Comparison of early life histories between two clupeid fishes (*Konosirus punctatus* and *Sardinella zunasi*) in Ariake Sound, Shimabara Bay, Japan

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Abstract: The clupeid fishes, *Konosirus punctatus* and *Sardinella zunasi*, are dominant in the larval ichthyofauna of Ariake Sound, Shimabara Bay, where they spawn in spring and spring to summer, respectively. The distribution of two species larvae partly overlapped in the inner estuaries in spring. To clarify the early life histories of both species, the pelagic, demersal and immigrated stages were collected with larva nets, a beam trawl and a seine net, respectively, in Ariake Sound in May 2006 and 2019. While egg and larva distribution of both species spatially fluctuated between two years, both larvae were fundamentally observed to aggregate in the inner parts of the sound. *K. punctatus* and *S. zunasi* used the littoral zone and the inner estuaries as their nursery grounds, respectively, but they overlapped to inhabit some estuaries. Then, the vertical distributions of larvae in the estuary showed that *K. punctatus* was aggregated in the surface layer, and *S. zunasi* was dispersed during all tidal phases. Thus, there is likely less serious competition of larval niche during early larval period between two species in the estuaries.

Keywords : *Ariake Sound, Konosirus punctatus, Sardinella zunasi, larval distribution*

1. Introduction

Shimabara Bay is the largest tidal flat region with the highest tidal range in Japan. Ariake Sound (Fig. 1), which is located in the innermost part of the bay, is characterized by having brackish, highly turbid water with strong tidal

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currents（INOUE, 1980; YAGI *et al.*, 2011）. The importance of this upper estuary as a nursery ground has been demonstrated in a wide variety of fish species, including clupeoid fishes, such as *Coilia nasus*（Engraulidae）, *Konosirus punctatus*, *Sardinella zunasi*（Clupeidae）, and *Ilisha elongata*（Pristigasteridae）. *Coilia nasus* is an endemic species（UCHIDA and TSUKAHARA, 1955）, and *S. zunasi* and *I. elongata* are likely local stocks in Shimabara Bay（TAKITA, 1980, 2000）. All of these species have closely spawning seasons and grounds, while their larvae inhabit the upper estuary from spring to summer（YAGI, 2010; YAGI *et al.*, 2011）. It is considered that some larval niche isolation exists between these species as a means of avoiding competition within the estuaries of the sound.

Spawning of these species in the Ariake Sound occurs mainly in spring in *K. punctatus*, in summer in *C. nasus* and *I. elongata*, and in both seasons in *S. zunasi*（TAKITA, 1966, 1967, 1978; WANG *et al.*, 2021a, b）. Consequently, in the inner estuaries of the bay, larvae of *K. punctatus* and *S. zunasi* occur both sympatrically and in abundance in spring, while larvae of *C. nasus*, *I. elongata* and *S. zunasi* occur both sympatrically and in abundance in summer（YAGI, 2010; YAGI *et al.*, 2011; WANG *et al.*, 2021a, b）. Due to food isolation and slight differences in distribution, larval niche competition was not considered to be intense between *C. nasus*, *I. elongata* and *S. zunasi* in summer（WANG *et al.*, 2021a, b）; however, the extent of larval niche competition between *K. punctatus* and *S. zunasi* in spring has not yet been clarified.

This study therefore compared the horizontal and vertical distribution of *K. punctatus* and *S. zunasi* over tidal cycles to clarify the potential for spatial differences in their use of nursery grounds in Shimabara Bay.

2. Materials and Methods

Konosirus punctatus and *Sardinella zunasi* eggs and larvae were collected in Ariake Sound in the morning（7:00–12:00）at around spring tides（full moon）in May 2006 and 2019（Table 1）. Pelagic eggs and larvae were collected by oblique tows using a larva net with a mouth diameter of 1.3 m. The mesh apertures of the nets were 0.5 mm at the sea and river-mouth stations, and 1 mm at river stations to avoid clogging of the net by suspended particles. To collect demersal juveniles, beam trawls（width, 1.5 m; height, 0.3 m; 2-mm mesh aperture）were performed using a modification of the method described by KUIPERS（1975）. Table 1 shows sampling stations of two years, and the sets of larva net and beam trawl were made during both flood and ebb tides at Stns. 2 and 4 in 2006. A small seine net（1 × 4 m, 1-mm mesh aperture）（KINOSHITA *et al.*, 1988）was also used to collect larvae and juveniles immigrated the littoral zone at Miike beach（Fig. 1）.

To examine differences in the size and vertical distribution of the two species relative to the tidal phase, discrete-depth horizontal tows in the surface and middle layers were conducted with a larva net, and a beam trawl on the bottom at Stns. 6–8 of the Rokkaku River（Fig. 1）. The horizontal towing in the middle layer were fundamentally followed ZHONG *et al.*（2003）to avoid contaminations with other layer samples. Two or three sets of the three categorized collections were made from flood to ebb tides on 14 May 2006.

The towing distances（m）of the larva net were measured by a flow meter（2030R, General Oceanics）, and towing depths（m）by a divers watch（Log Memory 1473, Casio）in 2006, and a depth recorder（DEFI-D10, JFE Advantech）in 2019, attached to the nets. The towing distances（m）of the beam trawl and seine net was moni-
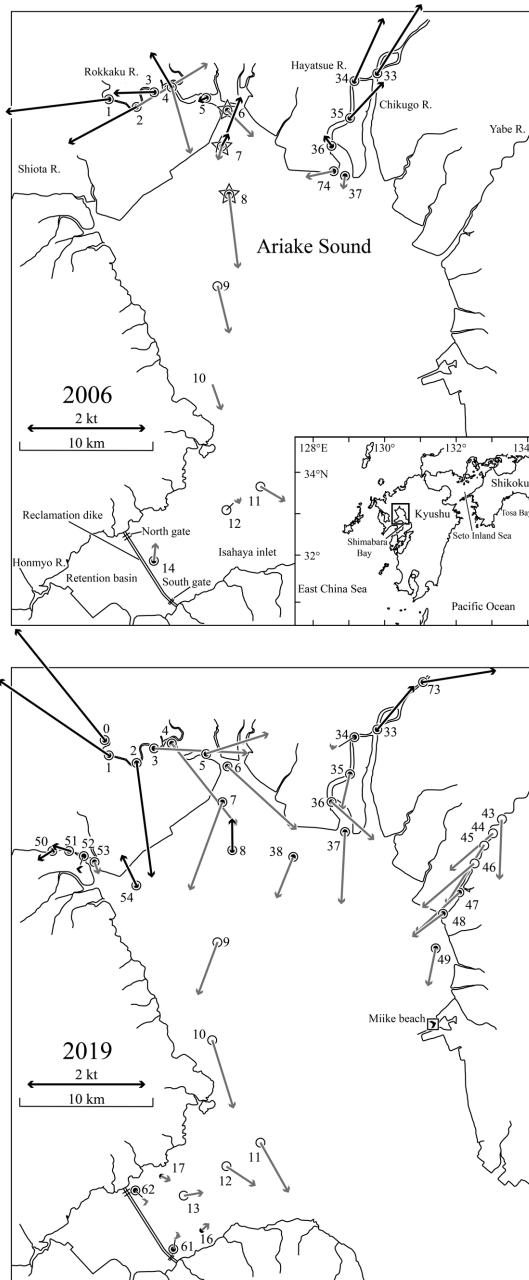
Fig. 1 Charts showing stations where fish were collected in Ariake Sound, Shimabara Bay, May 2006 and 2019. Open circles（Stns. 0–14, 33–38, 43–54, 61, 62, 73, 74）, solid circles（Stns. 0–8, 14, 16, 17, 33–38, 47–54, 61, 62, 73, 74）and the open square（Miike beach）indicate the stations where collections were made by a larva net for pelagic eggs and larvae, beam trawl for demersal juveniles and seine net for larvae and juveniles entering the littoral zone, respectively. Tidal sampling by discrete horizontal tows was performed from flood to ebb tides at Stns. 6–8（stars）in 2006. Solid（flood tide）and shaded（ebb tide）arrows show the tidal direction and speed（kt）at a depth of 1 m when surveys were made at each station.

Table 1. Sampling schedule for stations where fish collections (see Fig. 1) were made in Ariake Sound, May 2006 and 2019

Year	Date (May)	Station	
		Flood tide	Ebb tide
2006	12		8[*2], 9, 10[*2], 11, 12, 14
	13[*1]	1–5	2, 4, 6
	14	6[*3], 7[*3], 8[*3]	6[*3], 7[*3]
	15	33–36	37, 74
2019	16		9–13, 16, 17, 61, 62
	17	8, Miike	43–49
	18	33, 73	34–38, 6, 7
	19[*1]	50–52, 54	3–5, 53
	20	0–2	

[*1]: spring tide; [*2]: only observing water parameters; [*3]: tidal collection from discrete layers.

tored using a GPS (Colorado 300, Garmin in 2006; GPSMAP 64s, Garmin in 2019).

The number of individuals (n) was converted to density $(N: n \times 100 \, \text{m}^{-2})$ using the following equations:

$$N_{LN} = (n \times d \times 100)/(A \times D)$$

where A is the area (m^2) of the larva net, D is the towing distance (m), and d is the towing depth (m) for the larva net;

$$N_{BT, SN} = (n \times 100)/(w \times D)$$

where w is the width (m) of the beam trawl and seine net, and D is the towing distance (m) for the beam trawl and seine net.

All samples were initially fixed with ca. 10% field-water formalin. Eggs and larvae were immediately sorted and preserved in 10% formalin and 99% ethanol, respectively. Eggs and larvae of *K. punctatus* and *S. zunasi* were distinguished by UCHIDA (1958), MITO (1961), TAKITA (1966) and KURODA *et al.* (1983). The developmental stages of eggs and larvae were assessed by NAKAI (1962) and KENDALL *et al.* (1984), respectively. Unlabeled lengths indicate body length (notochord length for preflexion (including yolk-sac larva) and flexion larvae, and standard length for postflexion larvae). The mean body lengths at different tidal collection stations were compared by one-way ANOVA using the Games-Howell *post hoc* multiple comparison test using a significance level of $\alpha = 0.05$. To ascertain whether there was any difference in size preference on prey between the two fishes, a maximum of 100 specimens of each species that were collected from the two species most overlapped stations (Stns. 48 and 54 in 2019; Fig. 1) were randomly selected and their mouth size (SHIROTA, 1970) was measured. The data of mouth size were compared by ANCOVA using a significance level of $\alpha = 0.05$.

At each sampling station, temperature (℃) and salinity were measured at 0.5-m intervals from the surface to the bottom using STD (AST500-P, Alec Electronics), and turbidity measured at 1-m intervals from the surface to the bottom using a Water Quality Checker (WQC-22A, TOA DKK) in 2006. In 2019, these all physical parameters could be observed at 0.5-m intervals by a Compact-CTD (ASTD102, JFE Advantech). The current velocity was measured with an ADCP (WHSZ1200-I-UG12, RD Instruments) at 0.5-m depth intervals from a depth of 1-m to the bottom.

3. Results
Physical environment

Although it was same season between two years, water temperatures were markedly higher in 2019 (Fig. 2). In 2006, temperatures were somewhat higher in the rivers than sea, but there was little difference between the sea and rivers in 2019. Marked haloclines were observed between the estuary and upper river reaches, and these are attributed to the tidal exchange of water except the Shiota River in 2019. In 2006, Isahaya inlet blocked with the Honmyo River
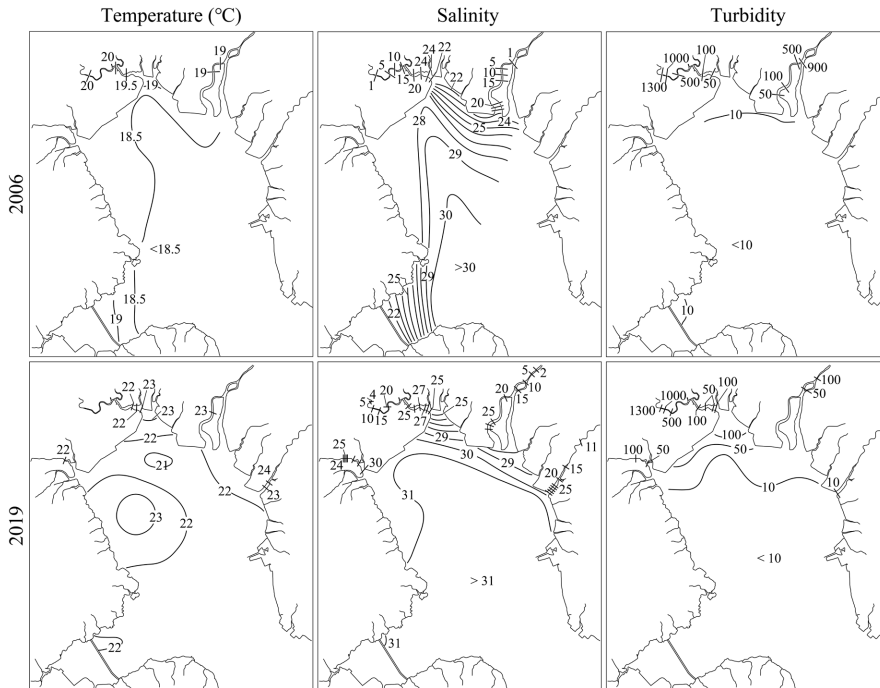
Fig. 2 Horizontal distribution of physical parameters at 0.5 m depth（turbidity measured at 1-m depth in May 2006）at each station when fishes were collected in May 2006 and 2019.

showed unusual halocline horizontally. Waters around estuaries were very turbid, while open bay and Isahaya inlet waters were relatively lower. In the rivers, much more turbid waters were born in the Rokkaku and Hayatsue Rivers in 2006, but the latter became considerably less turbid in 2019. Flood and/or ebb current speed ＞1 kt were frequently measured in the Rokkaku, Hayatsue, Yabe Rivers and open bay, whereas relative weaker current speeds were found in the Isahaya inlet and Shiota River（Fig. 1）.

Horizontal distributions of eggs and larvae

2006: A total of 9,684 *Konosirus punctatus* and 1,955 *Sardinella zunasi* eggs, chiefly at the A-stage of development, were collected outside the inner estuaries, both species being aggregated in Isahaya inlet. Inside rivers, little eggs were found in both species（Fig. 3）.

A total of 1,452 *K. punctatus* larvae（2.7–14.7 mm with a modal size at 10–11 mm）and 99 *S. zunasi* larvae（3.1–8.3 mm with a modal size at 3–5 mm）were sampled by the larva net, while the beam trawl captured neither *K. punctatus* nor *S. zunasi* larvae in any stations（Figs. 3, 4）. Like eggs, both larvae were more abundant in Isahaya inlet, but *K. punctatus* larvae were appeared inside rivers. Developmental stages of *K. punctatus* were earlier in the Isahaya inlet than Rokkaku and Hayatsue estuaries.

2019: A total of 9,804 *K. punctatus* and 3,780 *S. zunasi* eggs, chiefly at the B and C-stages of development, were collected from the Isahaya inlet to the inner estuaries, where the *K. punctatus* were more aggregated than the *S. zunasi*. The latter eggs were not observed in the Rokkaku
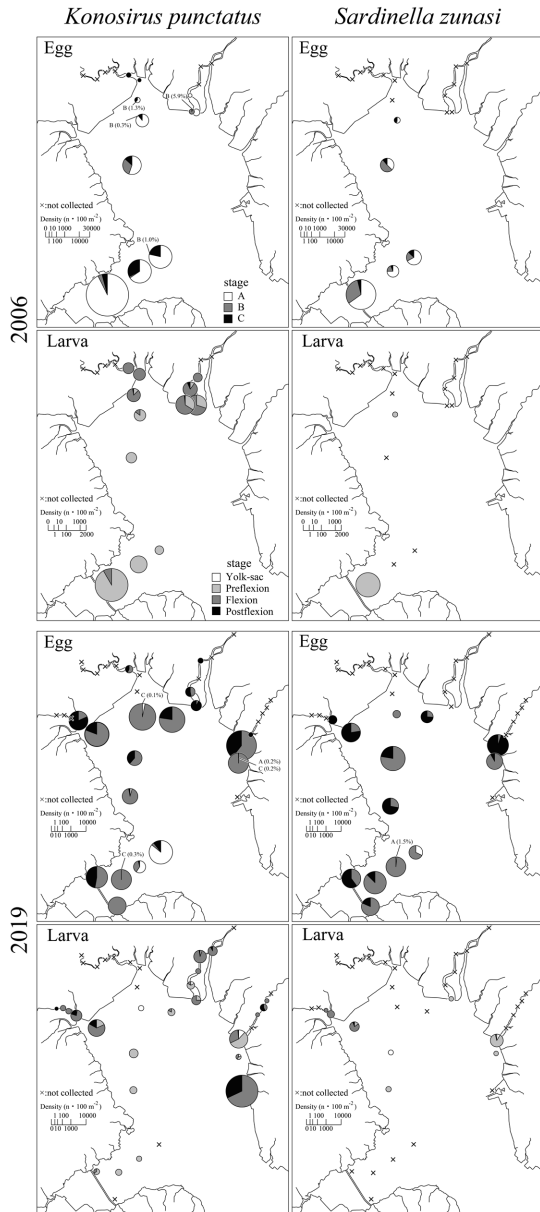
Konosirus punctatus   Sardinella zunasi

Fig. 3 Horizontal distribution of early stages of *Konosirus punctatus* and *Sardinella zunasi* collected by larva net and seine net in Ariake Sound, May 2006 and 2019. Densities at Stns. 7 and 8 in 2006 were averaged those of discrete horizontal tows for flood and ebb tides at each station, and at other stations, oblique tow data were used. The diameter of each circle is drawn in proportion to the square root of density ($n \times 100 \ m^{-2}$).

and Hayatsue Rivers. However, there were dominantly A-stages eggs of *K. punctatus* only near the mouth of Isahaya inlet (Fig. 3).

A total of 817 *K. punctatus* larvae (2.9–15.5 mm with a modal size at 9–10 mm) and 128 *S. zunasi* larvae (3.1–13.1 mm with a modal size at 3–4 mm) were collected using the larva net. Compared to eggs, *K. punctatus* larvae were found further upstream in rivers except the Rokkaku River, being scarce in the Isahaya inlet. The *S. zunasi* larvae were considerably scantier than *K. punctatus* larvae, being distributed almost in the mouth of the Shiota and Yabe Rivers, and absent in the Isahaya inlet. A total of 61,282 *K. punctatus* larvae [14,419 × haul^{-1} (ca. 50 m distance), mainly at the flexion stage, 9.4–16.4 mm with a modal size at 11–12 mm] were collected in the littoral zone of Miike beach, but no *S. zunasi* larvae being occurred at this site.

Tidal distribution

Dominant tidal currents entirely affected the vertical structure of the water column at Stns. 6 (river mouth), 7 (just outside the river mouth) and 8 (sea) (Fig. 5). Higher temperatures, lower salinities and higher turbidities were gradually accounting upper estuary. The current flowed up and down, mixing vertically, but was marginally stronger at the surface than in the bottom layers at all stations. Waters near the bottom were more turbid when current speed over 0.5 kt during both tides at three stations.

Most of *K. punctatus* eggs, predominantly with A stage, occurred at Stn. 8 and the eggs gradually developed as upper estuary. There, however, were only a few eggs and larvae of *S. zunasi* at only Stn. 8, where the *K. punctatus* eggs were more abundant in the surface and middle layers during flood and high tides, respectively. In *K. punctatus*, Stn. 7 yielded most larvae, being assembled at the surface in all stations (Fig. 6).
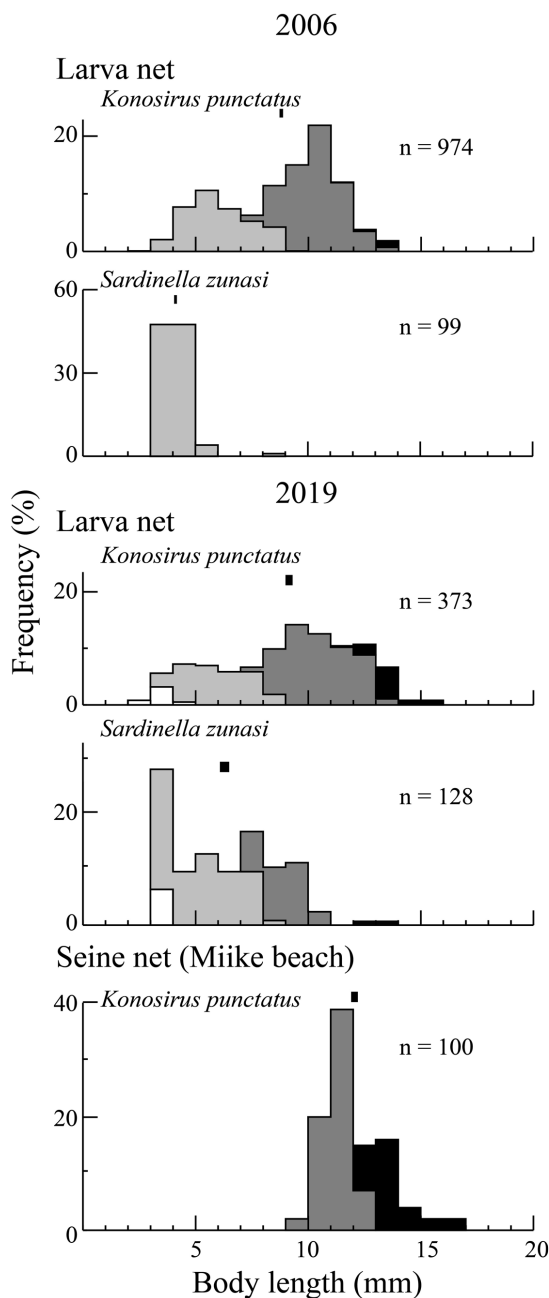
Fig. 4 Size and developmental-stage frequencies for *Konosirus punctatus* and *Sardinella zunasi* collected in Ariake Sound, May 2006 and 2019. The thick bar above each histogram denotes mean ± SE of body length. The patterns of larval developmental stages are the same as those in Fig. 3.

The larvae were more developed and larger at Stns. 6 and 7 than Stn. 8 (Fig. 7).

Comparison of mouth size

Larval mouth sizes were significantly larger in *Sardinella zunasi* than *Konosirus punctatus* especially under the flexion stage (Fig. 8).

4. Discussion

Temperatures were entirely ca. 3℃ higher in 2019 than in 2006. TAKEUCHI (2012) and our stocked data from 2002 to 2013 indicated temperatures suddenly fluctuated from ca. 19℃ in early May 2005 to 21–23℃ in later May 2002, 2003, 2009 and 2013. Thus, the differentiation between 2006 and 2019 should be attributable to seasonal rising for the short term rather than a global warming. Usually, there are hardly differentiation of salinities as ca. 30 between Isahaya inlet and open bay (YAGI *et al.*, 2011; TAKEUCHI, 2012; SIMANJUNTAK, 2016). Accordingly, the horizontal halocline in 2006 could be definitely due to discharging land waters from the retention basin by irregularly opening the north and south gates of the reclamation dike (Fig. 1) (per. commu. from Nagasaki Station, Kyushu Regional Agricultural Administration Office, 2006).

The eggs of both species were primarily at A and B-stages of development in May 2006 and 2019, respectively (Fig. 3). When ca. 28℃ in July 2016, most of *Sardinella zunasi* eggs were under C-stage (WANG *et al.*, 2021b). Accordingly, the difference of egg developmental stage between 2006 and 2019 seems to be attributed to the water temperature, i.e. higher temperatures in 2019 could accelerate to make both clupeid eggs develop.

In *S. zunasi*, although there is little differentiation in the horizontal distribution scale of the eggs between May (Fig. 3) and July (WANG *et al.*, 2021b), the larvae were hardly distributed in-
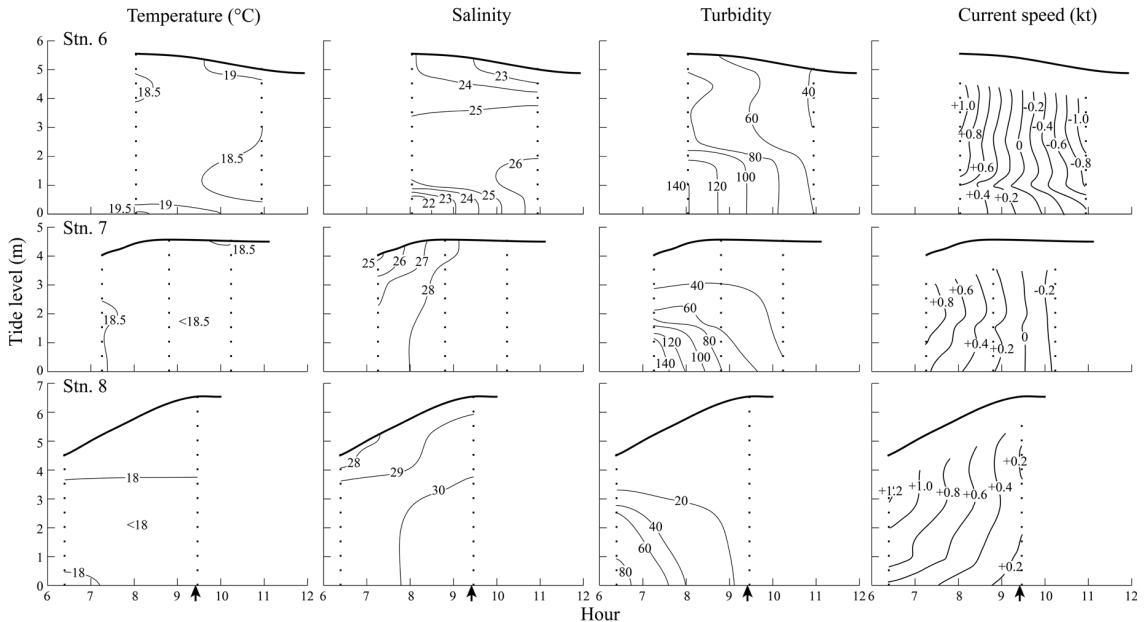
Fig. 5 Vertical profiles of physical parameters at Stns. 6–8 with the tidal level on 14 May 2006. Flood and ebb tide speeds are denoted as + and -, respectively. Arrows indicate the hour at high tide.

side the Rokkaku and Hayatsue Rivers in May. In August 2005 (YAGI *et al.*, 2011) and July 2016 (WANG *et al.*, 2021b), a rather number of *S. zunasi* larvae occurred in both the Rokkaku and Hayatsue estuaries. The reason for this difference is considered to be a seasonal variation. Compared to larvae of *Konosirus punctatus*, those of *S. zunasi* were more scarcely distributed in the both years. In July 2016, however, *S. zunasi* larvae abundantly occurred around inner estuaries and Isahaya inlet (WANG *et al.*, 2021b). These suggest that May is too early to distribute this species larvae in Ariake Sound. In the Isahaya inlet of 2019, *S. zunasi* tended to spawn actively, but no their larvae were appeared, so that this may show there was a large larval mortality from unknown cause, and also in July 2016, the Isahaya inelt hardly could accelerate to develop *S. zunasi* larvae (WANG *et al.*, 2021b). Furthermore, the Isahaya inlet was annually yield no more than a few larvae of this species in summer

of 2004–2011 (TAKEUCHI, 2012). However, *S. zunasi* larvae were previously predominately abundant in the Honmyo estuary (Fig. 1) in June 1979 (KINOSHITA, 2007; TAKEUCHI, 2012). Taken together, these findings suggest that the construction of a dike across the inlet blocking the Honmyo River (Fig. 1) in 1997 has had an adverse effect on the suitability of the Isahaya inlet for use as a nursery ground for *S. zunasi*. Hence, the present or absent of undeveloped larvae suggest that the now Isahaya inlet is suboptimal for early life history of *S. zunasi*.

Compared to the eggs, the *K. punctatus* larvae migrated upstream in Shiota, Hayatsue and Yabe Rivers, becoming more euryhaline. However, few *K. punctatus* larvae were collected in the Rokkaku River, suggesting that the extremely turbid waters of the Rokkaku River have an adverse effect on larval migration (Figs. 2, 3). In May 2019, a huge number of larger and more developed larvae than larva net collections of *K.*
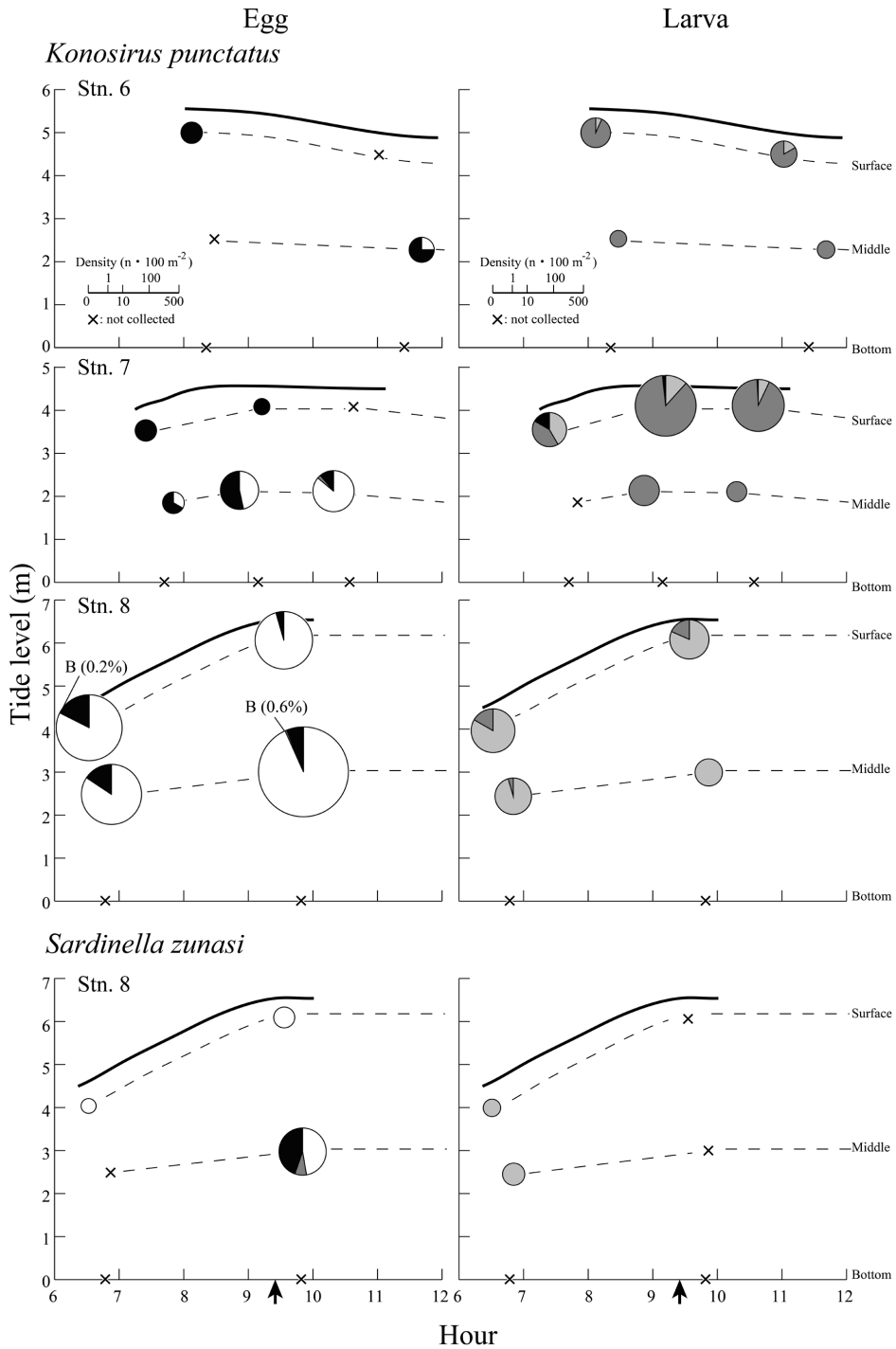
Fig. 6 Tidal vertical distribution for eggs and larvae of *Konosirus punctatus* and *Sardinella zunasi* at Stns. 6–8 on 14 May 2016. The patterns of developmental stages, diameter of each circle and arrows are the same as those in Figs. 3 and 5, respectively.
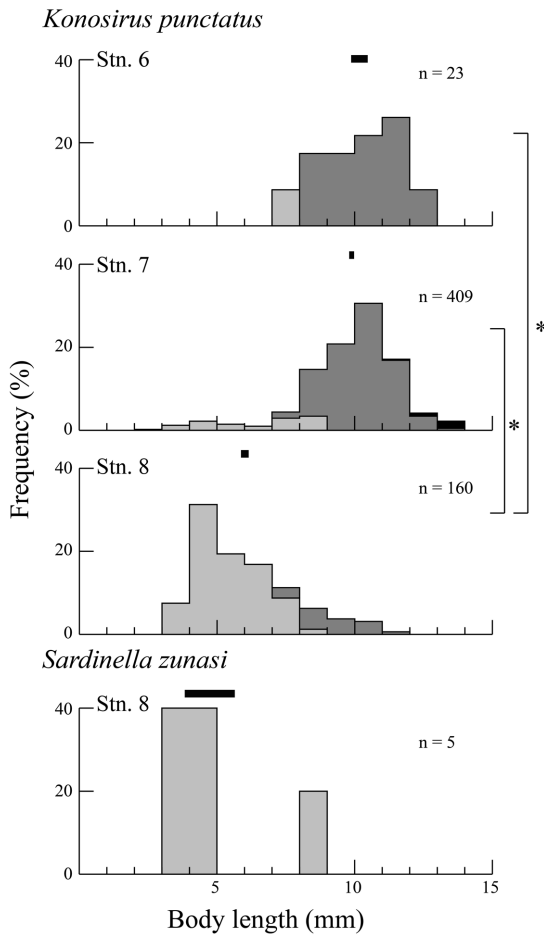
Konosirus punctatus

Sardinella zunasi

Fig. 7 Spatial comparison of the size and develop-ment-stage frequencies for *Konosirus punctatus* and *Sardinella zunasi* during tidal collections in 2006. The thick horizontal bar above each histo-gram denotes mean ± SE of body length. The pat-terns of larval developmental stages are the same as those in Fig. 3. *: Significant at $\alpha = 0.05$ be-tween the two stations.

punctatus occurred in Miike beach (Figs. 3, 4). Thus, they tend to be inshore when attaining to the flexion stage. This finding was corroborated by HIBINO *et al.* (2002) who demonstrated that *K. punctatus* larvae were the most abundant larvae in Miike beach. In other areas such as Tosa Bay in Shikoku, *K. punctatus* has been reported to be

the most dominant along surf zones of sandy beaches in spring (KINOSHITA, 1993; FUJITA, 2005). These findings imply that *K. punctatus* larvae use shallow coastal areas like Miike beach, where it relatively lower turbid (Fig. 2), as nursery grounds, rather than inner estuaries in the Ariake Sound. Prior to the construction of dike in the Isahaya inlet, indeed, KINOSHITA's (2007) and TAKEUCHI's (2012) data of 1979–1980 showed that the *K. punctatus* larvae were rela-tively uncommon in the Honmyo estuary, which had as visually turbid waters as those of Rokka-ku estuary. This phenomenon was observed in 2004–2009 (YAGI *et al.*, 2011; TAKEUCHI, 2012) un-til the present, indicating a nature of *K. puncta-tus* oneself. Before constructing the dike, *K. punctatus* larvae born in Isahaya inlet likely had used inner beaches of the inlet as their nursery ground.

In 2019 these two species were sympatrically distributed during the flexion and preflexion stages in the Yabe and Shiota estuaries, respec-tively (Fig. 3). Assessments of auxotrophic dif-ferentiation based on mouth size (Fig. 8) seemed to reveal a possibility of feeding competition and differentiation for flexion and preflexion larval periods in some estuaries, respectively. Then, in vertical distribution of *K. punctatus*, most abun-dant eggs under earlier developmental stage at Stn. 8 show that this station locates in the spawning grounds of this clupeid species. Subse-quently, the larvae became denser and larger at Stn. 7, being drastically aggregated at the sur-face in all stations irrespective tidal phases (Figs. 6, 7). These phenomena are likely attributed to not vertical but to the horizontal movement of larvae, which seem to move to shores such as Miike beach with relatively weak currents to avoid dispersing offshore during the ebb tide. There were only few *S. zunasi* larvae were cap-tured at Stn. 8 in the present study (Fig. 6), but
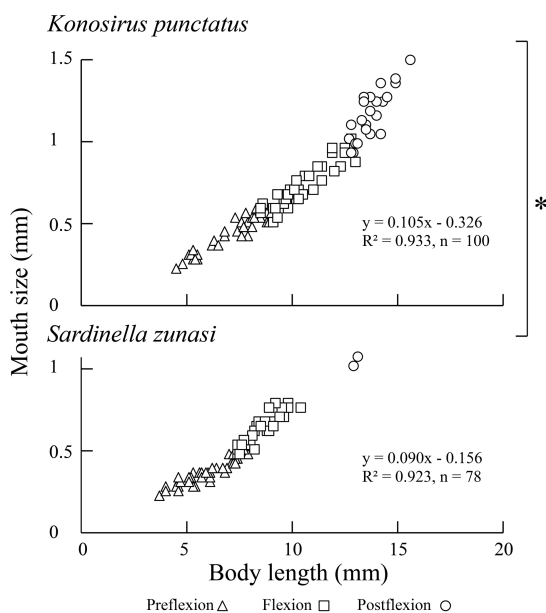
Fig. 8 Comparison of increment in mouth size with growth and development in *Konosirus punctatus* and *Sardinella zunasi* using collections in 2019. *: Significant at *α* = 0.05 between the two species.

WANG *et al.* (2021b) reported that this species larvae were vertically distributed throughout most layers during all tidal phases at Stn. 7 in July 2016. Thus, there may hardly occur serious niche competition between the two species.

In conclusion, four clupeoids, including also *Coilia nasus* and *Ilisha elongata*, overlapping their spawning and nursery grounds in the inner estuaries during spring to summer can vary vertical habitats and feeding habits each other (WANG *et al.*, 2021a, b), so that such niche isolation between closely related larvae likely facilitates the coexistence of these sympatric species in Ariake Sound, Shimabara Bay.

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