Spatial distribution of Japanese sardine, gizzard shad and Japanese anchovy larvae in the Sea of Hiuchi, central Seto Inland Sea, in the 1990s

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In contrast to the collapse of Japanese sardine *Sardinops melanostictus* population in the western North Pacific in the early 1990s, the annual catch of the Japanese sardine peaked in the Sea of Hiuchi, central Seto Inland Sea, Japan, in 1997. Larvae of the three clupeiform fishes, Japanese sardine, gizzard shad *Konosirus punctatus* and Japanese anchovy *Engraulis japonicus*, were simultaneously distributed in the Sea of Hiuchi during the late 1990s. In order to compare the early life histories of the three species, seasonal occurrence and spatial distribution of the larvae were investigated before (1982), during (1995–1998) and after (2008) the abrupt increase in Japanese sardine population in the Sea of Hiuchi. Corresponding with the trends in the annual fishery catch of each species in the Sea of Hiuchi, Japanese anchovy larvae were most dominant among the clupeiform species in 1982, Japanese sardine and gizzard shad larvae in 1995 and gizzard shad and Japanese anchovy larvae in 2008. Overlap in horizontal distribution was most evident between Japanese sardine and gizzard shad larvae. However, the pattern of vertical distribution differed between larvae of the two species; Japanese sardine larvae were more abundant in mid and bottom depths while gizzard shad in surface layer.

Key words: Japanese sardine, gizzard shad, Japanese anchovy, larvae, distribution, Seto Inland Sea

Introduction

Japanese sardine *Sardinops melanostictus* and Japanese anchovy *Engraulis japonicus* are small pelagic fish species distributed in the western North Pacific. Contrasting patterns of population oscillations in the two species have been reported in the western North Pacific as in other *Sardinops* and *Engraulis* species (Lluch-Belda et al., 1992; Schwartzlose et al., 1999; Takasuka et al., 2007). The Japanese sardine populations were abundant in the western North Pacific during the early and mid 1980s when the Japanese anchovy were scarce. Then the Japanese sardine populations collapsed after the late 1980s and Japanese anchovy populations increased. The alternations of dominant species, Japanese sardine and Japanese anchovy, in the pelagic fish community is considered to be associated with climate-induced ocean regime shifts (Lehodey et al., 2006; Takasuka et al., 2008). Recently, the optimal growth temperature hypothesis has been proposed to explain the population oscillation of Japanese sardine and Japanese anchovy in the western North Pacific (Takasuka et al., 2007).

The annual catch of the Japanese sardine in the Sea of Hiuchi (Fig. 1), central Seto Inland Sea, abruptly increased in the 1990s (Fig. 2), when the Pacific coast population had collapsed (Watanabe Y. et al., 1995). Occurrence of eggs and larvae of Japanese sardine in the Sea of Hiuchi in the late 1990s shows adult stock had immigrated to spawn into this area after the 1980s (Watanabe A. et al., 1995; Watanabe and Hashimoto, 2005). The increase in Japanese sardine population and alternation of dominant species from Japanese anchovy to Japanese sardine in the Sea of Hiuchi occurred about 10 yr after that in the western North Pacific. In the 1990s, when the Japanese sardine annual catch increased in the Sea of Hiuchi, annual average and lowest water temperatures in the central Seto Inland Sea were higher than those in the 1980s (Yamamoto, 2003; Uye and Ueta, 2004). Therefore, the optimal growth temperature hypothesis, which has been proposed to explain the population oscillation in the western North Pacific (Takasuka et al., 2007), may not well explain the alternation of dominant species from Japanese anchovy to Japanese sardine in the Sea of Hiuchi in the 1990s. There might have been another mechanism affecting population dynamics of Japanese sardine and Japanese anchovy in the Sea of Hiuchi.

In addition to Japanese sardine and Japanese anchovy, gizzard shad *Konosirus punctatus* is a dominant clupeiform fish in the Seto Inland Sea. In the Sea of Hiuchi, gizzard

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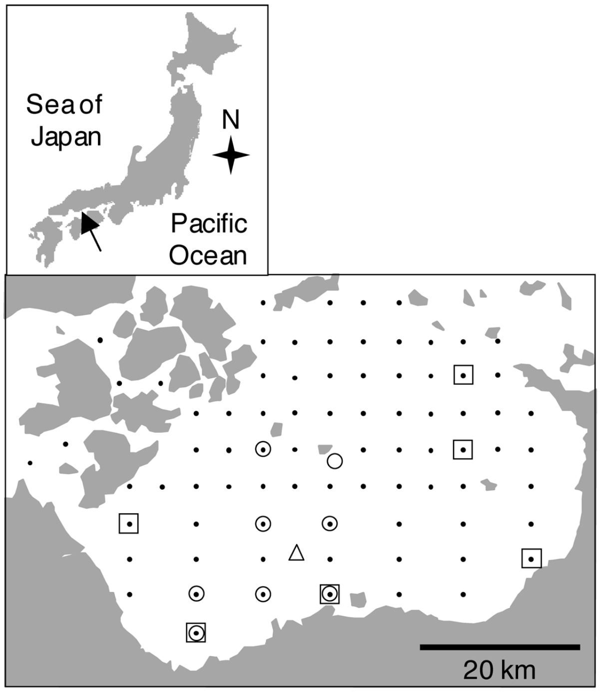

Figure 1. Map of the Sea of Hiuchi, the central waters of the Seto Inland Sea, showing the sampling stations where Japanese sardine, gizzard shad and Japanese anchovy larvae were collected. Monthly sampling was conducted at eight stations (open circles) from November 1997 to October 1998. Samples from six stations (open squares) were used for comparison of ichthyoplankton composition among three years (1982, 1995 and 2008). Intensive sampling for horizontal distribution of the larvae was conducted at 80 stations (dots) in 1995. Larval vertical distribution was investigated over periods of 24 hours at a station (open triangle) in the southern area.

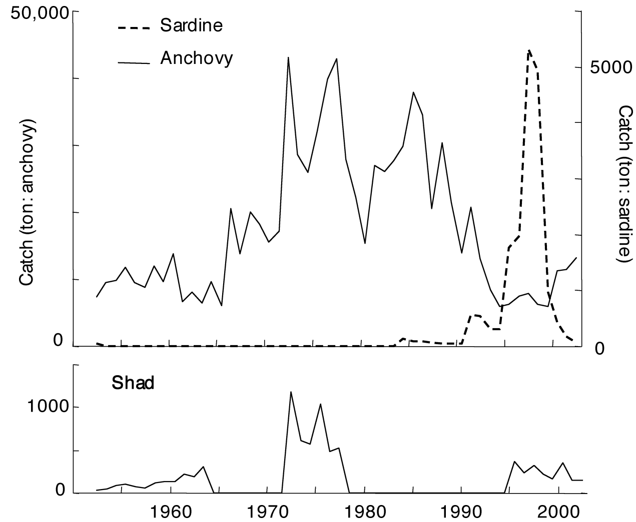

Figure 2. Annual catch of Japanese sardine, gizzard shad and Japanese anchovy in the Sea of Hiuchi, central Seto Inland Sea.

shad larvae were abundant in May and June when the larvae of Japanese sardine and Japanese anchovy also were abundant in the 1990s (Zenitani, 1998; Shoji et al., 2002). Analysis of ecological information on larvae of the three species in the Sea of Hiuchi during the 1990s would contribute to interspecific comparison of the early life histories and recruitment mechanisms of the three species which share common body morphology and feeding habits (Okayama Prefecture Fisheries Experimental Station, 1964; Okiyama, 1988).

In the present study, seasonal occurrence, horizontal and vertical distributions of larvae of Japanese sardine, gizzard shad and Japanese anchovy were investigated in the Sea of Hiuchi in order to compare larval spatial distributions of the three species. Ichthyoplankton surveys were conducted in the Sea of Hiuchi in three periods: before (1982), during (1995–1998) and after (2008) the period of Japanese sardine population increase. Intensive samplings to examine the horizontal distribution of the larvae (in 1995) and samplings over periods of 24 h (in 1997) were conducted to determine the spatial distributions of larvae of the three species.

Materials and Methods

Monthly larval sampling for seasonal occurrence from 1997 to 1998

Monthly larval sampling was conducted by RV *Hiuchi* (4.9 t) of Ehime Prefecture Chuyo Fisheries Experimental Station (EPCFES) from November 1997 to October 1998 in the Sea of Hiuchi, central Seto Inland Sea (Fig. 1). Oblique tow from the surface to 2 m above the bottom was made by using a conical larva-net (1.3-m mouth diameter, 6.9 m length and 0.5-mm mesh) at eight stations (from coastal to central area, covering the sea depth range between 5 and 35 m) in the central part of the Sea of Hiuchi. Further details of the sampling and list of fish larvae collected during the sampling are given in the previous study (Shoji et al., 2002). Abundance of the larvae was used for analysis of the seasonal occurrence in the present study.

Sampling for comparison among 1982, 1995 and 2008

Ichthyoplankton sampling was conducted in May and July, when the larvae of the three clupeiform species occurred (See the results section), in order to compare the larval fish composition among the three years from three decades: 1982, 1995 and 2008. Research cruises were carried out by RV *Shirafuji* (138 t) of the National Research Institute of Fisheries and Environment of Inland Sea (NRIFEIS) during 5–9 May and 10–14 July 1982, 24–28 May and 20–23 June 1995 and 13–15 June 2008 and by RV *Toyoshio* (256 t) of

Hiroshima University in 9–10 May 2008 in the Sea of Hiuchi. Oblique tow from the surface to 5 m above the bottom was made by using a conical larva-net (1.3-m diameter, 6.9 m length, 0.315-mm mesh: 1982 and 2008) and a bongo net (0.7-m diameter, 1.85 m length and 0.315-mm mesh: 1995) at six stations (Fig. 1). The stations for the sampling in 1995 and 2008 were fixed at the same location as those in 1982. The data from the six stations in 1995 were also used for the analysis of larval horizontal distribution using data from the intensive sampling in 1995 (see below).

Intensive sampling for horizontal distribution in 1995

Ichthyoplankton sampling was conducted at 80 stations covering whole areas of the Sea of Hiuchi (Fig. 1) to examine the horizontal distribution of the larvae of the three clupeiform species in May and June 1995, when larvae of the three species were abundant in the Sea of Hiuchi (see the results section). Research cruises were carried out by RV *Shirafuji* during 24–28 May and 20–23 June 1995 in the Sea of Hiuchi. Oblique tow from the surface to 5 m above the bottom was made by using a bongo net (0.7-m diameter, 1.85 m length and 0.315-mm mesh) at each station (Fig. 1).

24-hour samplings for vertical distribution

Samplings over periods of 24 hours were carried out during the cruise of the RV *Yuri* (4.9 t) of EPCFES, on 3–4 June 1997 (day: $n=5$, dusk: $n=1$, night: $n=3$; dawn: $n=1$). Four layers (0, 5, 10 and 20 m) were sampled by depth-discrete horizontal tows for 10 min with a conical larva-net (1.3-m mouth diameter, 6.9 m length and 0.5-mm mesh) at a station in the southern part of the Sea of Hiuchi, where clupeiform larvae were abundant (Shoji and Tanaka, 2005). Details of the samplings were shown in a previous study (Shoji et al., 1999a). Data on the clupeiform larvae abundance were used for the analyses of the vertical distribution in the present study.

Treatment of samples

Water temperature and salinity from the surface to bottom were measured with a CTD during each sampling. Ichthyoplankton samples were fixed in 10% formaldehyde-seawater solution on board and sorted later in the laboratory. The volumes of seawater filtered by the nets were measured by a flow-meter mounted in the mouth of the net. The number of larvae was converted to concentration (no. 1000 m^{-3}).

Results

Seasonal occurrence from 1997 to 1998

A total of 6,377 Japanese sardine (2.8–22.3 mm in body length: BL), 8,045 gizzard shad (3.3–13.7 mm BL) and 588 Japanese anchovy (2.6–11.5 mm BL) were collected by the monthly sampling from November 1997 to October 1998 (Fig. 3). Japanese sardine larvae were abundant from November to March and from May to June. Gizzard shad occurred from May to July. Japanese anchovy larvae occurred from April through December with a maximum abundance in June. Larvae of the all three species were abundant in May and June.

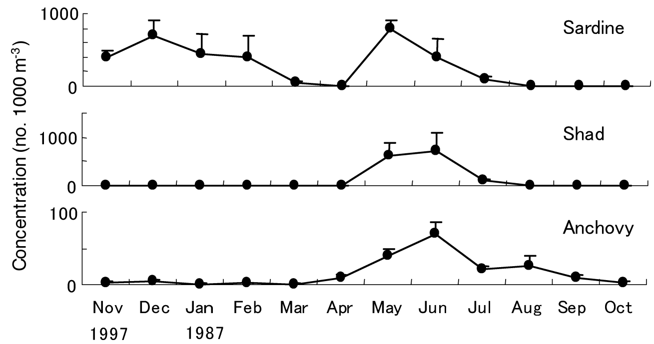

Figure 3. Seasonal changes in mean concentration (standard deviation as vertical bars) of Japanese Sardine, gizzard shad and Japanese anchovy in the Sea of Hiuchi.

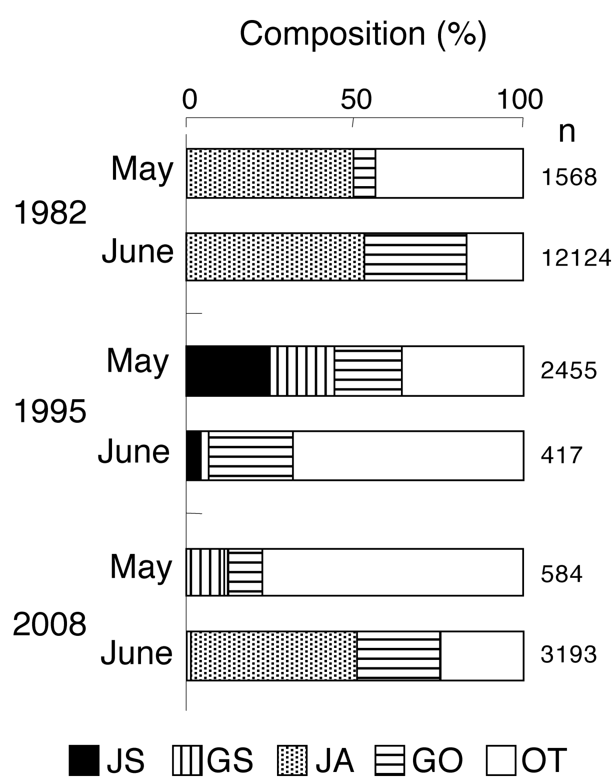

Figure 4. Numerical composition of ichthyoplankton in May and June 1982, 1995 and 2008 in the Sea of Hiuchi. JS: Japanese sardine; GS: gizzard shad; JA: Japanese anchovy; GO: Gobiidae; OT: others.

Comparison of ichthyoplankton community among 1982, 1995 and 2008

A total of 20,134 clupeiform larvae were collected by the sampling for comparison of composition of clupeiform larvae during the three decades (Fig. 4). Dominant clupeiform species differed among the years. In 1982, Japanese anchovy was most dominant in both May (49.2% in number of total ichthyoplankton) and June (51.9%) while the composition of Japanese sardine (0%) and gizzard shad larvae (<0.5%) was minimal in 1982. In May 1995, Japanese sardine (25.1%) and gizzard shad (18.4%) were dominant. In 2008, gizzard shad (11.1%) was dominant in May and Japanese anchovy (49.4%) in June.

Horizontal distribution in 1995

A total of 67,841 fish were collected during the intensive sampling at 80 stations for horizontal distribution in 1995, with 12,763 Japanese sardine, 11,773 gizzard shad and 659 Japanese anchovy larvae. Japanese sardine and gizzard shad larvae were more abundant in May than in June 1995, with higher concentration in the middle and northern area of the Sea of Hiuchi in May (Fig. 5). Japanese anchovy larvae were more abundant in June than in May. There was a significant correlation in the larval concentration between Japanese sardine and gizzard shad in May and June (Fig. 6), but no significant correlation was detected in the relationships between Japanese sardine and Japanese anchovy and between gizzard shad and Japanese anchovy.

Diel vertical movement of the larvae

Japanese sardine and Japanese anchovy larvae were abundant at sub-surface (5 m in depth) to bottom (20 m) layers and were less at the surface during the all sampling time periods (Fig. 7). Contrastingly, gizzard shad larvae were most abundant at surface to sub-surface layers through the day.

Discussion

Results from the monthly and decadal samplings showed that the three clupeiform species spawned in the Sea of Hiuchi and their larvae were distributed within the same area in May and June during the late 1990s. After the increase in annual catch of Japanese sardine in the Sea of Hiuchi due

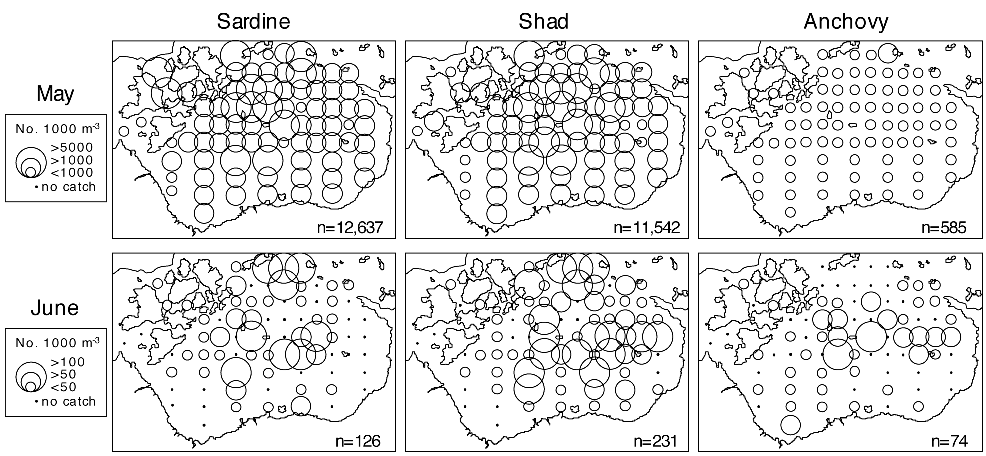

Figure 5. Horizontal distribution of Japanese sardine, gizzard shad and Japanese anchovy in May (top) and June (bottom) 1995 in the Sea of Hiuchi.

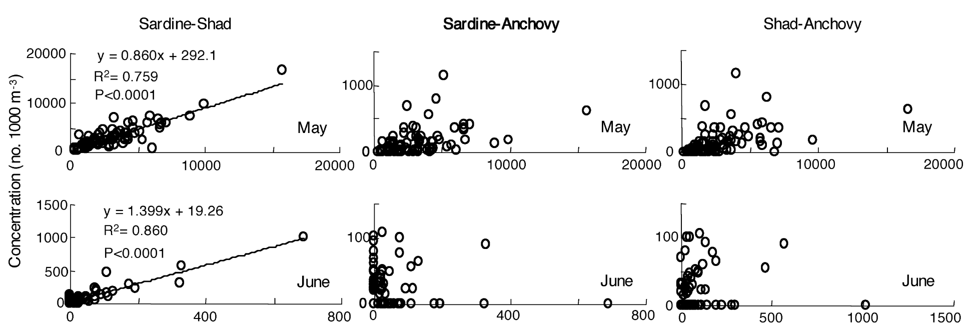

Figure 6. Plots of larval concentration of gizzard shad to Japanese sardine (left), Japanese anchovy to Japanese sardine (middle) and Japanese anchovy to gizzard shad (right) in May (top) and June (bottom) 1995 in the Sea of Hiuchi.

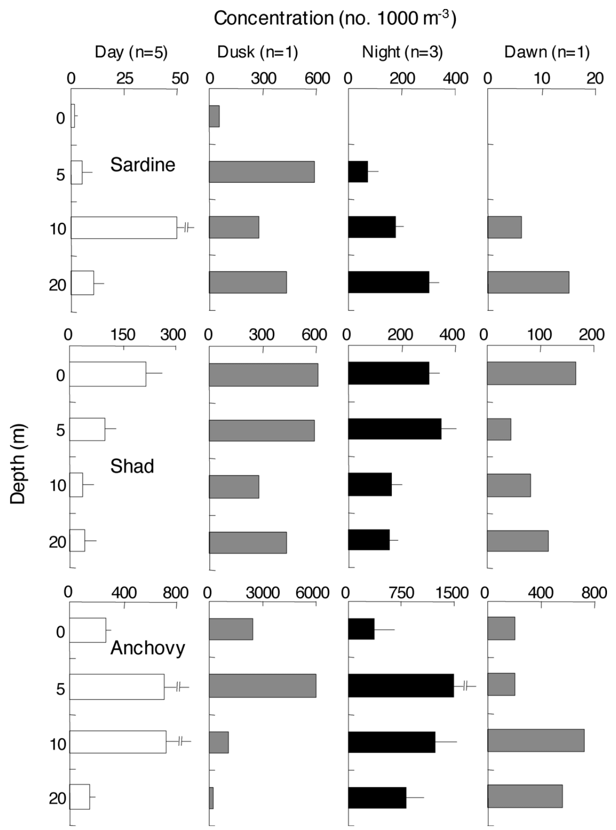

Figure 7. Mean concentration (standard deviation as horizontal bars) of Japanese sardine, gizzard shad and Japanese anchovy larvae at four different layers (0, 5, 10 and 20 m depth by discrete depth horizontal tows) at four different time of day (day, dusk, night and dawn) collected during the sampling for larval vertical distribution in 1997.

to the immigration of adult stock from the Pacific coast into the Seto Inland Sea, seasonal peak in the egg abundance was observed from April to May (Watanabe A. et al., 1995; Watanabe and Hashimoto, 2005). In addition, a previous research on hatch-date distribution by use of otolith microstructures showed that the Japanese sardine larvae and juveniles collected by a light trap in the Sea of Hiuchi from March 1996 to February 1997 originated from two separate spawning periods: late April to early June and mid October to mid January (Shoji et al., 1999b). Two separate seasonal peaks in spawning have been reported also in some of other *Sardinops* species, the Chilean sardine *S. sagax* and the South African sardine *S. ocellatus* (Le Clus, 1992; Lluch-Belda et al., 1992). Annual catch of Japanese sardine in the Sea of Hiuchi abruptly decreased after 1998 when biomass of adult Japanese sardine migrating from the Pacific coast to spawn in the Sea of Hiuchi decreased (Watanabe and Hashimoto, 2005). Japanese sardine egg production also decreased after 1999 corresponding with the decrease in annual catch of adult fish. Fishing is another possible factor which had accelerated the decrease in Japanese sardine population in the Sea of Hiuchi. The gill net fishery to catch mainly the Japanese sardine started in the 1990s in the Sea of Hiuchi since Japanese sardine was economically more valuable than the other two clupeiform fishes: Japanese anchovy and gizzard shad (Watanabe and Hashimoto, 2005).

Gizzard shad larvae were abundant in May and June, occurring with a low concentration in July in the Sea of Hiuchi in the 1990s. Although the annual catch of gizzard shad is not as large as that of Japanese anchovy in the Seto Inland Sea, gizzard shad eggs and larvae have been reported to occur from May to June (Okayama Pref. Fish Exp. Sta., 1964), sometimes at higher concentrations than those of Japanese anchovy in the Sea of Hiuchi (present study) and Osaka Bay (Yamamoto et al., 1997). Recent larval and juvenile fish surveys in Hiroshima Bay showed gizzard shad larvae occurred in the surf zones of the northern bay area in May (Iwamoto et al., 2009). Ecological information from juvenile to adult stages such as migration and spawning of gizzard shad is still limited (Kawasaki et al., 2006). Based on the results from the previous and present studies, however, it is plausible that gizzard shad spawned from May to June for recent decades in the Seto Inland Sea.

Japanese anchovy larvae occurred over a longer seasonal period (from April through December 1998) compared to the other two species in the Sea of Hiuchi. They were collected from May through October (seasonal peak in abundance: June) also in the 1960s in the central waters of the Seto Inland Sea (including Sea of Huchi and Bisan-set: Okayama Pref. Fish Exp. Sta., 1964). Although season and peak of spawning of Japanese anchovy have been reported to vary based on their stock size (Funakoshi, 1990), it seems that Japanese anchovy has been spawning in May and June in the Sea of Huichi for the recent 30 yr. Therefore, the three clupeiform species share the same spawning season (May to June) in the 1990s, when the Japanese sardine population increased in the Sea of Hiuchi.

The intensive sampling for horizontal distribution demonstrated that the larvae of three clupeiform species were widely distributed in the Sea of Hiuchi in May and June in the mid 1990s. Mean sea surface temperature of the sampling stations was 18.6±1.2 and 20.5±0.6°C in May and June 1995 and 19.0±1.3 and 19.4±1.0°C in May and June 1996 with higher temperatures at eastern part of the Sea of Hiuchi during the all cruises (Shoji and Tanaka, 2005). Larvae of the three species were abundant at the central area of the Sea of Hiuchi where the temperature ranged between 16–22°C. The egg-density-weighted-mean sea surface temperature estimated for Japanese sardine (18.1°C) and Japanese sardine (20.7°C) in the Pacific coast of Japan (Takasuka et al., 2007) are within the range of temperature in the Sea of Hiuchi.

Nevertheless, cross-species comparison of larval horizontal distribution demonstrated different patterns of larval horizontal distribution among the species. The optimum spawning temperature of Japanese sardine and Japanese anchovy (Takasuka et al., 2007) might have induced the difference in the larval horizontal distribution between Japanese sardine and Japanese anchovy within the Sea of Hiuchi. On the other hand, overlap in the larval horizontal distribution was more evident between Japanese sardine and gizzard shad in May and June 1995 and 1996 in the Sea of Hiuchi. The major spawning areas of Japanese sardine and gizzard shad seemed to have overlapped since eggs of the two species were abundant in the central and northern areas of Sea of Hiuchi during the cruises in 1995 and 1996 (Shoji et al., 2002).

Species-specific patterns in larval vertical distribution have been reported in many fish species (Okiyama, 1965; Last, 1980). For the three clupeiform species examined in the present study, larval vertical distributions have previously been investigated in the Seto Inland Sea and adjacent waters. Japanese sardine larvae were abundant in surface to mid layers (15–70 m in depth, depending on time and space) off the southwestern Pacific coast of Japan (Konishi, 1980). Gizzard shad larvae seemed to be concentrated in the surface layer in Osaka Bay (Yamamoto et al., 1997) and in 10-m layer in Kii Channel (Horiki, 1981) although there is still no information on their vertical distribution during the nighttime. Japanese anchovy larvae have been reported to be abundant in the sub-surface to mid layers in each area during daytime: 5 m layer in the Bisan Archipelago (Okayama Pref. Fish. Exp. Sta., 1964), 10–20 m layers in Kii Channel (Horiki, 1981) and 5–20 m layers in Osaka Bay (Yamamoto et al., 1997). During nighttime, concentration of Japanese anchovy larvae increase in the upper layers (0–5 m) probably due to decrease in swimming performance with expansion of their gas bladder (Okayama Pref. Fish. Exp. Sta., 1964; Uotani, 1973). So far, however, there has been no study on comparison of larval vertical distribution among the three species in the same area.

In the present study, species-specific patterns of larval vertical distribution has been demonstrated for the three clupeiform species in the Sea of Hiuchi. Japanese sardine and gizzard shad larvae were abundant in deeper layers than gizzard shad in the Sea of Hiuchi. Surveys on vertical profiles of physical conditions showed temperature was 21.5°C at surface and 16.2°C at bottom and salinity ranged 32.9–33.7 during the 24-h samplings for vertical distribution on 3–4 June 1997 (Shoji et al., 1999b). A thermocline was observed at the depths around 5–10 m throughout the sampling series. Gizzard shad larvae were more abundant above the thermocline while Japanese sardine and Japanese anchovy were more abundant bellow that. Physical conditions such as temperature and light intensity might have affected the vertical distribution of each species.

As conclusions, larvae of the three clupeiform species, Japanese sardine, gizzard shad and Japanese anchovy, were simultaneously distributed in the Sea of Hiuchi during the late 1990s after the increase in Japanese sardine population in this area. Among the three species, larval horizontal distributions of Japanese sardine and gizzard shad well overlapped but vertical distributions did not. Further investigation on larval spatial distribution together with physical conditions would lead to understanding the mechanisms how larval spatial distribution pattern differs among the three species.

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1990年代の瀬戸内海中央部燧灘におけるマイワシ，コノシロ，カタクチイワシ仔魚の空間分布

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太平洋岸マイワシ資源が1990年代前半に急減したのとは対照的に，瀬戸内海中央部の燧灘では1990年代後半に漁獲量が過去最大となり，ニシン目3種（マイワシ，コノシロ，カタクチイワシ）仔魚が同時期に出現した．3種の初期生活史の比較研究を目的として，燧灘におけるマイワシ漁獲量急増期（1995–1998年）とその前後（1982，2008年）に仔魚の出現と空間分布を調査した．漁獲量変動に対応して1982年にはカタクチイワシが，1995年にはマイワシとコノシロが，2008年にはコノシロとカタクチイワシが5–6月のニシン目仔魚のなかで優占した．3種の仔魚がいずれも比較的多く採集された1995年には，コノシロとマイワシの水平分布が最もよく重複した．表層付近に集中する傾向が強かったコノシロ仔魚と，中-底層で多く採集されたマイワシおよびコノシロ仔魚との間で鉛直分布パターンが異なった．

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