

CHARACTERIZING SPAWNING HABITATS OF JAPANESE SARDINE (*SARDINOPS MELANOSTICTUS*), JAPANESE ANCHOVY (*ENGRAULIS JAPONICUS*), AND PACIFIC ROUND HERRING (*ETRUMEUS TERES*) IN THE NORTHWESTERN PACIFIC

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ABSTRACT

We analyzed sea surface temperature, salinity, and depth in the spawning grounds of three small pelagic fishes, Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), and Pacific round herring (*Etrumeus teres*), to compare species-specific characteristics of spawning based on a long-term dataset of egg surveys off Japan from 1978 to 2004. A total of 133,294 samples were obtained by vertical tows of plankton nets. Temperature-salinity-depth plots of the spawning grounds of the three species indicated broad temperature and salinity ranges for anchovy, reflecting a wide distribution from coastal to offshore waters, compared to sardine. Spawning activities of round herring were observed in similar temperature but narrower salinity ranges compared to anchovy. These species-specific temperature/salinity characteristics reflect differences in the location and bottom depth distribution of their spawning grounds. Differential spawning strategies are also reflected in the species-specific relationships between spawning area and egg abundances.

INTRODUCTION

Small pelagic fish are generally characterized by marked fluctuations in population size. Such cyclic patterns seem to reflect or be influenced by climate changes, as indicated by long-term landing histories (Lluch-Belda et al. 1989; Schwartzlose et al. 1999). In any given ecosystem, however, the timing of population fluctuations and their extent differ between co-existing species of small pelagic fish. A typical example is the alternating dominance of sardine and anchovy in various regions of the world (Kawasaki 1983). In the northwestern Pacific, Japanese sardine (*Sardinops melanostictus*) populations peaked in 1988 and then abruptly decreased to near collapse in recent years, while Japanese anchovy (*Engraulis japonicus*) populations increased during the sardine's collapsing phases (fig. 1; Anonymous 2005). Conversely, the Pacific round herring (*Etrumeus teres*) population has had a smaller but stable biomass during the same periods, although its spatial distribution from the larval to adult stage overlaps with the Japanese sardine and Japanese anchovy along the coastal area (Hanaoka 1972; Tanaka et al. 2006).

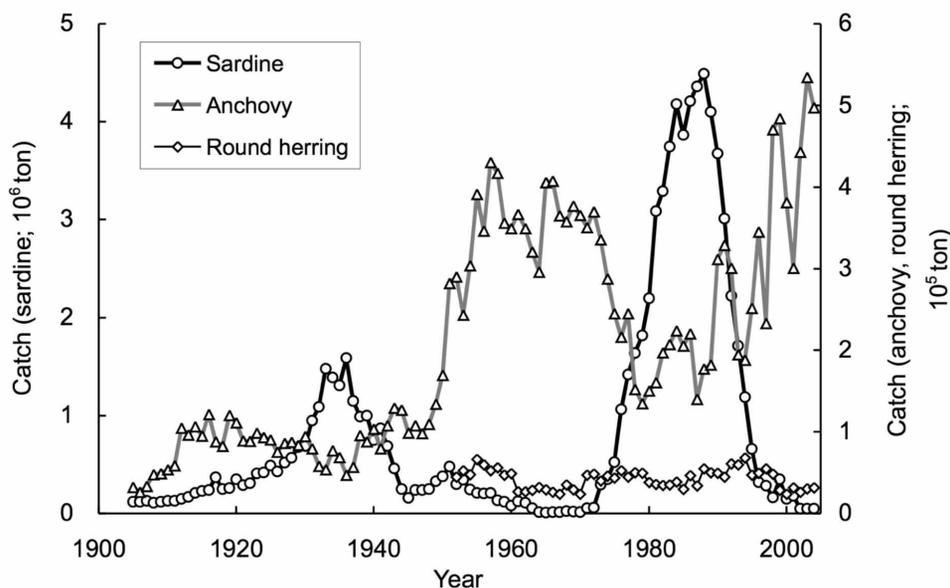


Fig. 1. Landing records of Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) off Japan from 1905 to 2004.

These patterns tend to be consistent with patterns in other ecosystems dominated by small pelagic fish and are attributed to differential responses to climate-related environmental changes. In this regard, characterizing spawning habitats of co-occurring small pelagic fish species appears critical to understanding these patterns, assuming that the physical conditions of the spawning habitats, crucial to their reproduction and subsequent survival of offspring, play a role in characterizing the spawning habitats.

The characteristics of the spawning grounds of pelagic fish have been described for temperature, salinity, bottom depth, and distance from coasts, and compared between different current systems (cf. van der Lingen et al. 2005). Temperature and salinity records are useful for detecting differences in the spawning habitats of small pelagic fishes with different population fluctuation patterns (Checkley et al. 2000). Sardine distributed in the northern Pacific might be a good example, as the characteristics of the spawning grounds in the northwestern Pacific are thought to be different from those in the northeastern Pacific, because these two populations increased simultaneously even though the temperature fluctuation patterns of the two areas have been quite different (Chavez et al. 2003). Sea surface temperature (SST) and salinity (SSS) in the spawning grounds of these fishes may provide information important to analyzing the synchrony of their population fluctuations.

The spatial overlap between the anchovy and sardine spawning grounds might be crucial from this point of view. However, the species-specific utilization of the spawning grounds should be analyzed before interpreting the consequences of the spatial overlap. There are two specific issues to be considered: the cross-shelf spatial preference and the area of the spawning ground. Spawning ground spatial preferences have been studied in several current systems (cf. van der Lingen et al. 2005), but no detailed analysis has been done in the northwestern Pacific. Relationships between spawning area (SA) and egg abundance (EA) have been analyzed for sardine and anchovy (Mangel and Smith 1990; Watanabe et al. 1996; Zenitani et al. 1998; Zenitani and Yamada 2000). Watanabe et al. (1996) reported a positive relationship between SA and EA for sardine; Zenitani and Kimura (1997) also reported a positive relationship between SA and EA for anchovy. However, the relationship between SA and EA among species has not yet been compared.

Long-term spawning data have been accumulated in various regions of the world to investigate spawning of small pelagic fish. The Japanese Fisheries Agency has conducted egg surveys of small pelagics since 1947, and small pelagic spawning habitats and egg production from 1978 to 1996 have been reported (Mori et al. 1988;

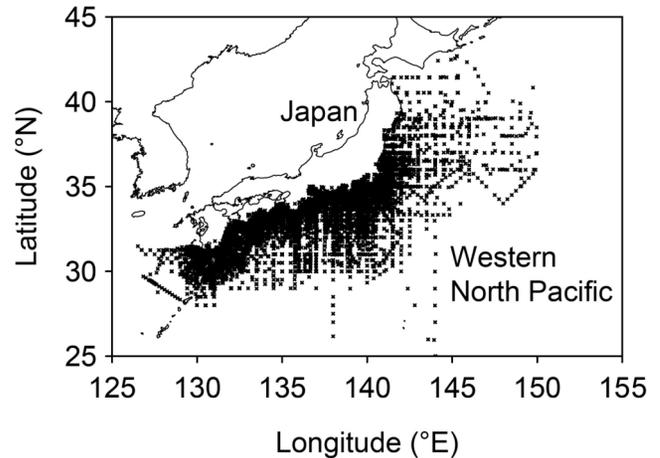


Fig. 2. Sampling stations of egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. Both fixed and unfixed stations are shown together. Redrawn from Takasuka et al. (2007).

Kikuchi and Konishi 1990; Ishida and Kikuchi 1992; Zenitani et al. 1995; Kubota et al. 1999). Recent information on the spawning habitats and egg productions off the Pacific coast of Japan has been reported in a series of Fisheries Research Agency annual reports (Anonymous 1997–2004). These reports suggested that the spawning area was affected by population size. However, the differences in the spawning habitat cannot be resolved by looking at the spawning ground distribution and estimates of egg production alone.

The present study characterizes the spawning habitats of three major small pelagic fishes (Japanese sardine, Japanese anchovy, and Pacific round herring), using Japanese Fisheries Research Agency datasets from 1978 to 2004. These long-term datasets, which covered the low and high population periods of both sardine and anchovy, were used to compare the species-specific environmental characteristics of the spawning grounds.

MATERIALS AND METHODS

Egg and larval surveys along the Pacific coast of Japan have been historically conducted by 18 prefectural fisheries research laboratories and two national research institutes of the Fisheries Research Agency since 1947. We use data from these surveys. The survey areas covered the major spawning grounds of Japanese anchovy and sardine off the Pacific coast (fig. 2), and survey cruises were conducted monthly, with more intense sampling during early spring. Egg and larva samples were obtained using vertical tows of a net with 0.33 mm or 0.335 mm mesh size from 150 m depth (or just above the bottom) to the surface, equipped with a flowmeter to estimate the water volume filtered. Sampling nets varied throughout the time period: from 1947 through 1990, “Marutoku-B” net (45 cm mouth diameter, 80 cm-long conical net), “Marunaka” net (60 cm mouth diameter,

150 cm-long conical net), and NORPAC net (45 cm mouth diameter, 180 cm-long conical net) was used (Nakai 1962); since 1991, long NORPAC net (45 cm mouth diameter, 65 cm + 130 cm-long cylindrical-conical net) were used for all egg survey cruises. Despite the changes of sampling gears, sampling efficiency was not significantly different throughout the years (Matsuoka 1995a, b; Zenitani 1998). For all survey years, net samples were identified, sorted, and counted for eggs of small pelagics. Temperatures and salinities at several layers were measured by reversing thermometers or CTD.

Temperature-salinity-depth plots for eggs of the three species were described using all SST, SSS, and bottom-depth data at the sampling station along with egg density (individuals per m³) from 1978 to 2004 off the Pacific coast of Japan (from 29°N 129°E to 42°N 145°E). Data from 1947 to 1977 were not used because the number of samples was limited (<800 stations per year) and because a portion of tows lacked flow-meter records. Egg densities (individuals per m³) were estimated from flow-meter filtering rates, towing distance, and tilt angle of the wire. Depth data were obtained from the website of the Japan Oceanographic Data Center (http://www.jodc.go.jp/data_set/jodc/jegg_intro_j.html, accessed on 8 Nov. 2006) from which average depth for each 0.01-square degree was estimated. Due to the large number of small islands and the complex topography of the area, bottom depth was used as a proxy for the distance from the coast.

Quotient analyses of bottom depth class were plotted to compare differences in distance from shore of the spawning grounds of the three species. The frequency of positive egg samples for all sampling stations (% eggs_D) was divided by the frequency (%) of this depth class in all sampling stations (% sampling station_D). The quotient in each depth class (Q_D) was calculated as (Twatwa et al. 2005):

$$Q_D = \frac{\% \text{ eggs}_D}{\% \text{ sampling station}_D} \quad (1)$$

Monthly egg abundance was calculated for each 15' square. The resolution has been updated from the 30' latitude × 30' longitude squares that have previously been used in the annual reports of egg and larval surveys (e.g., Mori et al. 1988; Kubota et al. 1999). Our calculation procedures were similar to Mori et al.'s (1988) and Kubota et al.'s (1999) except for the spatial resolution. First, the number of eggs was standardized to densities per m² for each tow. Then, egg density per 1 m² was calculated for each 15' × 15' square by arithmetically averaging egg densities of all tows conducted in the square for each month. Egg abundance in the 15' × 15' square *i* in month *j* (*E_{ij}*) was calculated using the egg density (number

per m²) in the square in that month (*D_{ij}*), with egg incubation time and survival rate being considered (Nakai and Hattori 1962):

$$E_{ij} = \frac{1}{s} \cdot \frac{d_j}{d'_{ij}} \cdot A_i \cdot D_{ij} \quad (2)$$

where *s* is the survival rate during egg stage (day⁻¹), which was 0.571 for sardine, 0.600 for anchovy and 0.571 for round herring (Watanabe 1983; Mori et al. 1988; Kubota et al. 1999; Watanabe T. unpubl. data), *d_j* is the number of days in month *j*, *d'_{ij}* is the egg incubation time in days in the square *i* in month *j*, and *A_i* is the area of the square *i* (m²). Mortality during egg stages was estimated from the long-term datasets providing egg stage. Estimated survival rates were used to compare relationships between egg abundance and spawning area between the three species. Area value of each square was estimated by the 20 m mesh GIS data (25000V; Hokkaido-chizu Co., Ltd.). Egg incubation time was estimated using a function of SST based on the Arrhenius' equation (Hattori 1983; Uehara and Mitani 2004; Watanabe T. 1983):

$$d_{ij} = \frac{1}{24} \cdot 10^{\left(\frac{a}{t_{ij} + 273} - b\right)} \quad (3)$$

where *t_{ij}* is the mean SST weighted by egg occurrence, *a* and *b* are constants (*a* = 4760, *b* = 14.6 for sardine, *a* = 4060, *b* = 12.2 for anchovy and *a* = 3656, *b* = 10.7 for round herring).

Annual relationships between spawning area and egg abundance were examined both for the total egg counts for each year and for the egg count during the peak spawning month of the three species. Total spawning area and egg abundance in a given year were calculated by simply summing up the monthly data from January to December for anchovy and from October of the previous year to September of the given year for sardine and round herring based on their specific spawning seasons (see Results). The relationships between total spawning area (during the whole spawning period) and annual spawning stock biomasses (SSB), estimated through virtual population analyses (Anonymous 2005), were also analyzed for sardine and anchovy. Relationships between spawning area, egg abundance, and SSB were also analyzed for the peak egg abundance month, which is February for sardine and June for anchovy.

RESULTS

A total of 133,294 stations were covered by the survey and 126,080 net samples were available for the present analyses (fig. 2). Mean sampling area coverage (sum of areas of 15' latitude × 15' longitude squares in which

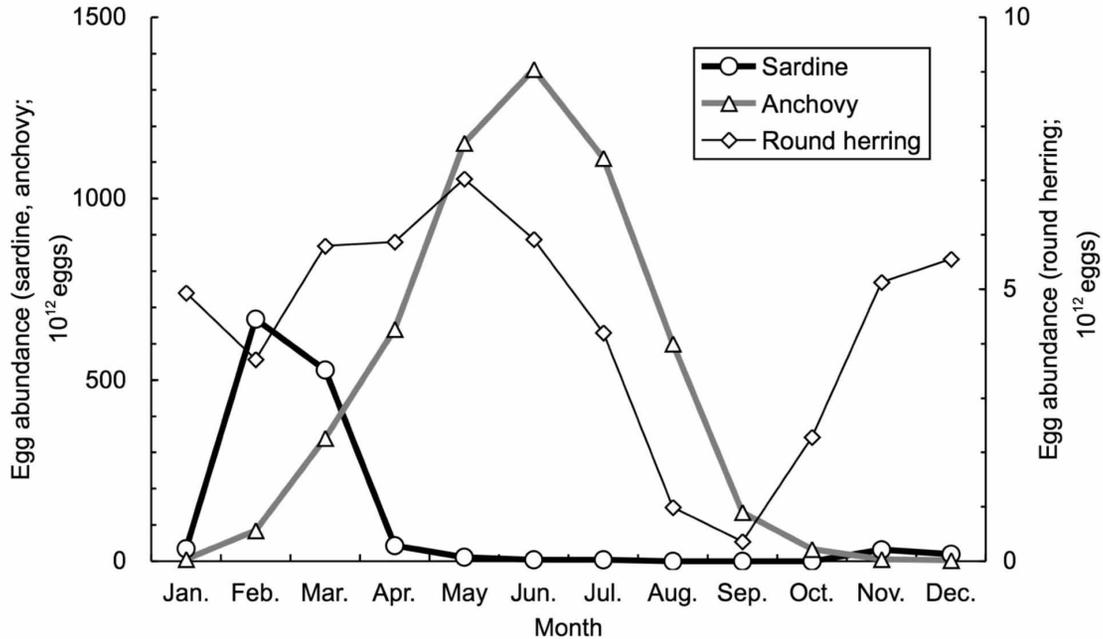


Fig. 3. Mean monthly egg abundance of Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) along the Pacific coast of Japan from 1978 to 2004.

sampling was conducted) ranged from 7.05×10^4 km² (September) to 14.58×10^4 km² (February). Number of samples (frequency of plankton net tows) per month during 1978 to 2004 ranged from 253 (September) to 456 (February). Annual total sampling area coverage and number of samples (summed for all months) have been almost constant since 1978, ranging from 92.50×10^4 km² (1978) to 128.31×10^4 km² (2004) and from 3,188 (1997) to 4,308 (1982), respectively.

A total of 10,890 positive samples were collected for spawning sardine, 24,718 for anchovy, and 10,420 for round herring from 1978 to 2004. Mean egg abundance per month indicated that the sardine spawning season, estimated as the period in which more than 95% of eggs were spawned, was from November to April, with peak spawning in February (fig. 3). The main spawning season of anchovy was from March to August with peak spawning in June. For round herring, the main spawning season was from October to July with a peak in May. While our recorded months of peak spawning for sardine and anchovy are slightly different from those in previous studies (Watanabe et al. 1996; Zenitani and Kimura 1997), the main spawning seasons are stable and thus the months of peak spawning calculated from the long-term data are appropriate for characterizing species-specific spawning behaviors.

Temperature-salinity-depth plots of the spawning grounds were described from the positive sampling data for the three species from 1978 to 2004 (figs. 4–6). Spawning activities of Japanese sardine were observed in the SST range of 10° to 25°C, and the abundant egg

distributions were observed mainly at salinities of 33.5 to 35.5 psu (fig. 4). Abundant spawning activities were not only observed in the shallow coastal waters but also in the surface waters of offshore areas over bottom depths of up to 5000 m. The salinity of the spawning ground was not, however, lower than 31 psu. The SST range in the offshore areas (deeper than 1000 m depth), was between 15° to 21.5°C, but abundant spawning (>100 eggs per m³) was only observed in SSTs of 18° to 21.5°C and in the high salinity waters.

The temperature-salinity-depth plots of the spawning grounds of Japanese anchovy indicated very wide temperature and salinity ranges, from 12° to over 30°C and mainly from 23 to 34.5 psu, respectively (fig. 5). Spawning activities of anchovy were observed both in shallow coastal areas and deep offshore areas (up to 5000 m bottom depth), and high egg abundances were not only observed in shallow, low salinity areas (less than 33 psu), but also in the high salinity offshore waters (up to 35.5 psu).

Temperature ranges of the round herring spawning grounds were from 10° to 30°C, which was similar to those of anchovy, although the eggs were concentrated only in a narrow SSS range of 30 to 35.5 psu (fig. 6). High densities of eggs were not observed in the surface waters of areas deeper than 3000 m, and spawning was not active in low salinity, coastal areas (<25 psu).

Results of the bottom depth quotient analyses of the spawning grounds indicated marked contrasts among the three species (fig. 7). The highest values of the anchovy depth quotient were found at the shallowest sampling

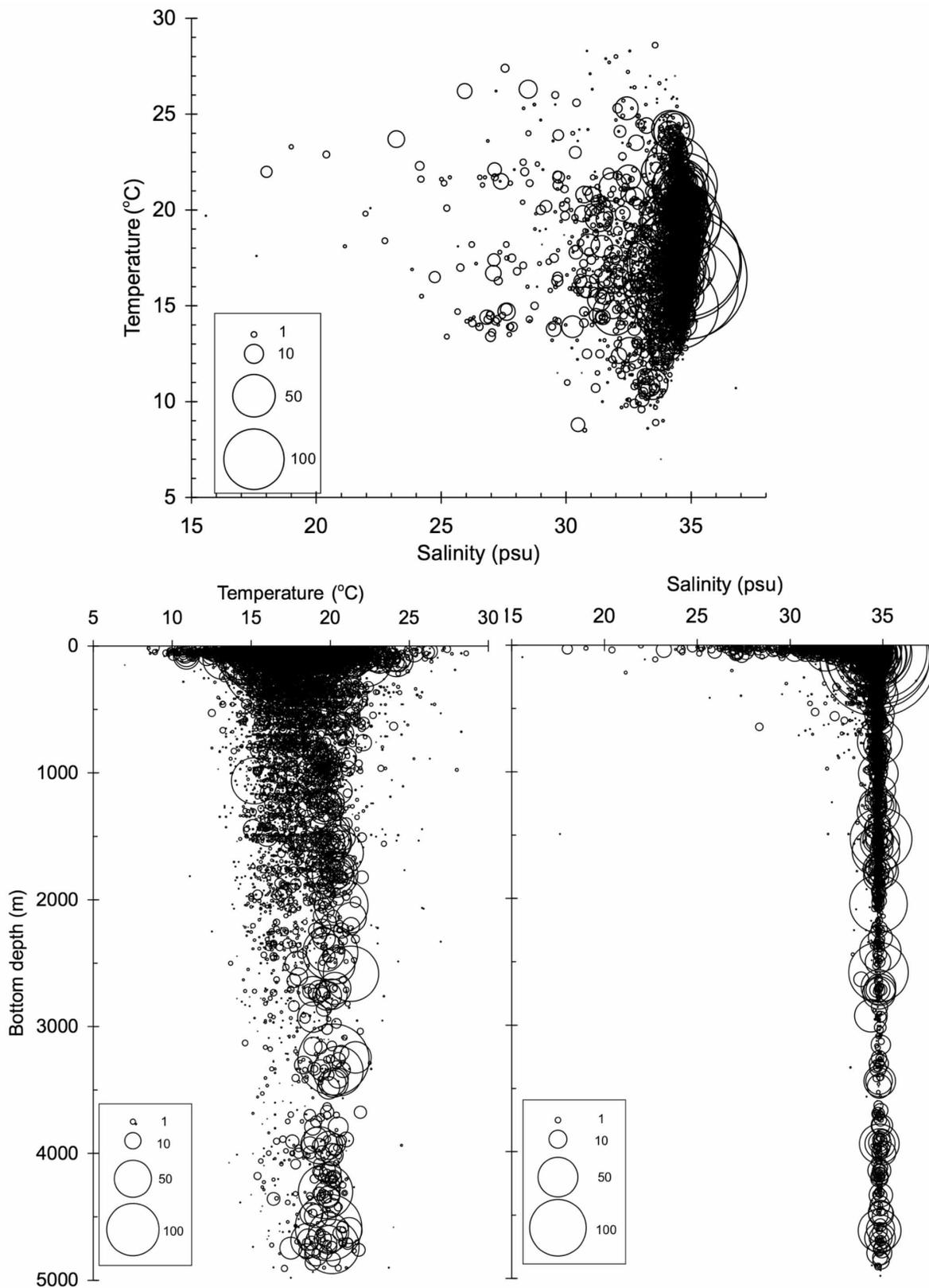


Fig. 4. Temperature-salinity-depth plots of the spawning grounds of Japanese sardine (*Sardinops melanostictus*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per m^3) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

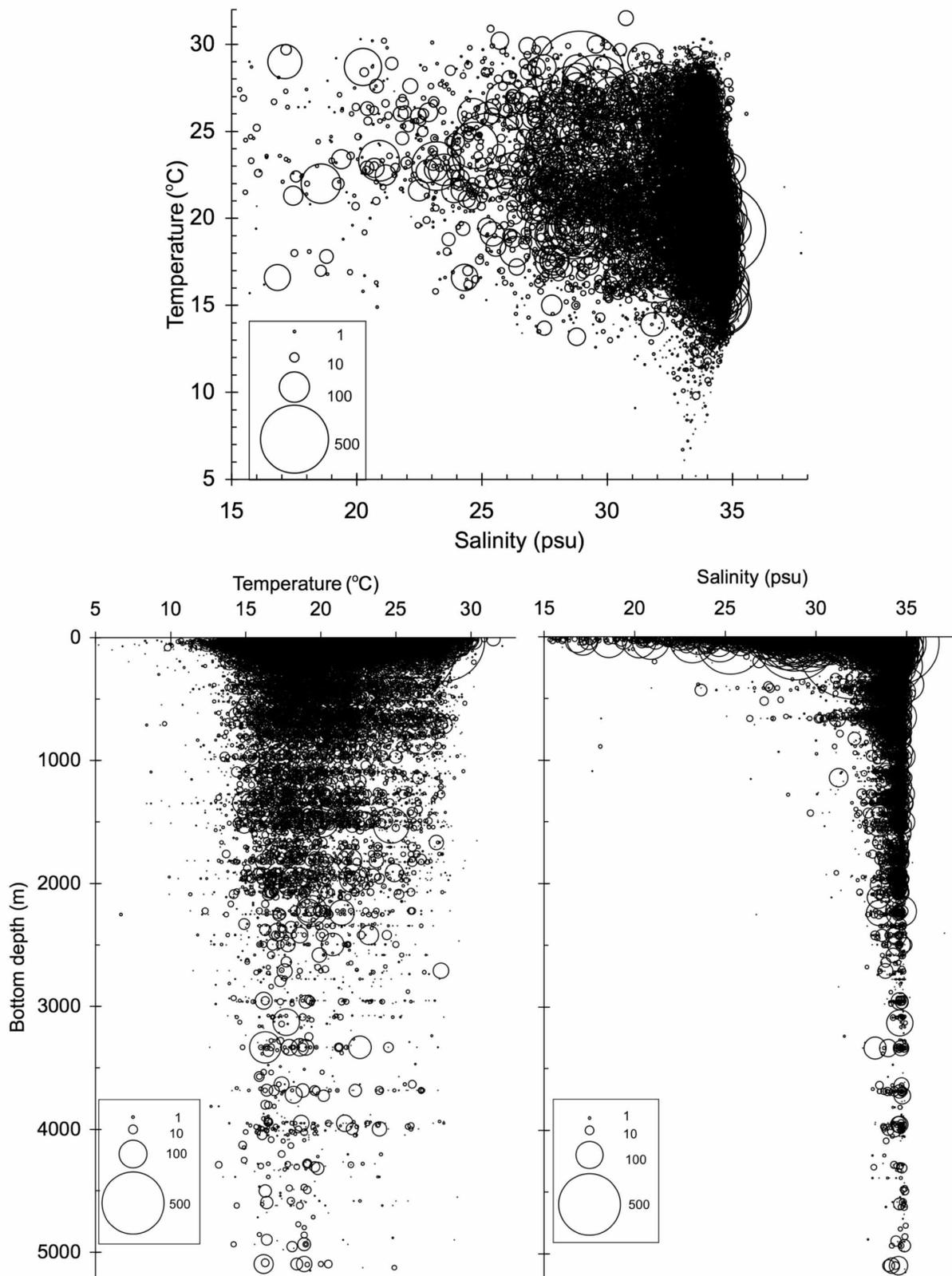


Fig. 5. Temperature-salinity-depth plots of the spawning grounds of Japanese anchovy (*Engraulis japonicus*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per m³) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

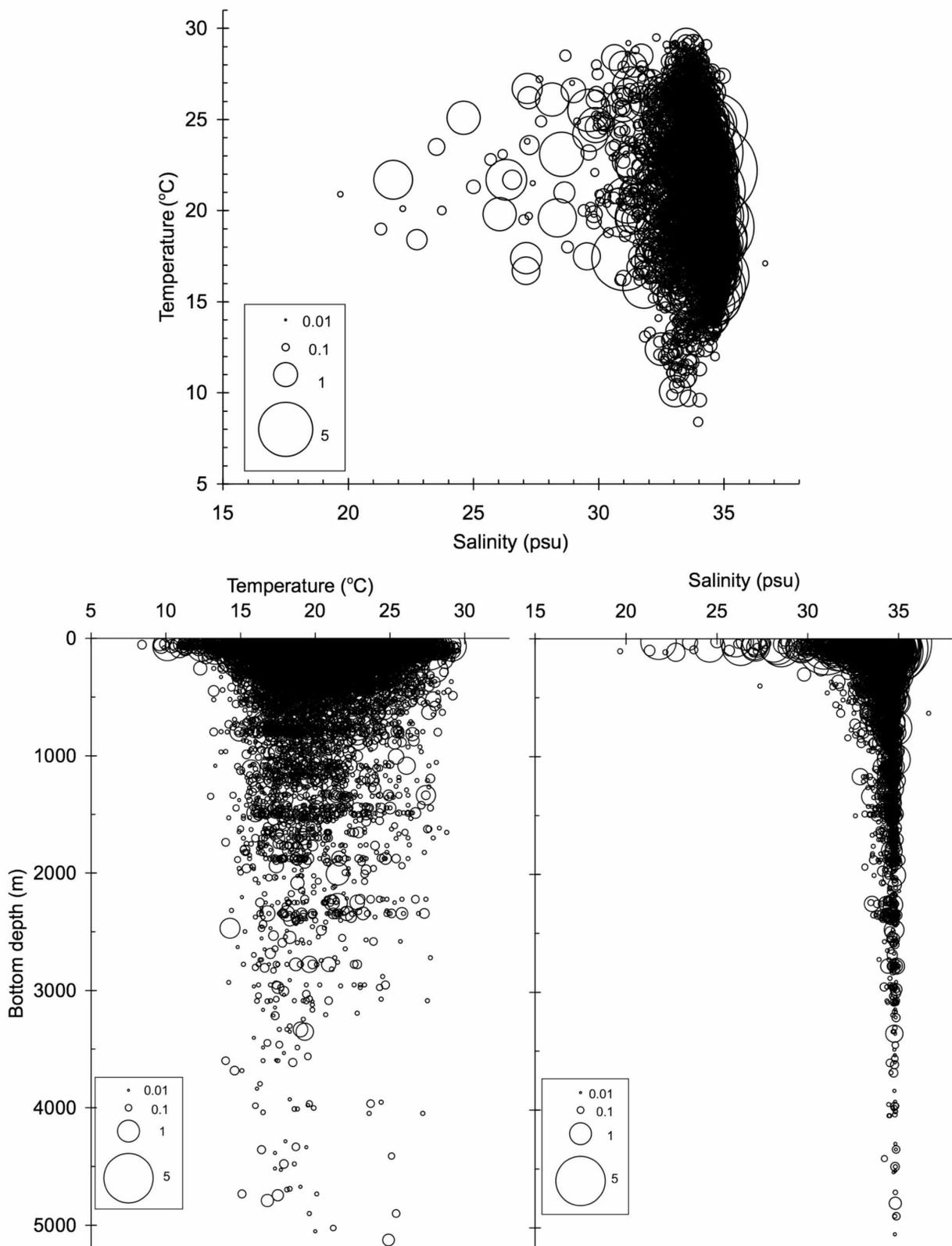


Fig. 6. Temperature-salinity-depth plots of the spawning grounds of Pacific round herring (*Etrumeus teres*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per m³) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

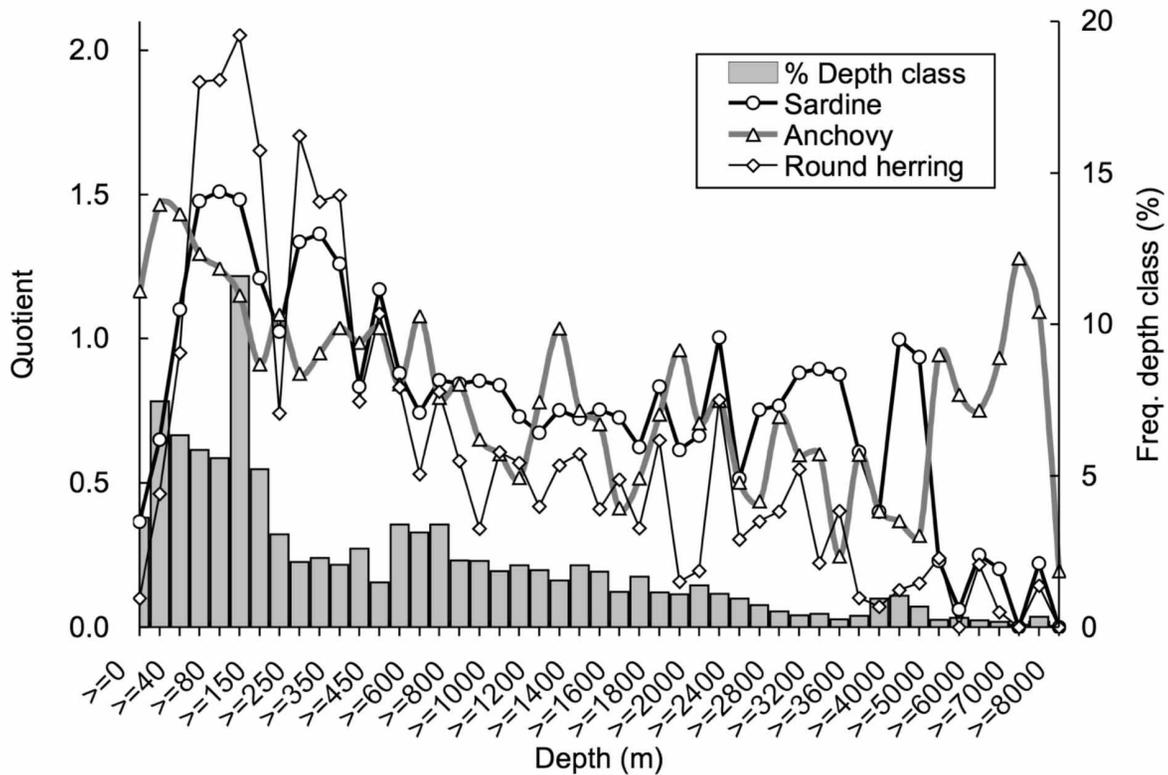


Fig. 7. Frequency distribution of depth class (histograms) and egg abundance/depth quotients (symbols and lines) for sardine (circle), anchovy (triangle), and round herring (diamond) along the Pacific coast of Japan from 1978 to 2004.

station (<60 m depth); for round herring they were at stations 80–400 m depth; and for anchovy they were around 1.0 at the same stations. Both sardine and anchovy had similar stable quotient values of less than 1.0 at stations 400 to 4000 m depth. The quotient for sardine decreased at stations deeper than 5500 m, although this was not the case for anchovy.

Significant species-specific log-linear relationships between egg abundance (EA) and the spawning area (SA) were observed for both sardine and anchovy, although no significant relationship between EA and SA was found for round herring because of its narrow egg abundance range in the time series (fig. 8). Relationships between EA and SA in the peak spawning period were not markedly different between sardine and anchovy. However, the total annual SA for anchovy was larger than that of the sardine because of its longer spawning season (fig. 8).

Significant species-specific relationships between SA and SSB both in the peak-spawning month and in the annual total were similar for sardine and anchovy (fig. 9). SA for anchovy was larger than that for sardine at the same SSB level, although the annual variance and the maximum value of SSB were much larger for sardine than for anchovy. Plots for round herring could not be computed due to uncertainties in stock estimation.

DISCUSSION

Temperature-salinity (TS) plots of the spawning grounds indicated differential patterns among the three species. Sardine spawning was characterized by a stenohaline pattern in the higher salinity range associated with offshore waters, and by a eurythermal pattern in the relatively low temperature of 10° to 25°C. Nakai et al. (1955) analyzed three years of egg survey data from 1949 to 1951 and reported that SST for sardine spawning ranged from 11.1° to 19.1°C and SSS ranged from 33.06 to 35.04 psu, while spawning mainly occurred at temperatures of 13° to 16°C and salinities of 34.00 psu. Ito (1961) summarized data to show that the main spawning temperature varied depending on latitude: from 17°–19°C in the southern areas, and from 14°–17°C in the northern areas of the Pacific coast of Japan. Kuroda (1991) reported that the temperature range of sardine spawning grounds was from 11° to 21°C and that the main spawning temperatures from 15° to 19°C were along the Pacific coast of Japan. These previous findings agree well with the present results and the temperature and salinity ranges analyzed in this study. Overall, SSTs of 10° to 25°C and salinities of 33.5 to 35.5 psu are typical Japanese sardine spawning grounds. The main spawning temperature range indicated in this study, 15°–21.5°C, also coincides with laboratory studies. Zenitani (1995)

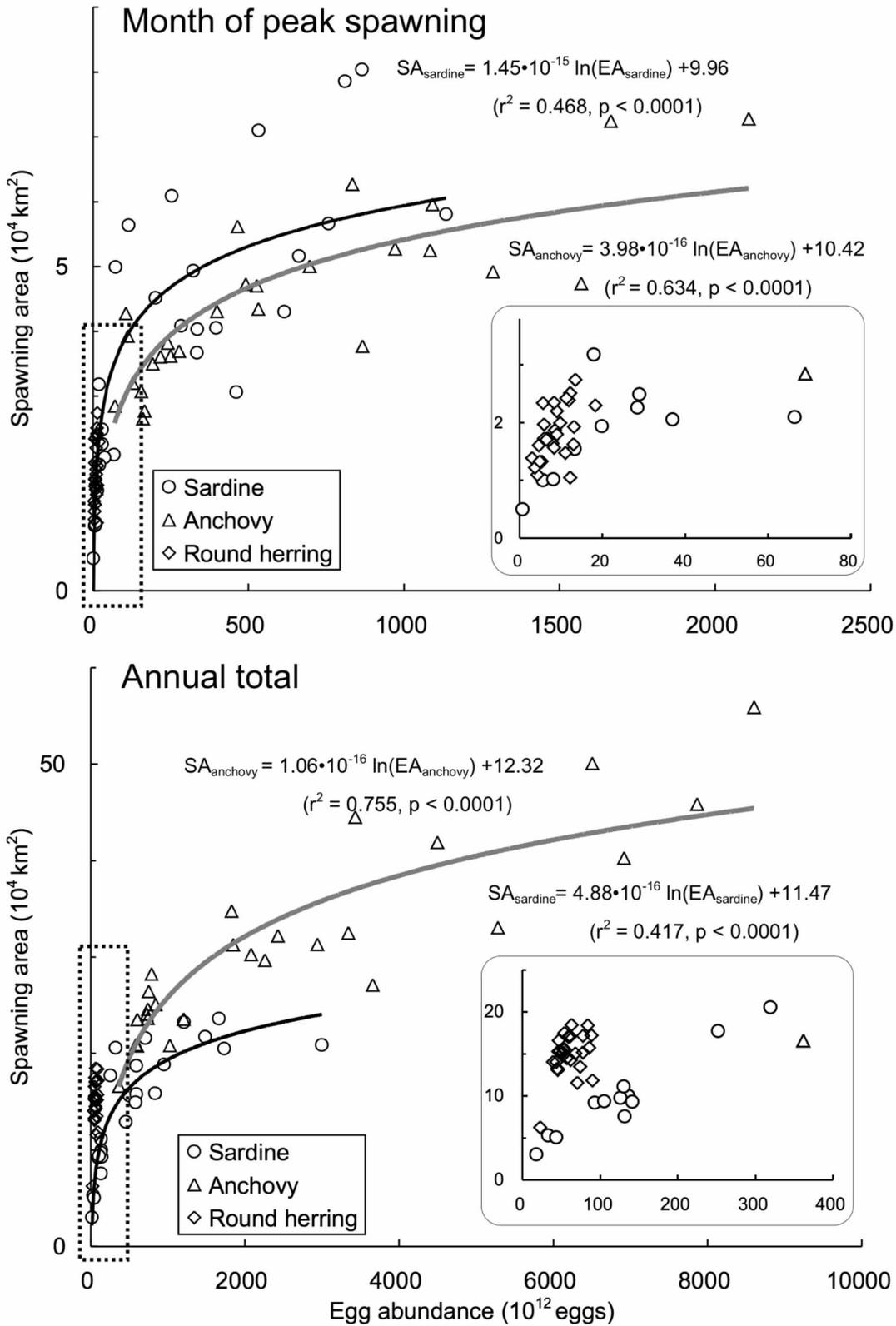


Fig. 8. Relationships of spawning area to egg abundance for Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) in the Northwestern Pacific from 1978 to 2004. Upper panel indicates the data in the month of egg abundance peak (February for sardine, June for anchovy, and May for round herring). Lower panel indicates data summed from October of the previous year to September for sardine and round herring and from January to December for anchovy. A close-up of the range enclosed by dotted line is shown in each panel.

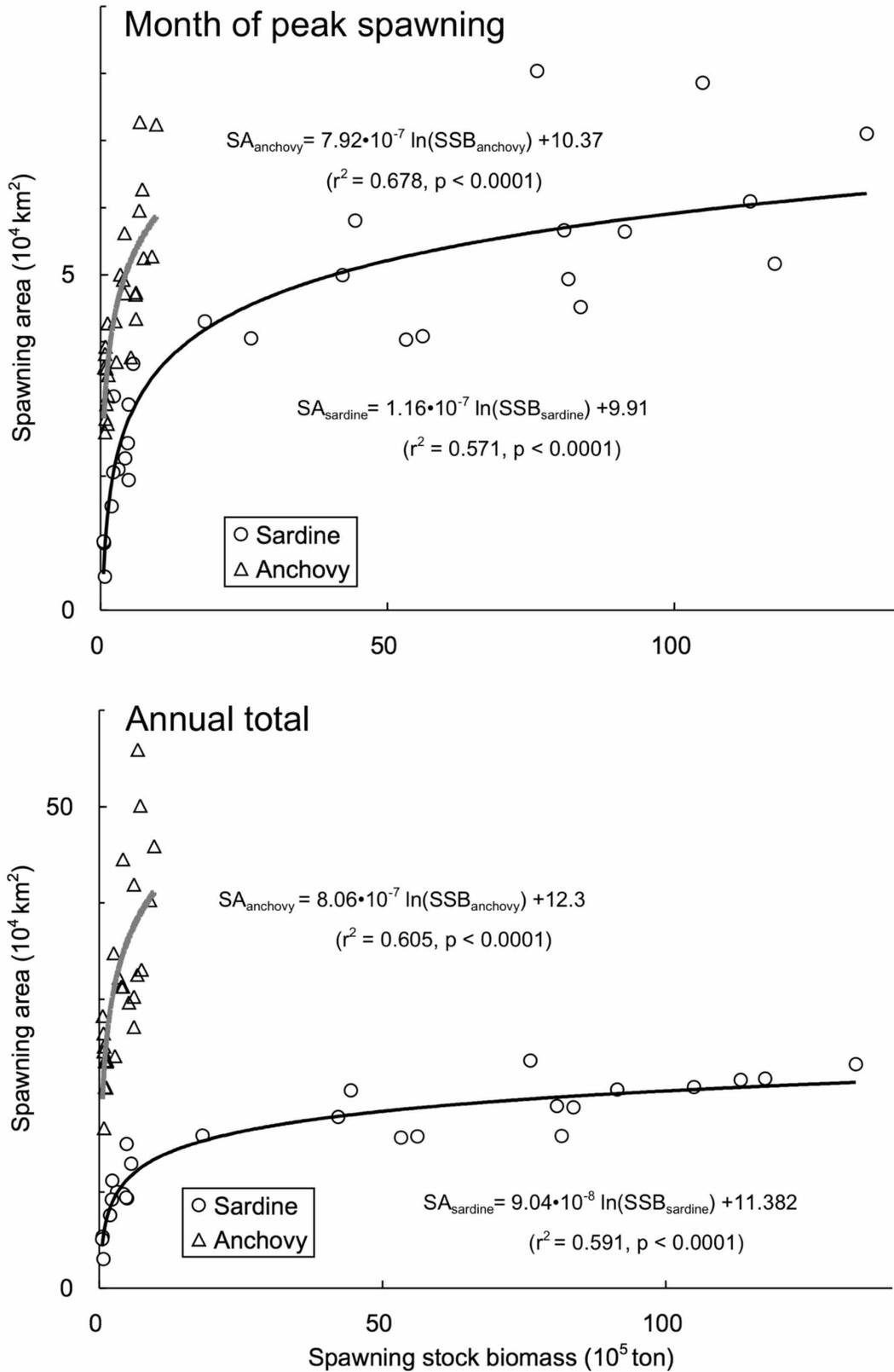


Fig. 9. Relationships of spawning area to spawning stock biomass for Japanese sardine (*Sardinops melanostictus*: circle), and Japanese anchovy (*Engraulis japonicus*: triangle) in the Northwestern Pacific from 1978 to 2004. Upper panel indicates the data in the month of egg abundance peak (February for sardine, and June for anchovy). Lower panel indicates the data summed from October of the previous year to September for sardine and round herring and from January to December for anchovy.

reported that embryo length and the yolk-sac volume of larvae hatched at 19°C was significantly larger than those that hatched at 15° and 23°C. Takasuka et al. (2007) pointed out that the optimum growth temperature was 16.2°C for Japanese sardine larvae. Therefore, the TS plot of the sardine spawning grounds reflects the physical environment preferable for larval growth.

Data from anchovy spawning grounds indicated a euryhaline pattern from estuarine (lower salinity) to offshore waters (higher salinity), and also a eurythermal pattern from 12° to over 30°C. Nakai et al. (1955) reported that the temperature and salinity in anchovy spawning areas was from 12.0° to 24.7°C (peak temperature: 17.7°C) and from 26.74 to 35.23 psu, respectively. Both temperature and salinity ranges were broader for anchovy than for sardine. Long-term data analyses in this study confirmed these results and indicated that the ranges of spawning temperature and salinity were broader than those reported in Nakai et al. (1955).

Spawning grounds of round herring were characterized by a eurythermal pattern from 10° to over 30°C, which is broader than the range previously reported in Nakai et al. (1955; 14° to 23°C). It was confirmed, however, that the salinity range of round herring spawning grounds was from 30.35 to 35.23 psu (Nakai et al. 1955), and that round herring are located in the high salinity stenohaline area between estuarine and offshore waters.

The different environmental characteristics of the spawning grounds of the three species could be associated with their specific spawning ground locations. This is particularly evident in the bottom depth of the spawning ground, used as a proxy for the distance from the coast. Both sardine and anchovy have the ability to expand their spawning grounds offshore, unlike round herring. Differences in TS where spawning activity occurred, however, reflect differences in the locations of sardine and anchovy spawning. TS plots of sardine spawning grounds, which indicated a stenohaline pattern in high salinity and a eurythermal pattern at relatively low temperatures, are consistent with a lack of spawning in the low-salinity and high-temperature coastal waters. The broader temperature adaptability of anchovy reflects active use of low-salinity coastal waters, along with offshore waters, for spawning. On the other hand, round herring can use neither near-coastal waters, because of its stenohaline spawning behavior, nor offshore waters.

The species-specific characteristics of the spawning grounds differ from other current systems, even when compared within the same genus. In upwelling-dominated systems, spawning grounds both for sardine and anchovy are characterized by relatively high salinity waters (>33 psu, van der Lingen et al. 2005). For example, off California, *Sardinops sagax* and *Engraulis mordax* spawned in a narrow salinity range from 32.5 to 33.5

psu, with sardine spawning in relatively lower-salinity offshore waters compared to anchovy (Checkley et al. 2000); and the main spawning temperature for anchovy was lower than that for sardine (Lluch-Belda et al. 1991). Similar spawning ground separation between *Sardinops sagax* and *Engraulis encrasicolus* was reported for the southern Benguela area, with sardine spawning located inshore and anchovy spawning offshore, although this pattern may not be consistent historically (Barange and Hampton 1997; Barange et al. 1999). These differences potentially are the result of adaptation to different current systems, i.e., western and eastern boundary currents, and may help explain the synchronicity in population fluctuations between areas related to fluctuating environmental characteristics. Further studies are needed to compare species-specific biological characteristics of small pelagics among different current systems.

Relationships between spawning area (SA), egg abundance (EA), and spawning stock biomass (SSB) also reflect the species-specific use of the spawning grounds. The present results indicated species-specific relationships between SA and EA, reflecting differential use of spawning grounds. Our results confirmed the positive relationship reported as $SA = 60.9 EA^{0.181}$ for sardine (Watanabe et al. 1996). Anchovy utilize a larger spawning area than the sardine (per unit of egg abundance) for the whole spawning season, although in the peak spawning month no large differences were observed between sardine and anchovy. The difference thus may be explained by the duration of spawning seasons, which was two months for sardine and five months for anchovy. The difference in spawning season duration might be attributable to the wide ranges of temperature and salinity of anchovy sardine spawning. Barange et al. (2005), however, proposed that differences in the use of space between anchovy and sardine might be due to more complex factors, such as different school structures of *Sardinops sagax* and *Engraulis encrasicolus* in the southern Benguela. The relationship between SA and SSB presented in this study also suggests a similar phenomenon where anchovy utilized a larger spawning area than the sardine.

Our results indicate that the preferred environment for spawning was partially explained by species-specific inshore-offshore spawning patterns, but also reflected species-specific patterns of space use, in terms of spawning area per unit of biomass. Furthermore, there is a possibility that species-specific physiological preferences may determine when, where, and how long small pelagic fish spawn eggs. Concerning this issue, Bellier et al. (2007) analyzed historical shifts of spawning grounds of *Engraulis encrasicolus* and *Sardina pilchardus* and concluded that the shifts in spawning grounds reflected changes in population size and demography as well as environmental con-

ditions. Watanabe et al. (1996) also reported the historical shifts of spawning grounds of Japanese sardine, showing that age structures of the spawners changed as population size fluctuated. The present study showed differences in spawning habitats among small pelagic fish in the Northwestern Pacific. Although spatial and temporal dynamics of spawning habitats needs further study, the species-specific patterns that are presented here are an essential step toward describing the spawning strategies of small pelagic fish in different ecosystems.

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