, which seemed to be an unreasonable assumption. However, perhaps the two different anchovy species have very different temperature optima for spawning, and likewise for the two different sardine species.

The present study was designed to examine species-specific temperature optima for anchovy and sardine with field-based evidence as a step toward basin-scale synthesis of anchovy and sardine fluctuations. We analyzed the updated long-term data set of the egg and larval surveys that were conducted off the Pacific coast of Japan to establish temperature optima of spawning of Japanese anchovy and Japanese sardine in the western North Pacific. These results were then compared with northern anchovy and California sardine spawning temperature optima obtained by Lluch-Belda et al. (1991) in the eastern North Pacific. We anticipate finding a simple theoretical solution to the large-scale synchronous phases of anchovy and sardine regime shifts despite the reversed temperature regimes across the North Pacific.

2. Materials and methods

The long-term data set of the egg and larval surveys was organized and updated to examine occurrence of Japanese anchovy and Japanese sardine eggs and larvae in relation to sea surface temperature. Monthly egg and larval surveys have been historically conducted by the national research institutes of Fisheries Research Agency and the prefectural experimental stations or fisheries research institutes off the Pacific coast of Japan (Fig. 2). In these surveys, a conical or cylindrical-conical plankton net with an opening mouth ring diameter of 45 or 60 cm and a mesh size of 0.330 or 0.335 mm was towed from 150 m or just above the bottom (if bottom depth <150 m) to the surface, to estimate the density of eggs and larvae of important commercial fish species. Sea surface temperature (SST) was measured simultaneously at the sampling stations. The survey areas and stations were organized to cover the potential spawning grounds of Japanese anchovy and sardine with an approximately consistent effort throughout the year, although

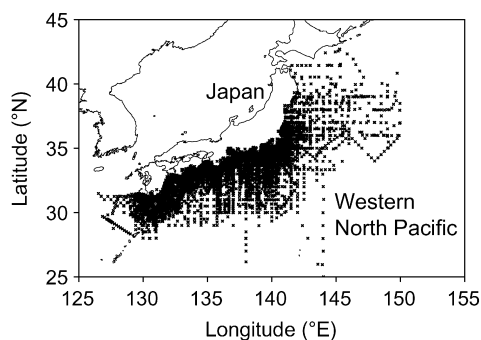


Fig. 2. Location of sampling stations of the egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. All sampling stations, including fixed and unfixed stations, are shown as crosses. A total of 102,660 samples of a vertical plankton net tow were obtained.

monthly surveys tended to be slightly more intensive during early spring. We adopted the recent 27-year data set comprising a total of 102,660 plankton net samples (tows) from 1978 to 2004 because over 3000 samples are taken each year during this period.

Species-specific temperature optima were determined for Japanese anchovy and sardine by the method of Lluch-Belda et al. (1991) to compare our results with those obtained in the California Current system through a uniform approach. This method focuses on occurrence of eggs and larvae (i.e. presence/absence) standardized by sampling effort in relation to a single factor (SST), based on the assumption that occurrence of eggs and larvae indicates spawning. A similar method has been adopted as a tool to characterize the spawning habitat of small pelagic fish with regard to physical or biological parameters (e.g. Twatwa et al., 2004; van der Lingen et al., 2005). Plankton net sample where eggs and/or larvae occurred was labeled a “positive” sample. All samples ($n = 102,660$) were grouped by SST intervals of 0.1 °C and sorted for “positive” samples of anchovy and sardine eggs and larvae (four categories of species-stage combination) independent of spatial location, month, or year. That is, each sample was assigned to one of 350 intervals from 0.0 to 35.0 °C. Then, the relative frequency (%) for each SST interval was calculated for only “positive” samples—those in which the species-stage combination was present. A similar relative frequency was calculated using all samples (including both positives and negatives). The latter provides an estimate of the distribution of sampling effort by SST. The ratio (quotient) of relative frequencies of “positive” samples versus all samples was regarded as a proxy for the temperature optimum for occurrence of eggs and larvae (hereafter called “spawning temperature index”) for each SST interval, under the assumption that the index distribution patterns (quotient curves) constructed by the data pooled over the long-term (1978–2004) represent species-specific spawning temperature patterns (see Discussion). A ratio of 1.0 for this index indicates that the species-stage combination was present in samples of that particular SST interval at the ratio expected if the eggs or larvae were distributed randomly by temperature (e.g. independent of SST). Ratios that exceed 1.0 indicate temperatures where egg or larval presence is greater than expected if they are independent of temperature. Thus, quotient indices that exceed 1.0 were assumed to be preferable or selected (whether active or passive) for spawning (Lluch-Belda et al., 1991). The densities of anchovy and sardine eggs were estimated for each positive sample, and the egg-density-weighted mean SSTs were calculated for all positive samples pooled for each species.

In the above analysis, samples were pooled for the whole data set period of 1978–2004 to detect species-specific patterns. Subsequently, the index was also calculated for the two divided periods of 1978–1991 (mainly sardine regime) and 1992–2004 (mainly anchovy regime) in the same way for the whole period. Spawning temperature patterns were then compared between these two periods to examine the effects of the period (i.e. phase or regime) on the spawning temperature patterns.

3. Results

Of the 102,660 tow samples taken from 1978 to 2004, Japanese anchovy eggs were found in 24,944 (24.3%) and larvae in 24,644 (24.0%) samples. Japanese sardine eggs occurred in 10,939 (10.7%) samples and larvae in 12,623 (12.3%) samples. Frequency distributions of SST considering all samples in number seemed to be unimodal with the peak at around 19–20 °C (Fig. 3a). The number of positive samples for anchovy eggs and larvae increased to ca. 16 °C, remained at a nearly constant number between 16 and 18 °C, and gradually decreased to almost zero at >30 °C. The number of positive samples for sardine eggs and larvae seemed to

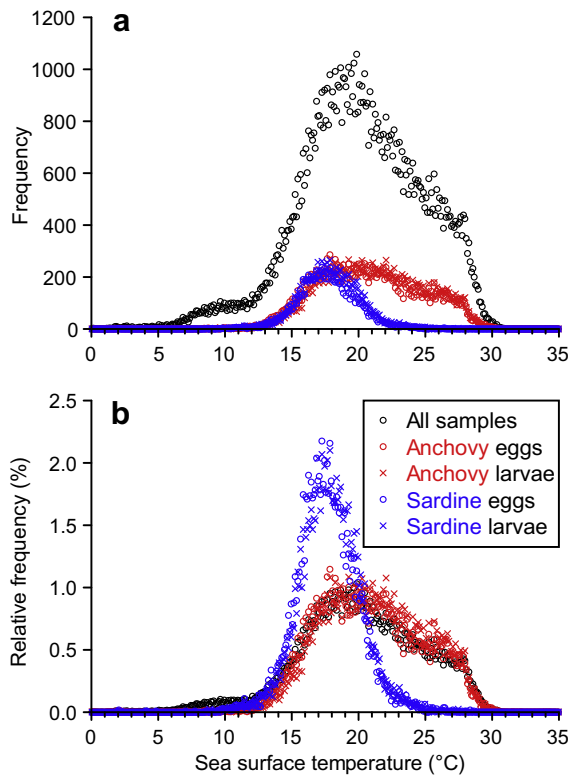


Fig. 3. Frequency distributions (a) and relative frequency distributions (b) of plankton net samples organized into the sea surface temperature (SST) intervals of 0.1 °C in the egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. The data are shown separately for all samples ($n = 102,660$), samples positive for anchovy eggs ($n = 24,944$), anchovy larvae ($n = 24,644$), sardine eggs ($n = 10,939$), and sardine larvae ($n = 12,623$).

follow the anchovy patterns at temperatures up to 18–19 °C, but rapidly decreased at higher temperatures with few positive sardine samples beyond 22 °C. Relative frequency at an interval of 0.1 °C marginally reached 1.0% at peaks around 19–20 °C for all samples and anchovy eggs and larvae, while it exceeded 2.0% for sardine eggs and larvae at around 17–18 °C (Fig. 3b).

The differences in distribution of the spawning temperature index were evident between Japanese anchovy and sardine (Fig. 4a). Although anchovy and sardine had unimodal distributions of the index, anchovy showed a plateau-like mode and sardine showed a steeply peaked mode. The spawning temperature index for anchovy eggs and larvae started to increase at ca. 9 °C. The index value for anchovy increased gradually until it exceeded 1.0 at 15–17 °C, and then continued to be stable with index values between 1.0 and 1.3 until the SST reached ca. 27 °C. Similarly, the index for sardine eggs and larvae also started to increase at ca. 10 °C. However, the index for sardine increased rather rapidly, with peak spawning indices >2.5 and >2.0 for sardine eggs and larvae, respectively, at 16–17 °C. The sardine index decreased rapidly at warmer temperatures. The SSTs at which the index values exceeded 1.0 ranged from 15.4 to 27.8 °C (ca. 12.4 °C range) for anchovy eggs, from 17.6 to 28.0 °C (ca. 10.4 °C range) for anchovy larvae, from 13.2 to 20.2 °C (7.0 °C range) for sardine eggs, and from 13.7 to 20.5 °C (6.8 °C range) for sardine larvae (Fig. 5). The mid-point of the SST range with the index >1.0 was at 21.6 °C, 22.8 °C, 16.7 °C, and 17.1 °C for anchovy eggs, anchovy larvae, sardine eggs, and sardine larvae, respectively. No clear SST differences were found between eggs and larvae for either species. Egg-density-weighted mean SST for all positive samples pooled was 20.7 °C for anchovy and 18.1 °C for sardine (Fig. 4a).

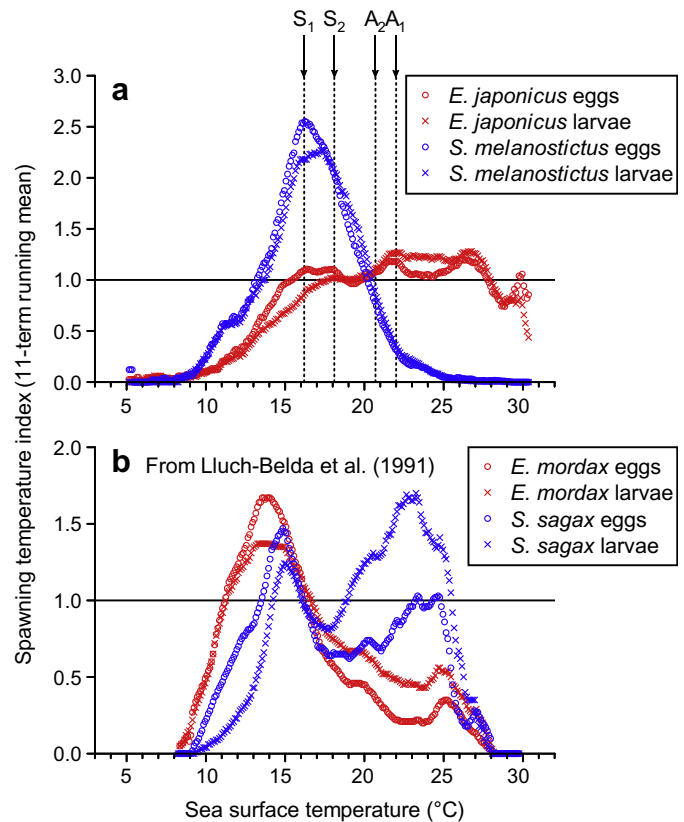


Fig. 4. Ratios of relative frequencies of positive samples versus all samples (spawning temperature index) for sea surface temperature intervals of 0.1 °C. (a) Spawning temperature index for Japanese anchovy (*Engraulis japonicus*) and sardine (*Sardinops melanostictus*) in the egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. The data are shown separately for samples positive for anchovy eggs ($n = 24,944$), anchovy larvae ($n = 24,644$), sardine eggs ($n = 10,939$), and sardine larvae ($n = 12,623$). The series were smoothed by 11-term running means (the plots are shown for the SST intervals at which 11-term running mean of frequencies of all samples exceeds 10). Horizontal line indicates the baseline ($y = 1.0$), above which temperatures are assumed to be preferred for spawning. A_1 (=22.0 °C) and S_1 (=16.2 °C): optimal growth temperatures for *E. japonicus* and *S. melanostictus* larvae, respectively (Takasuka et al., 2007); A_2 (=20.7 °C) and S_2 (=18.1 °C): egg-density-weighted mean SSTs for *E. japonicus* and *S. melanostictus*, respectively. (b) Spawning temperature index for northern anchovy (*E. mordax*) and California sardine (*S. sagax*) from the CalCOFI cruises. These were digitized and redrawn from Figs. 3 and 4 in Lluich-Belda et al. (1991).

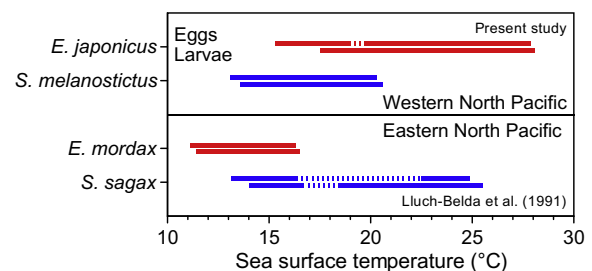


Fig. 5. Spawning temperature optimum ranges compared between anchovy and sardine and between the western and eastern sides of the North Pacific. Solid line segments are the spawning temperature index ≥ 1.0 , that is, the optimum ranges. Broken line segments are the spawning temperature index < 1.0 between the minimum and maximum of the optimum SST ranges.

The index of sardine eggs and larvae had a peak at 16–18 °C for both periods of 1978–1991 and 1992–2004, which was consistent with the peak for the period of 1978–2004. On the contrary, the mid-point of the range between the lowest and highest SSTs with

the index >1.0 was 24.9 °C and 24.0 °C for anchovy eggs and larvae, respectively, for the period of 1978–1991, while the mid-point was 20.5 °C and 21.1 °C for anchovy eggs and larvae, respectively, for the period of 1992–2004.

4. Discussion

4.1. Contrast between anchovy and sardine in the western North Pacific

The simple analysis using the huge data set of the egg and larval surveys identified temperatures preferred for Japanese anchovy and Japanese sardine spawnings in terms of temperature in spawning grounds off the Pacific coast of Japan. The differences in temperature-dependent spawning patterns were evident between anchovy and sardine in the western North Pacific. Japanese anchovy (*E. japonicus*) is a “warm” and “eurythermal” species, while Japanese sardine (*S. melanostictus*) is a “cool” and “stenothermal” species, in comparison. The mid-point of the range of SSTs at which the spawning temperature index of anchovy exceeded 1.0 was ca. 22 °C, and the marked peak of the index of sardine occurred at 16–17 °C. These temperatures exactly match the optimal temperatures for growth rates during the larval stage of anchovy and sardine (Fig. 4a), which were 22.0 °C and 16.2 °C, respectively, with the dome-shaped relationships between growth rates and SSTs in the field (Takasuka et al., 2007). Growth rates regulate survival potential of larvae through three growth-related mechanisms (Takasuka et al., 2004a): the “bigger is better” (Miller et al., 1988; Hare and Cowen, 1997), “stage duration” (Houde, 1987; Hare and Cowen, 1997), and “growth-selective predation” (Takasuka et al., 2003; Takasuka et al., 2004b) mechanisms. According to the “stage duration” mechanism, growth variability could lead to a hundredfold variation in mortality during the larval stage (Houde 1987). These three mechanisms could operate synergistically, serving as an amplifier in the growth–survival relationships. Therefore, small temperature fluctuations in the spawning grounds, owing to climate changes and ocean regime shifts, would cause substantial variability of larval survival potential as well as egg survival rate, potentially exerting dramatic impacts on population dynamics of anchovy and sardine. In addition, spawning success is temperature-dependent because temperature directly affects reproduction of Japanese anchovy (Funamoto and Aoki, 2002; Takasuka et al., 2005). Japanese anchovy and Japanese sardine migrate and spawn in the offshore waters as their stock sizes increase (Watanabe et al., 1996, 1997; Zenitani and Kimura, 1997; Takasuka et al., 2005). Such expansion/contraction of spawning grounds would also influence the temporal variations in spawning temperature and survival during early life stages.

The “optimal growth temperature” hypothesis (Takasuka et al., 2007) postulates that differential optimal temperatures for larval growth rates and fluctuations of ambient temperature between these optima simply cause the anchovy and sardine species alternations in theory. These two species do not always experience the same environments, as sardine spawning peaks in early spring, while anchovy spawning extends from spring to summer; however, their ambient temperatures for both larvae fluctuated mainly between their optimal growth temperatures. Although retrospective analysis using the time-series data of temperature, growth rates, larval survival, and biomass indicated both positive and negative aspects of the hypothesis, the “optimal growth temperature” concept would provide a possible biological mechanism of anchovy and sardine regime shifts (Takasuka et al., 2007). This idea can be theoretically applied to the differential spawning temperature optima of anchovy and sardine. The shifts from warm SST regime to cool SST regime would be favorable to Japanese sardine and vice

versa for Japanese anchovy and thus could be a trigger of sardine population flourishes by providing the preferable conditions for their vital parameters such as spawning and growth.

In previous studies, characteristics of the spawning grounds of Japanese anchovy (Zenitani and Kimura, 1997) and sardine (Watanabe et al., 1996, 1997) were described, based on egg and larval surveys off the Pacific coast of Japan. Those previous studies examined spatial and temporal variability of the spawning grounds and its relationships to population dynamics using the time-series data of the surveys. Conversely, the present analysis focuses on habitat conditions (SST) and spawning, regardless of season, year, and space, to detect species-specific spawning temperature optima. Such values would only be estimated accurately when data are accumulated for long periods, because there could be inter-annual fluctuations of spawning characteristics. Japanese anchovy (sardine) started to decrease (increase) in the early 1970s, as revealed in catch records (Fig. 1). The anchovy regime shifted to the sardine regime and then returned to the present condition. If a data set is limited to any specific phase of population dynamics, the index patterns would indicate the spawning temperatures specific to that phase but not species-specific spawning temperatures. In fact, for Japanese anchovy, the mid-point of the SST range of the index >1.0 was ca. 2–3 °C higher for the period of 1978–1991 (mainly the sardine regime) and ca. 1 °C lower for the period of 1992–2004 (mainly anchovy regime) than the mid-point detected for the whole data set period of 1978–2004 (ca. 22 °C), although no substantial difference in SST giving a peak of the index was observed between these two periods for Japanese sardine. Although spawning temperatures themselves may vary with phase (Twatwa et al., 2004; van der Lingen et al., 2005), species-specific optima should not differ among different periods by nature. Our updated data set spans for longer than a half cycle of the species alternations. Thus, we assumed that the spawning temperature patterns described for the whole data set period of 1978–2004 represented the picture averaged over the various phases (i.e. both high- and low-biomass phases) of the population dynamics and thus that the index represents the species-specific spawning temperature optimum with a fair degree of accuracy. This conclusion is supported by the fact that the detected spawning temperature optima are consistent with earlier observations of optimal growth temperatures (Takasuka et al., 2007). We note again that the egg and larval abundances are not taken into consideration in the determination of the spawning temperature index. The difference in egg-density-weighted mean SST for all positive samples pooled was less than that in the mid-point of optimal range or peak of the index (i.e. 22 °C and 16 °C) between anchovy and sardine (Fig. 4a); the annual egg-density-weighted mean SSTs have fluctuated between 16 and 22 °C for both species (Takasuka et al., 2007). However, the relationship between these two species (i.e. “warm” anchovy versus “cool” sardine) was confirmed.

4.2. Contrast between the opposite sides of the North Pacific

The relationship between anchovy and sardine in terms of spawning temperatures in the western North Pacific showed a marked contrast to the relationship observed for similar anchovy and sardine species in the eastern North Pacific (Figs. 4 and 5). The spawning temperature index, based on occurrence of eggs and larvae, enabled us to compare the spawning temperature patterns across the North Pacific through a uniform approach. Characteristics of spawning habitat of anchovy and sardine have been examined for various ecosystems (e.g. Lluch-Belda et al., 1991; Hernandez-Vazquez, 1994; Watanabe et al., 1997; Hammann et al., 1998; Twatwa et al., 2004; van der Lingen et al. 2005; Planque et al., 2007; references therein). But, comparison across the Pacific has yet to be conducted or discussed in the context of

synchronous species alternations, partly because past studies tended to target specific regions or seasons and partly because comparisons lacked the species in the western North Pacific.

Lluch-Belda et al. (1991) determined the preferred temperatures for spawning of northern anchovy (*E. mordax*) and California sardine (*S. sagax*) in the California Current system using the CalCOFI data set comprising some 19,500 samples obtained from 1951 to 1989. The index for temperature optimum for spawning exceeded 1.0 in the SST ranges from ca. 11.5 to 16.5 °C for northern anchovy eggs and larvae, with peak spawning associated with temperatures at 13–15 °C (Fig. 4b). On the other hand, the temperature peak associated with spawning of California sardine is multimodal with peaks at around 15 °C and 23 °C. Temperature associated with the presence of California sardine eggs and larvae ranged from ca. 13 to 25 °C (but with some temperature intervals within that range having index values less than 1.0). The bimodal patterns would not mean that California sardine have two extreme optima but rather that they respond to other environmental factors such as upwelling intensity that can control temperature (Lluch-Belda et al., 1991). In fact, California sardine showed peak spawning at 18–20 °C in the Gulf of California (Hammann et al., 1998). Although the period covered by the California data (1951–1989) differs from our data set period (1978–2004), such a difference per se would be of no matter in estimating spawning temperature optima as far as the data set period covers various phases to describe the averaged spawning temperature patterns. The California data set includes both species regimes, but tends to be more occupied by the anchovy regime. Thus, by an analogical inference from our data, there might be similar extent of biases (1–3 °C) in the estimates of optima of northern anchovy and California sardine; however, this would not be serious enough to change the relationship between anchovy and sardine. Therefore, by comparison, northern anchovy (*E. mordax*) is a “cool” and “stenothermal” species and California sardine (*S. sagax*) is a “warm” and “eurythermal” species in the eastern North Pacific. According to the across-Pacific comparisons, the spawning temperature optimum appears to be species-specific rather than genus-specific. In Fig. 5, the ranges of spawning temperature optima were extracted to compare anchovy and sardine and between the western North Pacific and the California Current system. The anchovy and sardine relationships were reversed between the opposite sides of the North Pacific in terms of species-specific temperature optima.

Why are anchovy and sardine regime shifts nearly synchronous despite the reversed temperature regimes for certain phases across the North Pacific? The reversed species-specific temperature optima under reversed temperature regimes would provide a possible theoretical solution to synchronous phases of anchovy and sardine alternations between the opposite sides of the North Pacific. This theory might also provide a possible explanation of the recent break of synchrony: e.g. California sardine populations increased after the early 1990s, while Japanese sardine populations have still collapsed. The winter SST at the Scripps pier increased after the early 1990s (Yatsu et al., 2008), suggesting that recent temperature conditions might be favorable to sardine but not to anchovy off California. If so, the theory could be consistent even with the asynchrony. In any case, what caused the time lags observed in the peaks of population abundance or asynchronous phases between the two ecosystems is hard to identify without further scrutinizing local temperature fluctuations, local population structures (Smith, 2005), and several other environmental factors (see below). But, the effects of fishing have also been of great concern. In addition to environmental factors, fishing impacts might be at least in part responsible for the timing of recovery of California sardine and Japanese sardine populations (e.g. Smith and Moser 2003; Suda et al., 2005; Yatsu et al., 2005).

Our synchrony-alternation model has focused only on temperature. It is obvious that no single factor is sufficient to explain everything related to fish population dynamics in complex marine ecosystems (Duffy-Anderson et al., 2005). Thus, we do not exclude that synergistic bottom-up effects (Noto and Yasuda, 1999; Beau-grand et al., 2003) like the influence of physics and wind on lower trophic levels (Cury and Roy, 1989; Lluch-Cota et al., 1999) and top-down effects (Frank et al., 2005) such as predation by piscivorous fish and fisheries (Suda et al., 2005; Yatsu et al., 2005) may also be important in controlling species dominance. For example, van der Lingen et al. (2006) proposed a trophodynamic process of anchovy and sardine alternations, based on differences in morphology of feeding organ and type and size of prey plankton between anchovy and sardine and their resource partitioning. The hypothesis by MacCall (2002) highlights differential impacts of current flow on habitats of anchovy and sardine. Interspecific interactions are also considered in unique hypotheses such as “school trap” (Bakun and Cury, 1999) and “School-mix feedback” (Bakun, 2001). Of note is a theoretical aspect that these multiple mechanisms are non-exclusive and can operate synergistically. Moreover, the components and the relative contribution of various factors to population dynamics might differ among ecosystems. In fact, Lluch-Belda et al. (1991) found differential spawning as a response to upwelling intensities between anchovy and sardine off the California coast. They attributed the complicated bimodal spawning temperature pattern of California sardine (Fig. 4b) to upwelling effects (see above). Bimodal patterns of spawning temperatures were not observed in the western North Pacific (Fig. 4a). Ecosystem differences exist in prey organisms and possibly predator fields, as well. All provide complexity. However, synchrony of anchovy and sardine regimes occurred for certain phases at least, probably mediated by climate teleconnections, despite the considerable differences in ocean systems, such as western boundary current system versus upwelling system. It is natural to believe that a dominant one of multiple mechanisms responsible for such large-scale events should be simple and direct because, if not, the phenomena would not have been repeated for more than a century at a basin-scale. Moreover, the simple and direct pathway should be based on a common factor beyond ecosystems. In our synchrony-alternation model, the impact of temperature on the species-specific spawning and growth temperature optima would provide a potential biological mechanism that could satisfy the above conditions for synchronous species alternations at a basin-scale.

Further questions need resolution, including why anchovy and sardine have contrasting temperature optima within a region and why their relationships contrast across the North Pacific. Why marked biological differences originate is still unknown, but it could be attributed to genetic and evolutionary backgrounds. In any case, comparisons of biological factors with a uniform approach will serve to orient further basic issues of biology, and at the same time, provide parameters for using the models. Further investigations need to consider differences and generalities of natural phenomena among ecosystems. Comparisons of different ecosystems should clarify the biological mechanisms of out-of-phase or synchronous alternation phenomena toward a basin-scale synthesis of multi-species regime shifts of pelagic fish.

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