Distribution of Japanese temperate bass, *Lateolabrax japonicus***, eggs and pelagic larvae in Ariake Bay**

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Abstract We collected eggs and larvae of the Japanese temperate bass, *Lateolabrax japonicus*, and present horizontal and temporal changes of distribution relative to development and growth during the species pelagic life history in Ariake Bay. Sampling was conducted from the inner to central region (11 sampling stations) of Ariake Bay using a plankton net (80 cm diameter, 0.5-mm mesh) from November 2000 to February 2001. Both eggs and larvae were collected most abundantly in mid-December. The CPUE of eggs in the surface layer was higher than the middle layer, which is in contrast to that at the larval stage. Most eggs were collected around the central and western regions of the bay. The distribution of eggs shifted vertically to the middle layer with development. Yolk-sac larvae were collected in the central region of the bay, and preflexion and flexion larvae were more abundantly collected in the inner region of the bay. The body length of larvae around the inner bay was larger than in the central region. The pelagic life history can be summarized as follows: eggs are distributed around the central region of the bay and eggs and larvae expand their distribution to the inner and shallower waters with growth. We conclude that the shift of vertical distribution in pelagic stages and the hydrographic features of the middle layer form one of the mechanisms enabling the inshore migration of *L. japonicus*.

Key words Pelagic life history · Transportation · Isolated population · *Lateolabrax japonicus* · Ariake Bay

The Japanese temperate bass *Lateolabrax japonicus* is commonly distributed in the coastal waters of Japan, except for northern parts of Hokkaido and Ryukyu Islands, and is one of the important commercial and recreational fishes. Many ecological studies have clarified that estuaries (Matsumiya et al., 1982; Hibino et al., 1999), eelgrass beds (Fujita et al., 1988), and the surf zone of sand-mud flats (Kanou et al., 2000; Hibino, 2002) located in inner bay areas are important nurseries for the juvenile stage of this species. The year-strength of juvenile abundance has been shown to vary within almost a tenfold range and is affected by the survival rate from hatching to postlarval stage (Matsumiya et al., 1985). However, compared to the ecological traits of juvenile fish, little is known about the pelagic life history. For example, pelagic eggs and larvae of *L. japonicus* have been sampled along the thermohaline frontal areas between more oceanic waters and bay waters (Watanabe, 1965; Horiki, 1993), and larvae move to the inshore nursery via the middle to bottom layer of the water (Ohmi, 2002). In

Ariake Bay, it is speculated that the spawning ground of *L. japonicus* is located in the central region of the bay around the Shimabara Peninsula (WJSFIPC, 1973) and that eggs and pelagic larvae disperse toward the inner region (Hibino, 2002). However, the temporal dispersal process still remains unclear. It is important to clarify the mechanism of transportation to favorable nursery areas in the pelagic life history for elucidating the factors inducing yearly fluctuations of this species.

Ariake Bay is geographically semienclosed, is connected by a narrow inlet to the East China Sea, and has many river inflows represented by the Chikugo River in the inner region. Accordingly, some of the biological aspects and physical characters of water change dramatically from the mouth to the inner region of the bay (Hirota, 1974; Inoue, 1980; Sato and Takita, 2000). Furthermore, the tidal range is the largest in Japan, which produces a dominant tidal current. Therefore, it is an appropriate area in which to examine egg and larval drift to the nursery waters for settlement in relationship to physical and hydrographic characters. In addition, *L. japonicus* distributed in Ariake Bay is the endemic population that originates from the natural hybrid of the ancestor between *L. japonicus* and the Chinese temperate bass *Lateolabrax* sp. (Yokogawa et al., 1997; Nakayama, 2002). This population is regarded as one of the continental relict populations, similar to other endemic fish species that are distributed only in Ariake Bay (Sato and Takita, 2000). Ecological information on the pelagic life history may give us evidence to consider why this endemic *L. japonicus* population is able to persist to the present day.

In this study, we present spatial and temporal changes in the distribution of *L. japonicus* eggs and pelagic larvae relative to their growth and development in the central to inner region of Ariake Bay. Also, we discuss the process of inshore transportation and endemic aspects of the early life stage of the Ariake population.

Materials and Methods

Field sampling was conducted from the inner to central region in Ariake Bay, Kyushu, Japan, during the spawning season of *Lateolabrax japonicus* reported by the previous studies (WJSFIPC, 1973; Ohta, 2004). Sampling was conducted five times: 21–22 November and 13–14 and 26–27 December in 2000 and 17–18 January and 17–18 February in 2001. Based on previous information of their spawning ground (WJSFIPC, 1973), 11 sampling stations (stns. W1– W6; C1–C5; Fig. 1) located by a global positioning system (GPS) were established to clarify the dispersal process during pelagic life stages. A small fishing vessel was hired to carry out the sampling. It took 2 days to complete one sampling schedule; namely, sampling of the western six stations was conducted on the first day and sampling of the eastern five stations on the second day. On both days, sampling was started from the innermost station in the morning (ca. 0800) and finished at the outermost station in the afternoon (ca. 1400) without taking into account tidal conditions. Eggs and pelagic larvae were collected using a quantitative larva net (80 cm diameter, ca. 3 m length, 0.5 mm mesh aperture) equipped with a flowmeter at the net mouth. The net was towed horizontally at the surface and in the middle layer for 10 min per station. For surface towing, the research vessel was moved at about 1.5 knot/h against the water current. For middle layer towing, the research vessel was moved as slowly as possible against the water current. The towing depths of the middle layer were adjusted by length of a buoy rope as half of the depth at stns. W1, W2, C1–C3, which were shallower than 20 m, and at 10 m in other stations more than 20 m in total depth. A depth data logger (diver's watch) was attached at the net ring and monitored the actual depth of the towing layer.

Net samples were fixed and preserved in about 5% formalin, and fish larvae and eggs were sorted under a binocular microscope in the laboratory. Eggs of the genus *Lateolabrax* and larvae of *L. japonicus* were identified

Fig. 1. Locality of sampling stations in Ariake Bay. *Dotted line* indicates the border between the inner and central region of the bay (see text)

according to Mito (1957) and Kinoshita and Fujita (1988). The abundance of individuals was shown by catch per unit effort (CPUE) calculated from the individual number and actual filtering volume estimated by counts of the flowmeter. The developmental phase was examined for all eggs and larvae, and the body length for larvae was measured. The developmental phases of eggs were divided into the following three phases: phase I, to presence of embryo; phase II, to differentiation of tail; and phase III, to hatching. The developmental phases in larval stages followed the methods detailed in Kendall et al. (1984). Notochord length of larvae was measured as the body length with a micrometer attached to a binocular microscope. Because the numerical collection of pelagic larvae was small (see Results), the data for body length distribution and developmental phase frequency in each of the sampling stations were integrated into two regions, namely, central (stns. W3–W6 and stns. C3–C5) and inner (stns. W1, W2 and stns. C1, C2) regions of the bay, after Sato and Takita (2000).

Water temperature and salinity were measured at every 2m from the surface to 20m depth using a portable STD instrument (YSI) at every sampling station.

Results

Water temperature and salinity. Water temperature and salinity for each sampling date and station are shown in Table 1. Averages of water temperature in surface and middle layers were highest in November (18.5° and 18.6°C), decreased seasonally, and were lowest in February (9.5° and 10.3°C). The water temperature was lower by 10°C in the inner region on January and February. Salinity gradients showed almost the same pattern along the bay during the sampling periods. Both the water temperature and salinity were lower toward the inner region of the bay, and were constant between surface and middle layer in November and December, but slightly different in January and February.

Distribution of eggs. Egg collection results are shown in Table 2. A total of 4304 *Lateolabrax* spp. eggs were collected during the sampling period. Total catch and CPUE of egg were the highest on 13–14 December. The catch number and CPUE for the surface layer were higher than the middle layer at the egg stages. Figure 2 indicates CPUE of eggs and the ratio of developmental phases in each of the sampling stations during the sampling period. A large amount of eggs was constantly collected around the central regions (stns. W4–W6, C4, C5) of the bay from November to January. On the other hand, only a few eggs were collected at the innermost sampling stations (stns. W1 and C1), with the exception of 13–14 December. On 17–18 January, eggs were not collected at the inner regions, in contrast to the results in December. In February, eggs were hardly collected with the exception of stn. C5.

The frequencies of the developmental phases were different between the surface and middle layer; overall, the more developed phase eggs (phases II and III) tended to collect more abundantly in the middle layer (Fig. 2). Developmental phases of eggs were different among the sampling stations. In November, the earliest phase (phase I) eggs were collected throughout the bay (stns. W2, W3, W6, C2, C4, and C5). In the later sampling, phase I eggs often occurred at stns. C4 and C5, in central regions of the bay. On the other hand, various developmental phases were collected mainly at each of the western sampling stations. In 26–27 December, a high ratio of phase I eggs was observed at stn. W2 inconsecutively. In addition, phase III eggs were often collected from the eastern to inner region (in December) or the edge of occurrence area (in January).

Characteristics of egg occurrence in water temperature and salinity diagrams are shown in Fig. 3. The ranges of salinity and water temperature at which eggs occurred were 29.1–31.7 psu and 10.3°–19.7°C, respectively. The majority of eggs were collected at 30.0–31.5 psu and 12.0°–17.0°C.

Distribution of larvae. Collection results of larvae are shown in Table 2. A total of 139 *L. japonicus* pelagic larvae [2.4–9.2 mm in notochord length (NL)], including the three developmental phases (yolk-sac, preflexion, and flexion), were collected during the sampling period. On 13–14 December, when the CPUE of larvae showed a maximum, larvae occurred at almost all the sampling stations irrespec-

Date	Sampling	Eggs				Larvae				
		\boldsymbol{n}		$_{\rm II}$	Ш	\boldsymbol{n}	CPUE	BL (mm)	Stage	Station ^a
$21 - 22$ Nov.	Surface	125	45.2	5.1	0.5	Ω				
	Middle	66	22.8	6.1	3.0	Ω	-			
13-14 Dec.	Surface	1741	746.3	261.4	206.4	40	28.0	$2.4 - 5.5$	Yo, Prf	All except W3
	Middle	985	523.0	206.0	205.4	72	64.5	$2.4 - 5.2$	Yo, Prf	All except C1
26-27 Dec.	Surface	597	332.9	51.7	90.3	6	4.3	$2.6 - 6.7$	Yo, Prf	W ₁ , W ₅ , C ₂
	Middle	350	203.9	40.9	69.2	17	15.0	$2.4 - 5.5$	Yo, Prf	W ₂ , W ₃ , W ₅ , W ₆ , C ₅
$17-18$ Jan.	Surface	355	194.9	37.4	31.6	Ω	–			_
	Middle	70	20.1	10.7	22.1	3	2.6	$8.2 - 9.2$	F	W ₂ , C ₁ , C ₂
17-18 Feb.	Surface	14	6.9	Ω	Ω	Ω				
	Middle		0.5	Ω	Ω	Ω				

Table 2. Collection results of eggs and larvae in each sampling date and towing layer

I, II, and III indicate developmental phases of egg (see text); data are shown by average of CPUE (catch per unit effort; individual number per $1000 \,\mathrm{m}^3$ water)

BL, body length; F, flexion, Prf, preflexion, Yo, yolk sac

a Larval fish were collected

Fig. 2. Catch per unit effort (CPUE; individual number per 1000 m³ water) and developmental phase of eggs collected in each sampling station and towing layers during the sampling period. *Open, shaded*, and *solid bars* indicate phases I, II, and III of egg developmental phases (see text), respectively. *Cross* indicates no egg was collected

tive of the bay regions. The CPUE of larvae of the middle layer was consistently higher than in the surface layer. Comparison of body length distribution and ratio of each developmental phase of larvae among the bay regions and towing layers are shown in Fig. 4. The frequency of each developmental phase showed a significant difference between the inner and central bay regions (χ^2 test: χ^2 = 28.7, *df* = 2, *P* < 0.001). The frequency of yolk-sac larvae was higher in the central region of bay than in the inner region. The frequencies of developmental phase between the surface and the middle layer were not significantly different in the central region but were different in the inner region (χ^2 test: χ^2 = 7.0, $df = 2$, $P < 0.05$). The body length of larvae collected around the inner bay region $(4.66 \pm 1.46 \text{ mm})$ was significantly larger than the central region $(3.49 \pm 0.67 \text{ mm})$; *t* test: $t = 6.1$, $df = 124$, $P < 0.001$). The body length of larvae collected in the middle layer was significantly greater than that in the surface layer for the central bay region (t test: $t = 2.8$, $df = 89, P < 0.01$) but not significantly so for the inner region (*t* test Welch: $t = 1.6$, $df = 15$, $P = 0.07$).

Fig. 4. Histograms of larval body length and the composition of developmental phases in the central and inner regions of the bay (see text). *Open, shaded*, and *solid bars* indicate yolk-sac (Yo), preflexion (Prf), and flexion (F) phases of larvae, respectively

Discussion

Dispersal process in the early life stages. The early developmental phase of eggs collected in this study might contain both *Lateolabrax latus* and *L. japonicus*. However, phase III of eggs and pelagic larvae collected at the same time were identified as *L. japonicus*. Body length of larval *L. latus* collected in the surf zone of the mouth of Ariake Bay was much smaller than *L. japonicus* even in the same season (Hibino et al., unpublished data), suggesting the spawning season of *L. latus* was later than that of *L. japonicus*. Matured adults of *L. latus* are rarely caught by the local fishery in Ariake Bay (Shimabara Fisheries Corporation, personal communication). Also, the spawning area of *L. japonicus* in Ariake Bay has been considered to be around the central region of the bay, adjacent to Shimabara Peninsula and Oyano Island, based on the results of catch reports of sexually ripe adults by the local fishery (WJSFIPC, 1973; Ohta, 2004). In this study, from the information mentioned previously, almost all the phase I *Lateolabrax* eggs were also thought to be eggs of *L. japonicus*. The phase I eggs were distributed around the wide area of the central bay, especially in November, suggesting the spawning area existed widely around the Shimabara Peninsula.

The spawning area of *L. japonicus* is generally located in the mouth of the bay where a thermohaline frontal region is formed between the outer water and the bay water, and eggs are also distributed densely there (Watanabe, 1965; Horiki, 1993). In Ariake Bay, the present study revealed that the eggs were distributed over the whole central region (Fig. 2), in contrast to previous studies. Because both water temperature and salinity changed horizontally toward the mouth of the bay (Table 1), the whole bay could be regarded as the frontal zone. These facts suggest eggs are distributed at the frontal zone, as shown in the previous studies.

According to Makino et al. (2003), the egg development of *L. japonicus* is affected by water temperature, and the probability of viable hatching is very low at water temperatures less than 10°C in rearing experiments. It has been reported that most wild eggs have been collected from 14°C to 20°C in other bays (Watanabe, 1965; Horiki, 1993). The surface water temperature of Ariake Bay decreased seasonally and was below 10°C, especially in the inner part, in January to February (see Table 1), being inappropriate for survival of eggs. In this study, egg distribution appeared to shift seasonally toward the mouth of the bay (Fig. 2), suggesting that decreasing water temperature was one of the limiting factors for egg distribution. However, further studies are needed to elucidate the seasonal shift of spawning area and egg survival probability against water temperature under the wild condition.

In this study, the eggs tend to collect more abundantly at the surface layer throughout the sampling periods (Fig. 2, Table 2). According to the previous studies by field surveys (Watanabe, 1965; Horiki, 1993) and rearing experiments (Makino et al., 2003), *L. japonicus* eggs are principally distributed in the surface layer of the water column. On the other hand, Ohmi (2002) stated that the distribution of eggs shifted to the middle layer in inshore regions with later developmental stage in Wakasa Bay. In this study, the total ratio of the well-developed eggs after presence of body trunk tended to be higher in the middle layer vertically (Fig. 2). This observation principally agrees with the results of Wakasa Bay (Ohmi, 2002), suggesting that *L. japonicus* eggs shift their vertical distribution to the middle layer or deeper with development so as to expand their horizontal area of distribution.

Most larvae were collected in the middle layer (Table 2) and the larger larvae were collected at the inner region of the bay (Fig. 4). These results showed that the larvae expand their distribution into the inner and/or shallow region via the middle layer temporally. Hibino (2002) stated that *L. japonicus* juveniles stay in the surf zone or estuaries around the central to inner regions of Ariake Bay as the favorable nurseries, suggesting that the larval drift must be a directional process in relationship to the distribution layer and water current. Ohmi (2002) speculated that the gravitational circulation in the estuarine region plays an important role for larval drift to the inshore region through the middle to bottom layer. However, for the winter season of Ariake Bay, the spawning season of *L. japonicus*, water mixing progresses additionally in response to the large tidal amplitude, making the gravitational circulation weaker. On the other hand, the northward mean current is developed in the middle to bottom layer during the winter season, which compensates for the seasonal (northern) wind-driven currents (Kitani, 2003). Also, this inner directional current is dominant around the central part of the bay (Tanaka et al., 2002; Kitani, 2003). The importance of a compensatory current for larval transport into the bay is indicated in the Japanese sand lance *Ammodytes personatus* in relationship to the yearly strength of larval abundance (Funakoshi and Nakamura, 1995). This northward current could also play an important role for

the inward-directed expansion of larval *L. japonicus* distribution and year-strength of juvenile abundance. However, a strong current that flows toward the outer part of the bay also occurs around the western part of the bay and surface layer (Kitani, 2003; Odamaki et al., 2003), and therefore it is not easy to explain egg and larval transportation simply. Further studies are needed, especially on seasonal compensatory current and their yearly fluctuations, in relationship to the abundance of juvenile fish occurring in the inner region.

Characteristics of pelagic life for the Ariake population. Nakayama (2002) revealed that *L. japonicus* in Ariake Bay is the endemic population of hybrid origin between *L. japonicus* and *Lateolabrax* sp., using amplified fragment length polymorphism (AFLP) markers and mitochondrial DNA. In comparison of the water temperature range in which eggs occur, *Lateolabrax* sp*.* is between 15° and 25°C, and *L. japonicus* in Tokyo Bay and Kii Channel is commonly dominant at 14°–20°C, suggesting that the results of the present study are almost same as the latter. As for the dominant salinity range, on the other hand, *Lateolabrax* sp. is between 25.0 and 32.3 psu in Bohai Bay, China (Wu et al., 1983), suggesting that it is lower than that of *L. japonicus*, 32.5–34.7 psu in Tokyo Bay (Watanabe, 1965) and 34.1–35.0 psu in the Kii Channel (Horiki, 1993). In this study, the majority of eggs were collected at 30.0–31.5 psu (Fig. 3), being intermediate between the reports of *L. japonicus* and *Lateolabrax* sp. already mentioned. These ecological characters of the Ariake population might be derived from the genetic background of this hybrid-origin population. Lower salinity conditions for hatched egg distribution may help to isolate the endemic population in Ariake Bay from the other local populations.

Nakayama (2002) also suggested that the Ariake population should be composed of subpopulations having different genetic characteristics, and that some independent spawning grounds occur. It was difficult to identify the subpopulation from the egg distribution in the present study, because all developmental egg phases were collected at the same time. However, eggs were distributed extensively from north to south around the Shimabara Peninsula, and early-phase eggs were collected nonconsecutively at some of the inner stations, which may indicate the existence of two or more spawning grounds. Further studies are needed to elucidate the population structure in Ariake population from genetic aspects using the present materials.

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