Importance of estuaries and rivers for the coastal fish, temperate seabass *Lateolabrax japonicus*

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Contents

Abstract

Estuaries have huge impacts on coastal environments. River plume supplies nutrient-rich water into the coastal areas and stimulates primary production. In addition, freshwater input induces important density currents, e.g., the estuarine circulation. Estuaries are also important as nurseries for many fishes in all over the world. However, the importance of estuaries for coastal fishes has not been fully recognized in the Asian area including Japan. The temperate seabass *Lateolabrax japonicus* is one of the most important fishery species in Japan. This study is about the importance of the Yura River estuary in the Tango Sea, Japan on the early life history of temperate seabass.

Impacts of river discharge on larval temperate seabass recruitment towards coastal nursery grounds in the Tango Sea

Planktonic larvae and settled early juveniles were collected from 2007 to 2013 in the Tango Sea. Planktonic larvae distributed mainly in the Tango Sea from January to February. On the other hand, settled juveniles distributed in the bottom layer with the depth ranged from 5 m to 10 m from February to March. The recruitment index (RI), which is defined as medians of settled juveniles divided by those of planktonic larvae, showed higher values in 2009 and 2012 than in the other years. The lowest RI was observed in 2007. The river discharge during January and February (planktonic larval period) showed significant positive relationship with RI ($R^2 = 0.76$). There are two plausible mechanisms; first, the larger freshwater input induces stronger estuarine circulation, which enhances effective larval transportation to the coastal area. Second, the river water provides nutrients to the coastal area and stimulates the primary production leading to better prey environment for temperate seabass larvae.

Distributions and size ranges of temperate seabass juveniles in the Tango Sea

Juveniles of temperate seabass were collected in the coastal area of the Tango Sea and the Yura River estuary from 2008 to 2012 in order to evaluate their distribution. Juvenile temperate seabass was collected in the most of stations along the coastal area of the Tango Sea in April 2012. It is considered that they use various environments, e.g., eelgrass, seagrass beds and sand beach, as nurseries. In addition, a lot of juveniles were collected in the lower part of the Yura River in blackishwater and freshwater conditions from March to August in 2008-2012. The Yura River estuary is also an important nursery for juvenile temperate seabass.

River ascending mechanisms of juvenile temperate seabass in the stratified Yura River estuary

River ascents of juvenile temperate seabass were monitored by seine net surveys from 2009 to 2012. Timings of the river ascending changed year-to-year. Juveniles started to ascend in the beginning of March in 2009, while in the mid April in the other years. This difference came from the cumulative temperature and the saltwedge dynamics in the Yura River estuary. Difference in temperature would change the metamorphosis rate of larvae and juveniles, affecting the ability of osmoregulation and swimming speed of juveniles. Saltwedge dynamics monitored by the conductivity loggers showed that the distance of juvenile ascent was coincided with the saltwedge intrusion. This indicates that small juveniles with poor swimming ability use the saltwedge intrusion to ascend the river efficiently.

Feeding ecology of juvenile temperate seabass in the Yura River estuary

Stomach contents of juveniles were analyzed from 2008 to 2012. The temperate seabass juveniles mainly fed on copepods and mysids both in the coastal area of the Tango Sea and Yura River estuary. The dependency on the mysids increased from standard length (SL) of 15 mm to 25 mm, and main stomach content was mysids for juveniles larger than 25 mm SL. The maximum size of food contents increased from 2 mm to 15 mm with the growth of juveniles from 15 mm SL to 25 mm SL. Most of prey items smaller and larger than 2 mm were comprised of copepods and mysids, respectively. The mean size increased with the size of juveniles. On the other hand, the mean number of stomach contents decreased with growth of juveniles. As the results, stomach content index increased with the size of juvenles. These results mean that the size shift of prey items to larger size (from copepods to mysids) is important for juveniles to gain energy efficiently. The size and abundance of mysids were larger and higher in the estuaries than in the coastal area. It is thus considered that the estuary provides better prey condition for juvenile temperate seabass than the coastal area.

Migration ecology of juvenile temperate seabass: a carbon stable isotope approach

Carbon stable isotope ($\delta^{13}C$) was applied for estimation of migration dynamics of temperate seabass juveniles between the Yura River estuary and the adjacent coastal area. $\delta^{13}C$ values of mysids, which are the most important prey items for this species, were consistently enriched in the coastal area, while relatively depleted in the estuary. $\delta^{13}C$ of juveniles in the coastal area were enriched, while those in the estuary were getting depleted, consistent with the $\delta^{13}C$ difference in prey items. Fish migration between the coastal area and the estuary were analyzed by separating juveniles into four migration groups based on individual $\delta^{13}C$ values; river ascending group, short resident group, long resident group and surf zone group. The results showed that many juveniles migrated upstream from April to June, and most of them stayed in the estuary at least until July. A part of juveniles started to go back to the sea after June.

Growth and migration patterns of juvenile temperate seabass in the Yura River estuary - combination of stable isotope ratio and otolith microstructure analyses

Using $\delta^{13}C$ and otolith analyses, body conditions and growth rates were compared among migration groups. The river ascending group showed lower growth than the surf zone group before river ascending. However, longer resident juveniles in the river showed, at last, the growth rate caught up with or even overcome that of the surf zone group. Body conditions of each group showed similar patterns as indicated by otolith analyses. It was concluded that the juveniles which experienced lower growth rate ascend the river by being put out from the surf zone by the better growth juveniles. However, the residence in the estuary enabled juveniles to achieve the similar or even higher growths than the residence in the coastal area. This pattern would come from higher temperature and better ambient prey condition in the estuary than in the coastal area during the juvenile stage.

Main factor of the mortality during the estuarine juvenile stage of temperate seabass

Mortalities of juveniles in the Yura River estuary from April to the end of June were evaluated from 2008 to 2012. Daily mortality rates were estimated for each sampling interval. Fine scale field sampling during the observational periods including large flood events showed no direct effects of flood events on the juvenile mortality. They would rather deteriorate due to density-dependent mortality. Given the prey conditions during the sampling periods, not the top-down control, but the bottom-up control, i.e., the juvenile competition for prey items, would be important for mortality of the juvenile temperate seabass in the estuary.

Relative contribution of the estuarine nursery areas to temperate seabass adult population in the Tango Sea revealed by otolith Sr:Ca ratio

Otolith Sr:Ca ratio was introduced to evaluate the contribution of estuarine nursery to the temperate seabass population in the Tango Sea. Otolith Sr:Ca ratios of juveniles collected in the freshwater area, blackish area and coastal area were analyzed to determine the criterion to distinguish whether individuals used the river or coastal area as nurseries. Otolith Sr:Ca ratios of adult seabass collected around the Tango Sea were also analyzed. Sr:Ca ratios of juveniles collected in the freshwater and blackish area significantly decreased, while juveniles collected in the coastal area showed higher values from the primordial to the edge of the otoliths. According to their Sr:Ca chronologies, thirty nine from 107, corresponding to 36 % of adult seabass were estimated to use the estuary as the nursery during their juvenile stage. As the nursery area of estuaries is considerably smaller than the coastal areas, the estuary play significantly important role for seabass juveniles as a nursery.

Chapter 1

General introduction

Pritchard (1967) defined the estuary as a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage. This region is characterized by its high productivity because of the large inputs of nutrients by river plume (Lalli and Parsons, 1997). Estuarine systems are thus considered to be among the most biologically productive and valuable ecosystems world-wide since many of the larger marine species which use estuaries as nursery areas are of commercial and recreational importance (Costanza et al., 1997; Kennish, 2002). Martinho et al. (2012) pointed out that larger river discharge from estuaries to coastal area improves the recruitment of planktonic larvae of various coastal fishes into the coastal nursery areas. Estuaries also have roles as nurseries for juveniles (Ray, 1997; Beck et al., 2001; Albe, 2005; Elliott et al., 2007). Much emphasis has been placed on the need to preserve estuarine environments in order to ensure the survival of important fisheries in the North America, tropical Indo-Pacific, European area, tropical Africa, temperate and subtropical Australia, and subtropical and temperate southern Africa (Elliott et al., 2007). However, the study in Asian region including Japan is still scarce. As a result, the importance of estuaries has not emphasized as much as tidal flats and eelgrass beds in Japan (Ministry of Agriculture, Forestry and Fisheries, 2011), even though the importance of river-estuarine systems to supply the information for achieving the sustainable coastal fisheries. On the other hand, these areas are always exposed by urbanization of their watersheds because of overpopulation and uncontrolled development in coastal watersheds, leading to alteration and loss of habitats for coastal biota (Nichols et al., 1986; Beck et al., 2001; Kennish, 2002; Albe, 2005). For example, Nichols et al. (1986) reported the modification of estuarine environment in the San Francisco Bay by human activities. Diking and filling of most of its wetlands have eliminated habitats for fish; introduction of exotic species has transformed the composition of its aquatic communities; reduction of freshwater inflow by more than half has changed the dynamics of its plant and animal communities and wastes have contaminated its sediments and organisms. It is important to know the detailed roles of river-estuarine systems in the production of coastal fisheries to achieve the conservation of river-estuarine systems and sustainable coastal fisheries.

Recruitment variability occured in the early life histories of marine fishes is still one of the most important issues in marine fisheries ecology, because it determines the production of fishes (Houde, 1989). Early life histories of marine fishes are often composed of two life stages; planktonic larval stage and settled juvenile stage (Lalli and Parsons, 1997; Bailey and Houde, 1989; Shoji and Tanaka, 2008). Feeding habits, habitat usage and life style of marine organisms change drastically between these two life stages (Pittman and McAlpine, 2001). Some previous studies pointed out that survival mechanisms of the larvae and juveniles are different; density-independent mechanism in the larval stage, while density-dependent mechanism in the juvenile stage (Bailey and Houde, 1989; Shoji and Tanaka, 2008; Martinho et al., 2012). Therefore, the roles of river-estuarine systems on the early life histories of coastal fishes would be different between these two life stages. It is thus necessary to evaluate the roles of river-estuarine systems in both these two stages to understand the importance of river-estuarine system for the early life history of marine fishes. (Pittman and McAlpine, 2001; Martinho et al., 2012).

The temperate seabass *Lateolabrax japonicus* is an important euryhaline species for Japanese coastal fisheries (Shoji et al., 2002). This species usually spawns around the bay mouth during winter season (Kuwatani, 1962; Watanabe, 1965; Hayashi and Kiyono, 1978; Hibino et al., 2007). The planktonic larvae are transported onshore (Ohmi, 2002; Hibino et al., 2007), then they settle around nearshore area and reside there for one month

(Ohmi, 2002) or directly appear around coastal areas (Fujita et al., 1988; Arayama et al., 2002). Juveniles utilize various coastal environments as nurseries after early spring, e.g., eelgrass beds (Hatanaka and Sekino, 1962a; Kinoshita, 2002), sandy beach (Iwamoto et al., 2010; Nakane et al., 2010), tidal flats (Hibino et al., 2002; Tamura et al., 2013) and estuaries or blackish lakes (Matsumiya et al., 1982; Kinoshita, 2002; Yamazaki, 2002; Iwamoto et al., 2010). Most of studies on juvenile ecology in estuaries have been conducted in the Chikugo River estuary (Islam et al., 2011). Juveniles ascend the Chikugo River estuary from March and gather in the estuarine turbidity maximum (ETM), which positions around the lower salinity area, to feed on the larger copepods and refuge from predators (Islam et al., 2011). However, some genetic and morphological studies revealed that the seabass population in the upper Ariake Bay is different from other areas in Japanese coasts (Kinoshita et al., 1995; Yokogawa et al., 1997; Nakayama, 2002). In addition, the hydrological conditions in the Ariake Bay are unique because of its extreme strong tidal currents and consequent high turbidity (Suzuki, 2010). These facts suggest the necessity of studies on temperate seabass ecology in other estuaries and coasts to know the intrinsic ecology of temperate seabass in the Japanese coasts.

The target field of this study is the Yura River estuary and the Tango Sea (Fig. 1-1). The Tango Sea is located in the northern part of Kyoto Prefecture, Japan, facing the Sea of Japan. It is approximately 336 km^2 and approximately 60 m deep at its center and 80 m deep at the mouth. This area is characterized by its small tidal range (< 0.5 m, Kasai et al., 2010). Therefore, tidal current is small in this field. The Yura River is the largest river flowing into the Tango Sea and the environment in the Tango Sea is affected by the freshwater from this river. The Yura River is a 146 km long, located in central Japan, comprising a catchment area of approximately 1880 km^2. The annual average discharge of the Yura River is ca. 50 m^{3}s^{-1}. On the Sea of Japan side, northwesterly winter winds off the Asian continent bring heavy snow, making the catchment area one of the snowiest regions in Asia. In contrast, the area is subjected to cyclonic rain depressions in summer. The river discharge is therefore high in winter and early spring because of snow melting, while generally low in summer and autumn with sudden increases (Fig. 1-2). It is therefore expected that the balance between stratification and mixing in the estuary changes seasonally. The lower-most 10 km of the Yura River estuary are strait and 100–500 m wide with a 3–5 m deep, nearly flat riverbed concluding in a shallow sill at the mouth. Seawater easily intrudes into the river, since the riverbed is lower than the sea surface until ca. 15 km upstream from the river mouth. The typical tidal range in the estuary is less than 0.5 m, so that the Yura Estuary is classified as a microtidal estuary. Therefore the effects of tidal currents on the physical and biological conditions are negligible.

The goal of this thesis is to estimate the function of the Yura River and its estuary on both the planktonic larvae and the settled juvenile stages of temperate seabass in the Tango Sea, the Sea of Japan. This thesis conducted the long-term and comprehensive surveys to reveal the various roles of river and estuary on temperate seabass. In Chapter 2, impacts of the river flows on the planktonic larvae recruiting to coastal area were estimated by long-period surveys in the Tango Sea. In Chapter 3, distributions of temperate seabass juveniles in coastal area and estuaries after planktonic stage were investigated by a 6 years survey. The river ascending mechanisms and the importance of the hydrological condition in the estuary were evaluated by multi-year field surveys in Chapter 4. Feeding ecology of juveniles was determined by stomach content analyses of juveniles to reveal the importance of estuarine nurseries in Chapter 5. The stable isotope ratio was applied to clarify the migration dynamics of juveniles between the estuary and coastal habits from the spring to summer in Chapter 6. The relationship between migration pattern and growth and body conditions was estimated by the combination of carbon stable isotope ratio and otolith microstructure analysis in Chapter 7. In Chapter 8, the importance of density-dependent mortality and effects of unstability of estuarine environments on the juvenile mortality were clarified. Finally, the contribution of estuarine nurseries to the adult population of seabass was estimated quantitatively by otolith Sr:Ca ratios in Chapter 9.

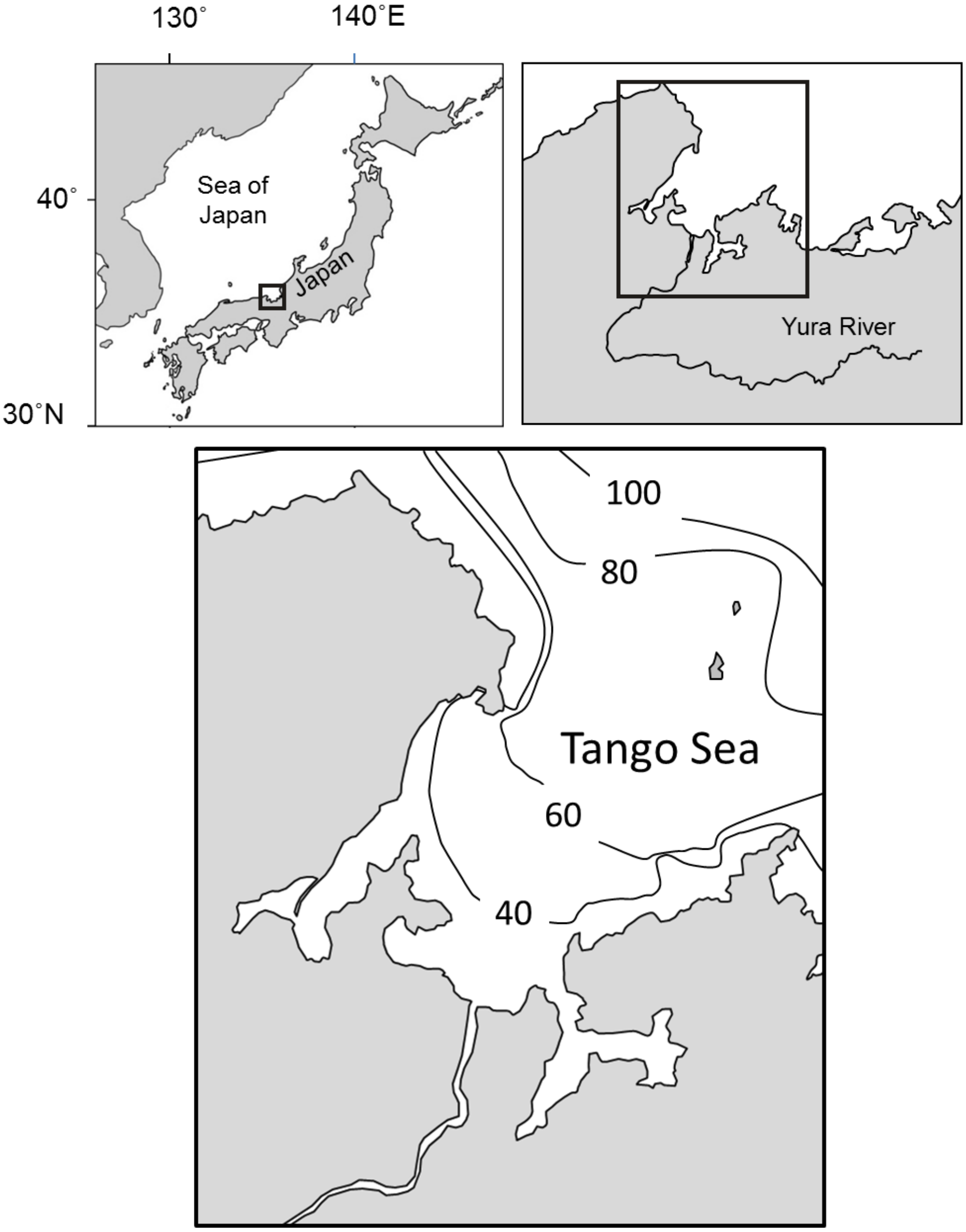

Fig. 1-1 Sampling field of this study.

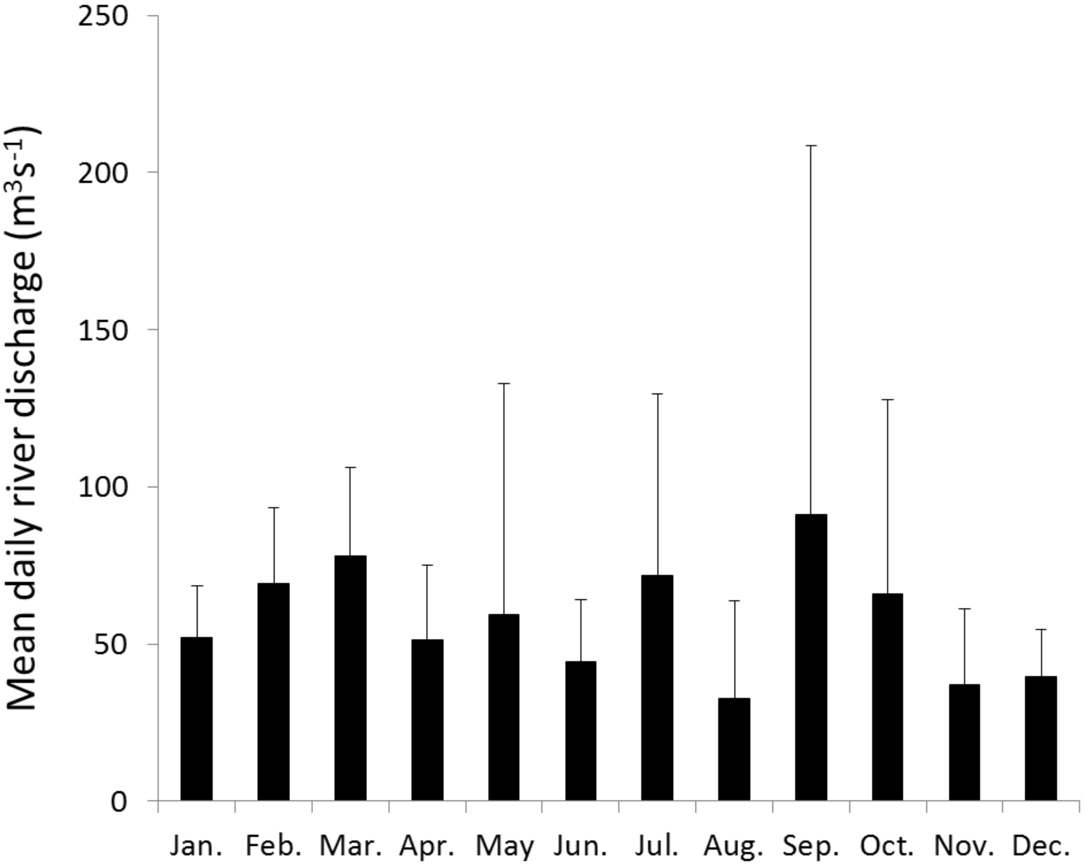

Fig. 1-2 Monthly change of mean daily Yura River discharge during 2004 and 2013. Vertical bars indicate the standard deviations.

Chapter 2

Impacts of river discharge on larval temperate seabass recruitment towards coastal nursery grounds in the Tango Sea

Introduction

The recruitment in the early life stage of fisheries resources is affected by mainly two factors; physiological process, e.g., transportation by water currents (Kasai et al., 2008), and biological process, e.g., predation (Takasuka et al., 2003 and 2004) and starvation (Cushing, 1995). Many environmental factors could affect and modify these processes. For example, wind has an effect of transport of larvae into inside or outside of the nursery area (Kasai et al., 1992; Yamashita et al., 1996; Fox and Aldridge, 2000). High temperature could cause stratification and low productivity in the ocean leading to high mortality of larvae of fish (Yasuda et al., 2000). The mechanism is complex and it is thus important to find the main factors affecting the recruitment to manage the stocks of fisheries resources.

River plume is also considered to have huge impacts on the coastal environment through both physical and biological processes (Kimmerer, 2002; Vinagre et al., 2007). For example, when river plume flows into semi-closed coastal areas, fresh water mix with salt water, resulting in average flows seaward in the surface layer, while landward flows in the lower layer. This two-way movement of water is called estuarine circulation (Dyer, 1973). Some marine species are considered to use this net landward current in the lower layer to immigrate to estuarine nursery areas (Kimmerer, 2002; Burke et al., 1998). In addition, river water often provides nutrients to coastal areas. This stimulates primary production in coastal areas leading to secondary production and good prey environments for larval fish (Salen-Picard et al., 2002; Harada et al., 2009).

The temperate seabass is considered to spawn around the Kanmuri Island in the Tango Sea mainly from the mid-January to mid-February

(Ohmi, 2002). Then larvae distributed in and around the Tango Sea during January and February and then settled in coastal areas in March (Ohmi, 2002; Islam et al., 2010). However, the mechanisms of their onshore migration and the fluctuation of the recruitment are unknown.

The objective of this chapter is to evaluate the effects of environmental factors on the recruitment of temperate seabass in the Tango Sea.

Materials and methods

Field sampling

Sampling surveys were conducted from 2007 to 2013. Cruises were conducted from mid-January to mid-February for collecting planktonic larvae and from mid-February to March for settled juveniles. Planktonic larvae were collected at stations indicated in Fig. 2-1b by obliquely towing an ichthyoplankton net designed by the Ocean Research Institute (ORI). The net (ORI net, hereafter) had 1.6 m mouth diameter and 1.0 mm cod-end mesh size. It was towed obliquely from the bottom to the surface. Settled juveniles were collected by 5 minutes tows of a beam trawl with 0.4 m^2 mouth opening (2 m width and 0.2 m height) with 2 mm mesh size at stations with water depths of 5 m and 10 m (Fig. 2-1c).

Daily river discharge of the Yura River measured in Fukuchiyama (Fig. 2-1a) was obtained from Ministry of Land, Infrastructure, Transport and Tourism. Wind data were measured by Automated Meteorological Data Acquisition System at Miyazu (Fig. 2-1b). Daily water temperature at the depth of 12 m measured in Miyazu (Fig. 2-1b) was obtained from Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Center.

Data analysis

Given the spawning season and migration schedule of this species in the Tango Sea (Ohmi, 2002; Islam et al., 2010), the median density of planktonic larvae from mid-January to the mid-February in each year was considered as the representative density. The median density of settled juveniles from the mid-February to the end of March in each year was calculated as the representative value of settled larval density. With these densities, recruitment index (RI) was estimated as follows;

$$RI = \ln(\frac{D_S}{D_P}),$$

where D_P means the median planktonic larval density and D_S the median settled juvenile density in each year.

North and East wind component intensities, river discharge and daily temperature were averaged from mid-January (15 Jan.) to the mid-February (15 Feb.), which coincides with the planktonic period of seabass larvae. The relationships between RI and these environmental factors were explored by the Peasson's regression analyses.

Results

D_P fluctuated from 1.7 to 27.1 ind.100 m^{-3} during the sampling years (Fig. 2-2a). D_S varied between 5.0 to 388.3 ind.100 m^{-3} (Fig. 2-2b). RI ranged from 0.3 to 3.7, reflecting the large variation in D_S (Fig. 2-2c).

Mean river discharge during planktonic period varied between 25.8 m^3s^{-1} in 2010 and 88.4 m^3s^{-1} in 2009 (Fig. 2-3a). Mean daily water temperature showed lowest value in 2011 (11.2 °C) and highest in 2007 (12.7 °C; Fig. 1-3b). Mean north wind component intensity varied between 0.3 ms^{-1} in 2010 to 0.6 ms^{-1} in 2008 (Fig. 2-3c). Mean west wind component intensity changed from 1.5 ms^{-1} in 2009 to 1.9 ms^{-1} in 2013 (Fig. 2-3d).

Relationship between each physical parameter and RI showed that only river discharge presented a significant positive relation with RI ($P \leq 0.01$, Table 2-1). Higher RI were observed in years with higher river discharges over the larval stage (Fig. 2-4). Other environmental factors showed insignificant correlations with RI.

Discussion

The range of fluctuation in D_S was larger than D_P during the sampling years (Fig. 2-2). This indicates that the survival and transport processes during the onshore migration are very important for the variation in recruitment of this species. The effects of the river discharge were significant on the variation of RI of temperate seabass (Fig. 2-4). The river discharge is considered as an important factor for explaining the variation of recruitment of many species (Kimmerer, 2002; Vinagre et al., 2007; Vinagre et al., 2009). There are mainly two possible mechanisms on this phenomenon through biological and physiological processes.

River flow has a large impact on the biological production in coastal area by supplying the nutrients and organic matters (Salen-Picard et al., 2002). Copepod is one of the most important foods for larvae of many coastal fishes (Nunn et al., 2011). Its production could be based on the primary production caused by inputs of nutrient-rich river water. The production of copepods in the Chesapeak Bay was affected by the discharge of the Susquehannna River (Kimmel and Roman, 2004). This mechanism could affect the larval mortality, because starvation leads directly to decease of fish larvae (Cushing, 1995; Shoji and Tanaka, 2006a).

The river flow also changes the current dynamics in the coastal area. Loading the river plume into coastal area induces the estuarine circulation. In this case, surface water flows offshore and middle and bottom waters flow onshore. The acoustic Doppler current profiler survey revealed that water flows into the head of the bay in the middle and bottom layer during the winter season in the Tango Sea (Zenimoto et al., unpublished data). The temperate seabass would use this current to migrate onshore. Actually, the larvae of this species distribute mainly in the middle layer of the Tango Sea (20 m depth, Ohmi, 2002). Larvae of Japanese flounder were also distributed in not the surface but bottom layer consistently in the Tango Sea and considered to use this current to immigrate into nursery area because the tidal current is too weak to transport the larvae (Burke et al., 1998). Kimmerer (2002) found positive relationships between river flow and recruitments of many fishes in the San Francisco Bay. However, primary production had no correlation with secondly production and recruitments of fishes. He emphasized the importance of physical mechanism associated with the river plume in larval stage of fishes.

The effects of estuarine circulation on larval fishes would be different depending on the vertical distributions of larvae. Larvae show various pattern of vertical distributions also in the Tango Sea. For example, larvae of flatfishes distribute in the middle or bottom layers in the Tango Sea (Kuwabara and Suzuki, 1982 and 1983a; Burke, 1998). On the other hand, rock fishes, black seabream and Japanese whiting distribute in the surface layer (Kuwabara and Suzuki, 1983 b and c). In addition, the Yura River discharge fluctuate seasonally (Kasai et al., 2010). Effects of the river discharge on the larval recruitments would be different among species according to their spawning season and larval vertical distributions. More studies on the relationships between the recruitment of various larval fishes and the river discharge are necessary to reveal the role of the river discharge.

Ohmi (2002) and Hibino et al. (2007) found seabass larvae distributed in the middle layer of the Tango Sea and Ariake Bay, respectively. In the Ariake Bay, seasonal north wind blows in winter and the northward mean current is developed in the middle to bottom layer, because water is always well mixed in the Ariake Bay (Kitani, 2003). This wind induced current is considered to be important for migration of temperate seabass larvae into the nursery area in the Ariake Bay (Hibino et al., 2007). This study found no relationship between recruitment and north-south and east-west wind components (Table 2-1). North wind component was generally weak in the Tango Sea (Fig. 2-3). This would be one reason why no significant relationship was detected between north-wind and RI. Different environmental conditions among the fields would lead to different mechanism of immigration. It is important to clarify the mechanism of recruitment variability for each field to achieve the region-specific fisheries management.

Recent human activities have changed river discharge. For example, extracting water by human for agriculture and industries reduces the discharge and has huge impact on estuarine and coastal ecosystems (Gillson, 2011). It is expected that human-induced global warming can also affect the river discharge through changing the precipitation (e.g. Allan and Sodern, 2008). Exceeding utilization of river water as industrial and daily life water would lead to loss of river water input to estuaries and coastal area and affect the recruitment of larvae (Fernández-Delado et al., 2007). It is thus important to recognize the importance of supply of the freshwater to the coastal area for the conservation of the coastal fishes.

Table 2-1 Correlation coefficient *(r)* and *P*-value for each parameter and recruitment index (*RI*)

Parameters	*r*	*P*-value
River discharge	0.872	0.01
Temperature	−0.073	0.88
North wind component	0.026	0.96
West wind component	−0.075	0.87

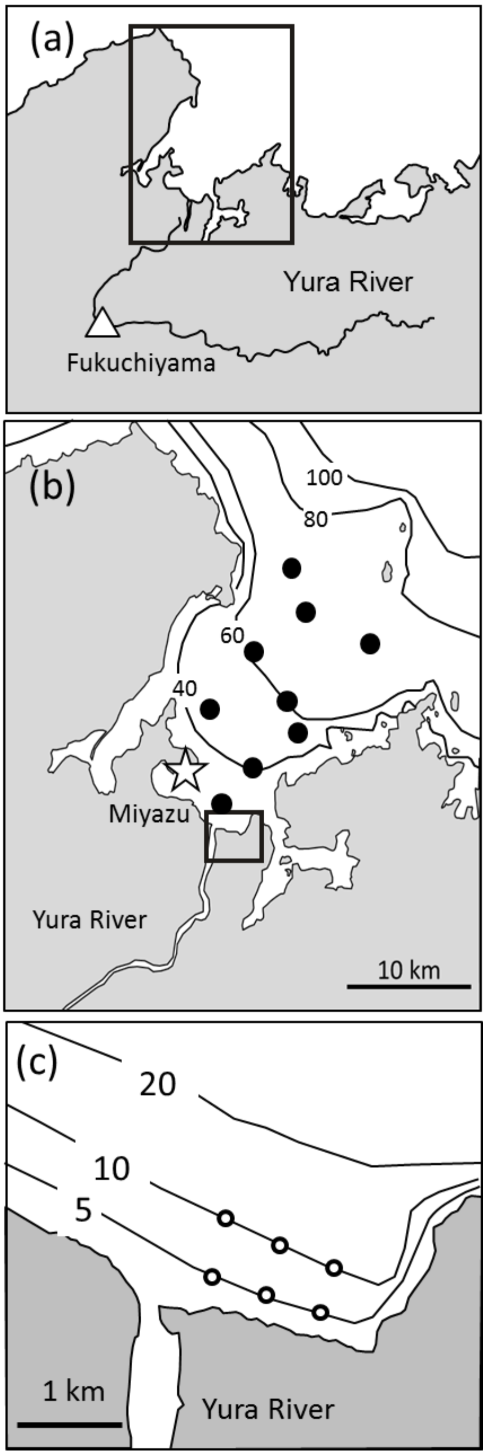

Fig. 2-1 The map of study area. Closed and open circles indicate the stations for ocean research institute (ORI) net and beam trawl net, respectively. River discharge was measured at Fukuchiyama indicated by a triangle in (a). Daily temperature and wind data were observed at Miyazu indicated by a star in (b).

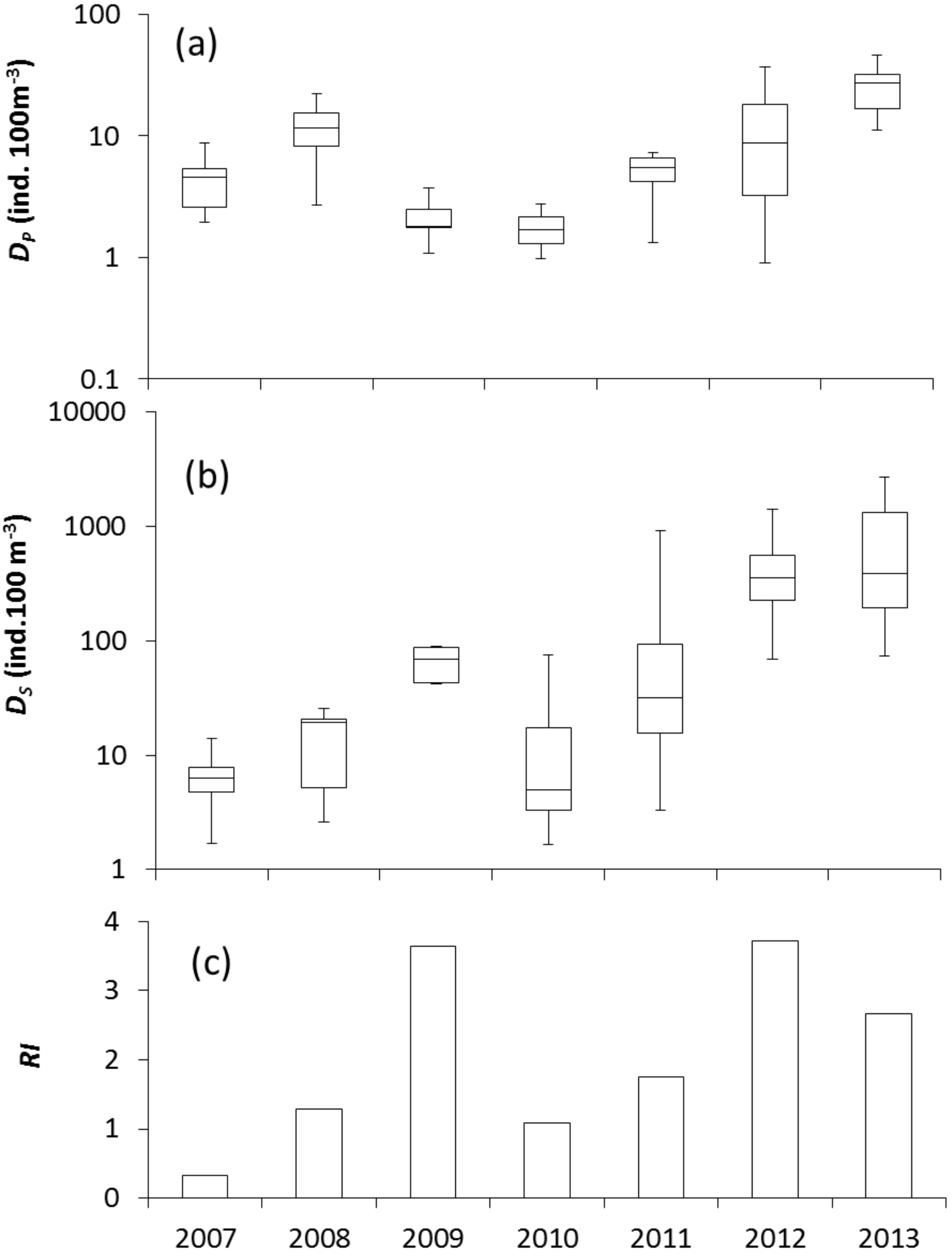

Fig. 2-2 (a) Density of planktonic larvae collected by ORI net (D_P) and (b) settled juveniles collected by beam trawl (D_S). Center horizontal lines, boxes and whiskers show median values, 25th, 75th percentiles, and maximum and minimum values, respectively. (c) Recruitment index (RI).

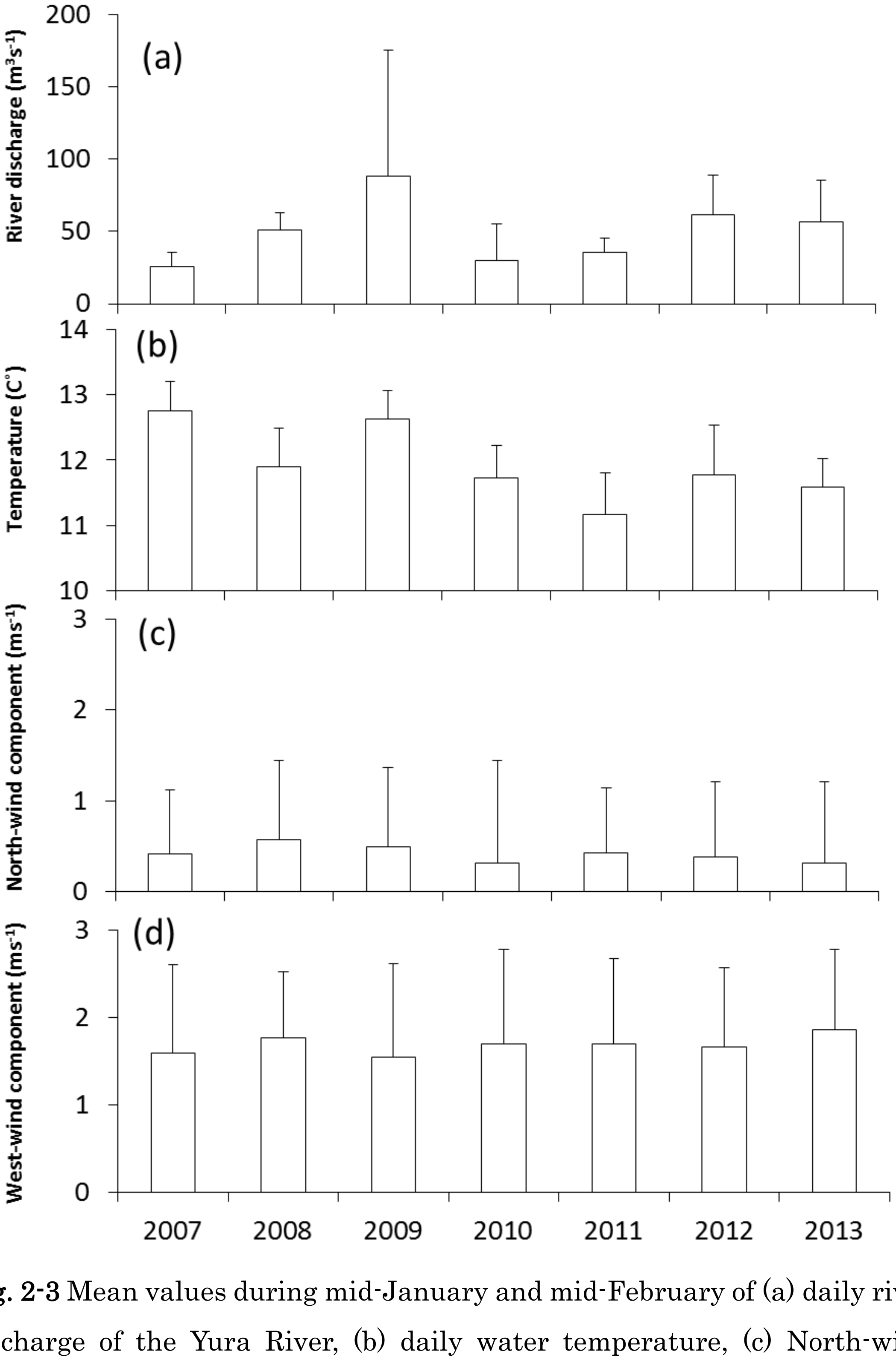

Fig. 2-3 Mean values during mid-January and mid-February of (a) daily river discharge of the Yura River, (b) daily water temperature, (c) North-wind component and (d) west wind component. Vertical bars indicate the standard deviations.

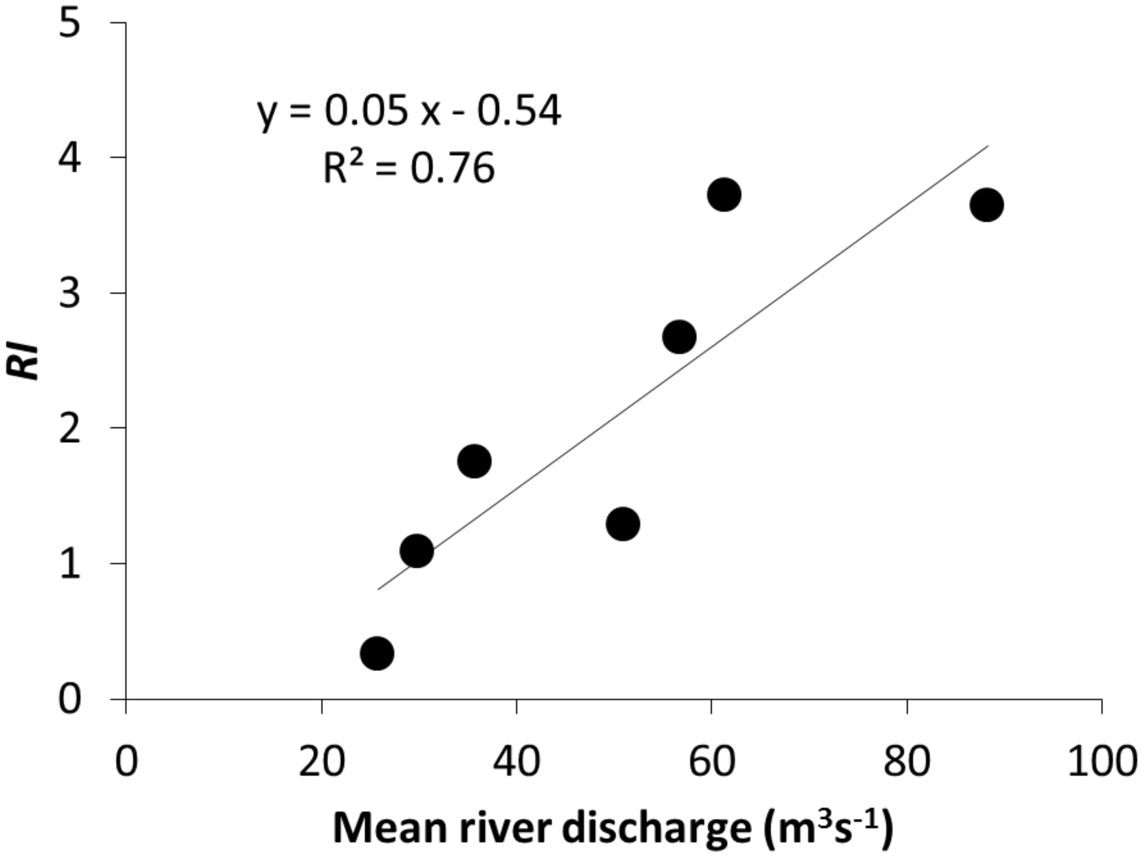

Fig. 2-4 Relationship between mean river discharge during mid-January and mid-February and recruitment index (*RI*).

Chapter 3

Distributions and size ranges of juvenile temperate seabass in the Tango Sea

Introduction

In general, during the early part of the juvenile period, temperate seabass migrates from open water areas into coastal areas including estuaries, surf zones and eelgrass beds (Tanaka and Matsumiya, 1982; Kinoshita, 2002). The ecology of juveniles has been thoroughly investigated especially in the Chikugo River estuary, Japan (Islam et al., 2011). The Chikugo River estuary is characterized by its large tide and subsequent productivity (Suzuki et al., 2007). In the Chikuogo River estuary, some early juveniles (ca. 20 mm SL) ascend the river in March then inhabit the upper estuary, including the freshwater zone (Matsumiya et al., 1982; Matsumiya et al., 1985; Suzuki et al., 2008a), while others reside in the lower estuary or in the littoral zone (Matsumiya et al., 1985; Hibino et al., 2006). For early juveniles of temperate seabass, their migration to the freshwater zone has been reported only in the Chikugo River estuary. The reason of this has been considered to be both unique hydrological condition (Hibino et al., 2007; Suzuki et al., 2007; Hirai, 2002) and genetic uniqueness of seabass in the Ariake Bay (Nakayama, 2002). Strong tidal currents form the estuarine turbidity maximum (ETM) in the upper Chikugo River estuary (Suzuki et al., 2007), where prey items are abundant (Hibino et al., 1999). High turbidity in the ETM would also have an important role as the refuge from predators for juveniles (Shoji and Tanaka, 2006b). In addition, the temperate seabass in the Ariake Bay is the hybrid between *L. japonicus* and Chinese seabass *L.* sp. (Nakayama, 2002). The Chinese seabass is considered to have higher ability of osmoregulation than *L. japonicus* (Hirai, 2002). This genetic uniqueness thus would lead to high ability of osmoregulation of seabass in the Ariake Bay. However, the information of distribution of juvenile temperate seabass in other fields has been scarce to compare with the Ariake Bay.

Distribution of juveniles is the information to know potential nurseries (Dufour et al., 2009). Information of distribution of juvenile temperate seabass is limited in the Tango Sea. Ohmi (2002) reported juveniles migrate to the surf zone near the Yura River mouth. However, it is not clarified whether juveniles migrate to upstream of the Yura River or remain in the littoral zone after aggregation around the river mouth. In addition, broad distribution pattern along the coastal line of the Tango Sea is also unknown.

Remarkably strong turbidity maximum zones, which are formed by the strong tidal currents in the upper Chikugo River estuary (Suzuki et al., 2007), are not observed in the estuaries facing to the Sea of Japan (Kasai et al., 2010). These differences in environmental conditions may lead to different migration and/or feeding habitats of the juveniles. However, no surveys have been previously conducted on the distribution of the juveniles in the rivers along the Sea of Japan side. The main objective of this chapter is therefore to determine the temporal distributions of juvenile temperate seabass around the Tango Sea and in the microtidal Yura River estuary. Two surveys were conducted; 1) samplings covering the whole area of the Tango Sea and 2) ca. multi-year frequent surveys along the estuary to investigate the upstream migration of juveniles.

Materials and methods

Twelve stations located along the coast of the Tango Sea were selected for broad area sampling (Fig. 3-1, Table 3-1). Honjo, Tomari, Sezaki, Mihama and Nohara are sand beaches facing to open sea. Tai, Amanohashidate, Kunda and S1 are sand beaches in inner part of the Tango Sea. Iwagahana, Satohami and Maizuru are characterized by dense seagrass beds.

Estuarine samplings were conducted at 6 stations indicated in Fig. 3-1. Five stations were set up along the lower reaches of the river from the mouth to 15 km upstream (R1-R5, Fig. 3-1). The distances from river mouth were 0.5, 4.0, 6.5, 9.0 and 15.0 km at R1, R2, R3, R4 and R5, respectively. Almost riversides of the stations are free from bank protection. Another station (S1) was set on the sand beach adjoining the river mouth (1.0 km from the river mouth, Fig. 3-1). The bottom was sandy at S1, R1 and R2, while muddy at R3, R4 and R5.

In order to collect temperate seabass juveniles, a seine net (0.8 m×10 m, 1.0 mm mesh aperture at the cod end) was towed along the bank or shoreline. About 3 minutes tow was performed two times at each station. Sampling depth was 0.3 – 1.2 m at every station. Bottom water temperature and salinity were measured with an environmental monitoring system (YSI 556 MPS, YSI Inc., U.S.A.) at the same time as seine net towing. Collected juveniles were sorted and frozen using dry ice immediately after seining or preserved in 90 % ethanol. These samples were transported to the laboratory and the former was kept in a freezer until further analyses.

Broad area sampling was conducted from 10 to 12 April, 2012 (Table 3-1). Estuarine samplings were conducted one - four times per one month from March or April to July or August in 2008 – 2012 (Table 3-2).

Care of the fish and all procedures were done following the guidelines for the use of fishes in research of the Ichthyological Society of Japan (2003).

The standard length (SL) and wet body weight (BW) of samples were measured.

Results

Temperature and salinity ranged from 11.8 to 14.8 ˚C and from 27.0 to 33.7 at stations of broad area sampling, respectively (Table 3-1). Temperature increased from ~8 ˚C in the beginning of March to ~29 ˚C in the end of August in the estuarine samplings (Fig. 3-2). There was no clear difference in temperature among the river stations. However, temperature at S1 and R1 was mostly lower than those at the other stations after May. Salinity fluctuated from 12.8 to 34.0 (mostly over 25.0) at S1, while it showed seasonal change in the river (Fig. 3-2). Generally, stations in the river showed lower salinity (almost 0) in March and salinity sometimes increased at some stations after April. Salinity was different among stations in the river. It was almost freshwater condition and rarely exceeds 1.0 at R4 and R5 (Fig. 3-2). At R2 and R3, salinity was almost 0 until April and sometimes exceeded 1.0 but almost remained below 5.0 after May except for 2011 (Fig. 3-2). Salinity at R2 drastically increased after May and reached to 23.2 in the middle of June in 2011 (Fig. 3-2). Salinity was often higher than 1.0 in April and exceed 5.0 after May at R1 (Fig 3-2).

Juveniles were collected in most part of the shoreline of the Tango Sea in broad area sampling (Fig. 3-3). Standard lengths of juveniles ranged from 12.2 to 22.2 mm (Table 3-1). Median size of juveniles was ca. 15 mm SL at Honjo and Tomari (outer bay stations) and ca. 18.5 mm SL at the other stations (inner bay stations; Table 3-1 and Fig. 3-3). Median size was significantly smaller at Tomari than at the other stations except for Honjo and Amanohashidate (Kruskal-Wallis test following Scheffe's test, $P \leq 0.05$).

Five years estuarine sampling revealed that the juvenile temperate seabass migrated to S1 at first during March or April with the median size of ca. 16-20 mm SL (Figs. 3-4, 3-5 and 3-6, Table 3-2). Then they ascended the river mainly in April with the median size of 17-21 mm SL (Figs. 3-4 and 3-6; Table 3-2). Median size increased after immigration from ca. 20 mm in April to 50-80 mm SL in July. Most of juveniles were collected at R2, R3, R4 and R5 from April to June every year. Many juveniles were caught again at S1 and R1 in June and July (Fig. 3-4). After August, small numbers of juveniles were collected.

Discussion

This study showed juveniles were not only distributed around river mouth, but also along the various environments of shoreline of the Tango Sea in mid-April with the median size of ca. 15 mm to 20 mm SL (Fig. 3-3). No juveniles were collected at Nohara, Mihama and Sezaki in this study, but a previous survey showed that they were distributed in the western part of the Tango Sea (Yube Y, personal communication). Therefore, juvenile seabass can utilize the most part of coastal areas of the Tango Sea as nurseries. It is also considered that they utilize various environments as nurseries, i.e., sand beach in both inner and outer bay, seagrass beds and eelgrass beds after early juvenile stage. The smallest size of juveniles collected was 12.2 mm SL (Table 3-1) almost matching with the minimum size of juveniles collected by seine net surveys in the Tokyo Bay (Tamura et al., 2013). All characters concerning swimming function became complete in number in this size (Tamura et al., 2013). This implies that juveniles larger than this size start to swim actively and select various environments along the coastal line as nursery areas (Tamura et al., 2013).

Smaller juveniles tended to be found in the outer part of the Tango Sea (Fig. 3-3). Similar pattern was found in the Tokyo Bay, Tosa Bay and Hiroshima Bay (Arayama et al., 2002; Fujita, 2004; Iwamoto et al., 2010). Arayama et al. (2002) also found that the residence period was shorter (within one month) in the outer part of the bay than inner tidal flats by year-round surveys. They concluded that the sand beach in the outer part of the bay functions as nursery habitat for shorter period than the sand beach in the inner part of the bay for temperate seabass. Fujita (2004) also reported smaller size range and shorter residence of juveniles in sand beaches facing to the Pacific Ocean than the Shimanto estuary. On the other hand, this study revealed that juveniles had larger size range in the sand beaches along inner bay, seagrass beds and eelgrass beds (Fig. 3-3, Table 3-1). In addition, juveniles continued to occur in the sand beach adjacent to river mouth (S1) until July in 2008 (Fig. 3-5). These results mean that sand beaches in inner bay play a role as nurseries for longer-periods. Tsujino et al. (1995) reported continuous occurrence of seabass juveniles in a sand beach adjacent to the Ochiai River mouth in the Osaka Bay. Kanou et al. (2000) and Hibino et al. (2002) also reported that juvenile temperate seabass occurred for a long period (a few months) in the tidal flats in the bottom of the Tokyo Bay and Ariake Bay, respectively. Kinoshita (1998) showed that many species use the surf zone in short periods in their juvenile stage. He considered that the surf zone plays an important role for juveniles of these species as a place for their metamorphosis. This study showed that the surf zone would have functions not only as a place for their metamorphosis but also as a nursery area for temperate seabass juveniles.

This study found that a certain number of early juveniles of ca. 20 mm SL migrate into the freshwater zone of the stratified Yura River estuary in March or April, while other juveniles reside in the coastal area (Figs. 3-4, 3-5 and 3-6). The two migratory pathways of early juveniles of the temperate seabass were observed in the well-mixed Ariake Bay and Chikugo River estuary (Hibino et al., 2002; Suzuki et al., 2008a), although hydrographic conditions and genetic characteristics of fish populations are considerably different between the two estuaries (Nakayama, 2002; Suzuki et al., 2007; Kasai et al., 2010). This indicates that the two way migration is the native and common ecology of juvenile temperate seabass, independent of their hydrodynamics. This also suggests that the early life history of this species depends more intensively on the river water than previously considered. It is necessary to investigate the distribution in the other estuaries to confirm the generality of the migration of juveniles into freshwater as well as residence in the sea water and brackish water.

The previous studies in the Chikugo River estuary, which is well-known as a strong tide estuary, showed that seabass juveniles select the flood tide to achieve effective upstream transport (Ohta, 2004; Islam et al., 2007). A similar migrating mechanism was also reported for American eels *Anguilla rostrata* in the Penobscot River estuary (James and Robert, 1982) and many flatfishes in various estuaries (Gibson, 1997). In the Yura River estuary, however, the tidal range is considerably small and strong tidal current is not induced (Kasai et al., 2010). Therefore, juveniles would ascend the Yura

River through the bottom layer which is occupied by sea water rather than the tidal stream transport. The timing of salt wedge intrusion in the Yura River estuary varied annually according to the river discharge in early spring (Kasai et al., 2010). This suggests that the timing of river ascending of juveniles would fluctuate from year to year. Actually, the timing of river ascent of juveniles were varied among years from the beginning of March (2009) to mid-April (2011) (Fig. 3-4). This point is discussed in Chapter 4.

The distribution of juveniles might be related to ambient prey abundance and/or refuge from predators. In the freshwater zone, juveniles were abundant at R2 and R3 every year (Fig. 3-5). Iwamoto et al. (2010) also reported that seabass juveniles were abundant at the middle part of the Ohta River estuary, where is 4-8 km upstream from the river mouth with salinity ranged from 1 to 12. They considered that the ambient prey abundance would be an important factor for juvenile distribution in the estuary. Fujita et al. (2007) and Shoji et al. (2006b) reported the distribution of seabass juveniles coincided with that of their prey items in the Rokkaku River estuary and Chikugo River estuary, respectively. This might be applicable to the Yura River estuary, although the hydrographic condition is considerably different from the other estuaries. The prey abundance and the feeding ecology of seabass juveniles in the Yura River estuary will be shown in Chapter 5.

Table 3-1 Environmental conditions and juvenile size and number collected in broad area sampling in 2012

Station	Habitat type	Date	Temperature (°C)	Salinity	Median SL (mm)	SL range (mm)	n
Amanohashidate	Sandy beach	10 Apr.	14.8	30.8	17.9	14.5–21.5	176
Tai	Sandy beach	10 Apr.	13.5	32.7	19.1	16.6–22.2	18
Kunda	Sandy beach	10 Apr.	12.9	33.6			0
S1	Sandy beach	10 Apr.	13.1	27.2	19.2	16.3–22.6	7
Maizuru	Seagrass beds	11 Apr.	13.0	30.6	18.6	14.1–21.8	86
Nohara	Sand beach	11 Apr.	11.8	33.5			0
Mihama	Sand beach	11 Apr.	12.1	33.6			0
Sezaki	Sand beach	11 Apr.	12.3	33.7			0
Honjo	Sand beach	12 Apr.	14.1	29.9	15.1	12.4–17.4	6
Tomari	Sand beach	12 Apr.	14.2	31.4	15.3	12.2–19.9	27
Iwagahana	Seagrass beds	12 Apr.	13.4	33.0	18.6	16.6–21.2	21
Satohami	Seagrass beds	12 Apr.	13.2	27.0	18.5	15.7–22.2	86

SL: standard length n: number of juveniles collected

Table 3-2 Number of sample (n), mean, median, maximum and minimum value of standard length (SL, mm) and body weight (BW, g) of juveniles

Year	Date	**Coastal area (S1 + R1)**									**Lower estuary (R2+R3)**									**Upper estuary (R4 + R5)**								
			SL				BW					SL				BW					SL				BW			
		n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum	n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum	n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum
2008	18 Apr.	150	20.6	20.7	26.4	15.7	0.13	0.12	0.29	0.04	309	20.6	20.5	25.5	15.7	0.12	0.11	0.25	0.05	11	18.4	17.6	20.3	16.4	0.09	0.09	0.11	0.07
	24 Apr.	112	21.7	21.7	25.8	18.0	0.15	0.15	0.26	0.08	84	21.7	21.1	33.0	15.5	0.15	0.13	0.54	0.05	17	22.2	21.8	27.0	19.0	0.15	0.13	0.34	0.07
	1 May	78	24.7	24.7	29.6	19.5	0.23	0.23	0.39	0.11	65	22.3	21.9	29.3	17.1	0.16	0.15	0.45	0.05	14	23.6	23.9	28.9	20.9	0.20	0.20	0.42	0.11
	8 May	50	28.2	28.2	32.8	22.3	0.38	0.38	0.58	0.16	73	24.2	24.4	30.8	17.1	0.20	0.19	0.46	0.06	19	24.7	25.2	32.0	19.8	0.26	0.20	0.93	0.10
	16 May	142	29.0	29.0	38.5	19.0	0.42	0.40	0.96	0.08	69	25.6	25.3	35.2	18.8	0.26	0.22	0.68	0.22	22	27.7	26.7	34.7	21.8	0.35	0.30	0.70	0.15
	23 May	16	32.9	32.7	38.5	27.1	0.60	0.58	0.98	0.28	40	26.6	26.0	39.1	18.6	0.33	0.28	0.98	0.09	8	26.7	26.4	34.3	23.3	0.34	0.30	0.70	0.22
	29 May	12	36.3	35.6	44.9	32.1	0.86	0.78	1.66	0.57	67	29.4	28.6	42.4	21.9	0.50	0.43	1.36	0.18	2	35.8	35.8	38.0	33.6	0.83	0.83	0.99	0.67
	6 Jun.	217	40.6	40.4	50.3	30.0	1.13	1.11	2.11	0.44	50	31.4	31.0	48.3	23.0	0.56	0.50	1.82	0.20	7	39.0	33.8	57.1	30.0	1.34	0.67	3.46	0.54
	13 Jun.	0									24	37.4	36.6	50.8	26.2	0.96	0.76	2.36	0.25	10	40.2	39.2	59.4	27.1	1.37	1.06	4.16	0.38
	19 Jun.	16	54.2	54.5	68.5	45.9	2.71	2.67	5.28	1.74	30	41.0	40.7	60.2	26.7	1.27	1.10	3.20	0.31	21	47.0	47.7	64.8	30.2	1.68	1.75	3.14	0.32
	26 Jun.	2	43.7	43.7	55.4	31.9	1.85	1.85	3.18	0.51	14	42.4	48.9	57.3	26.1	1.41	1.78	2.78	0.27	3	42.1	41.4	52.0	33.0	1.39	1.37	2.25	0.55
	3 Jul.	0									7	46.1	46.3	53.0	35.9	1.66	1.53	2.40	0.70	13	55.6	49.5	87.0	41.7	2.49	1.94	7.26	1.40
	10 Jul.	1	51.7	51.7	51.7	51.7	2.18	2.18	2.18	2.18	2	48.9	48.9	51.0	46.7	2.07	2.07	2.34	1.79	2	57.4	57.4	73.8	40.9	1.21	1.21	1.21	1.21
	16 Jul.	6	70.5	73.4	78.0	54.0	6.80	7.27	9.71	2.47	7	52.5	55.3	63.1	36.6	2.51	2.63	3.80	0.68	0								
2009	9 Mar.	0									2	18.7	18.7	18.7	18.6	0.08	0.08	0.08	0.07	n.d.								
	18 Mar.	41	16.9	16.7	21.5	13.0	0.06	0.06	0.12	0.02	5	18.5	18.2	20.2	17.1	0.08	0.07	0.10	0.06	n.d.								
	26 Mar.	3	17.5	18.1	18.2	16.3	0.07	0.06	0.09	0.05	9	19.4	19.3	21.2	16.6	0.09	0.09	0.13	0.05	n.d.								
	2 Apr.	19	17.9	17.7	21.7	14.5	0.07	0.06	0.13	0.03	9	17.8	16.6	20.7	16.4	0.07	0.06	0.12	0.04	n.d.								
	15 Apr.	6	20.0	19.9	21.2	19.0	0.08	0.08	0.10	0.06	78	21.8	21.8	28.7	17.8	0.14	0.13	0.33	0.05	23	23.5	22.7	27.2	20.5	0.18	0.15	0.31	0.10
	21 Apr.	35	17.7	17.8	24.7	12.8	0.08	0.08	0.25	0.02	39	24.2	24.2	29.6	18.0	0.23	0.22	0.46	0.07	25	24.7	24.5	29.7	20.5	0.25	0.23	0.46	0.14
	27 Apr.	0									47	22.6	21.1	30.8	16.3	0.19	0.14	0.50	0.04	25	25.5	25.7	31.7	20.7	0.28	0.27	0.53	0.13
	12 May	1	21.9	21.9	21.9	21.9	0.07	0.07	0.07	0.07	84	29.6	29.1	40.6	20.2	0.47	0.40	1.23	0.12	34	34.4	35.3	41.2	23.4	0.77	0.84	1.31	0.22
	19 May	2	28.9	28.9	30.2	27.5	0.51	0.51	0.60	0.42	48	30.0	29.5	45.0	20.8	0.54	0.49	1.60	0.14	32	32.3	31.7	48.2	24.6	0.62	0.53	2.03	0.27
	1 Jun.	0									79	36.1	37.0	52.6	22.7	0.90	0.81	2.55	0.18	43	43.1	43.5	61.1	26.2	1.56	1.36	4.36	0.25
	16 Jun.	6	36.5	36.0	46.1	31.5	0.88	0.85	1.57	0.52	26	39.2	37.9	52.2	27.7	1.15	1.00	2.45	0.43	46	46.2	46.7	61.4	28.6	1.94	1.83	3.52	0.42
	1 Jul.	22	57.2	59.2	70.9	40.4	4.02	4.11	7.16	1.96	14	46.7	43.6	63.3	37.2	2.05	1.54	4.42	0.93	58	57.9	61.2	71.0	43.8	4.26	4.21	8.36	1.63
	15 Jul.	106	57.9	56.7	95.1	38.6	3.66	2.91	13.30	1.16	7	53.4	49.0	79.4	43.1	3.10	2.01	9.17	1.26	49	49.3	46.7	56.9	42.4	2.11	1.84	3.37	1.28
	18 Aug.	14	70.3	68.8	92.6	55.8	5.98	5.38	12.50	2.73	2	70.2	70.2	94.0	46.5	5.87	5.87	10.03	1.70	0								

n.d.: no data

Table 3-2 Continued.

Year	Date	Coastal area (S1 + R1)									Lower estuary (R2+R3)									Upper estuary (R4 + R5)								
			SL				BW					SL				BW					SL				BW			
		n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum	n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum	n	Mean	Median	Maximum	Minimum	Mean	Median	Maximum	Minimum
2010	31 Mar.	31	17.9	18.0	20.2	15.0	0.07	0.07	0.10	0.05	0									n.d.								
	16 Apr.	8	19.9	19.4	23.0	18.3	0.11	0.10	0.15	0.08	3	23.2	22.0	26.7	20.9	0.19	0.19	0.27	0.12	n.d.								
	28 Apr.	86	20.6	20.5	26.2	15.4	0.14	0.14	0.29	0.05	123	21.6	21.6	25.3	17.1	0.15	0.15	0.25	0.05	0								
	14 May	2	22.3	22.3	25.5	19.2	0.18	0.18	0.27	0.08	41	24.3	24.9	35.4	16.7	0.24	0.23	0.74	0.05	23	27.3	27.8	36.7	20.5	0.34	0.35	0.73	0.11
	16 Jun.	12	44.8	43.4	56.1	33.0	1.78	1.45	3.45	0.69	16	36.5	33.7	48.4	29.2	0.92	0.68	2.18	0.44	0								
	21 Jul.	25	83.5	85.3	108.0	64.2	13.14	13.58	29.95	5.55	3	44.6	47.2	51.5	35.1	1.79	2.04	2.45	0.87	1	56.1	56.1	56.1	56.1	3.09	3.09	3.09	3.09
	27 Aug.	3	91.7	92.3	109.4	73.4	15.09	15.50	21.20	8.58	2	87.2	87.2	99.5	74.9	12.64	12.64	18.15	7.13	0								
2011	31 Mar.	18	15.9	15.8	18.2	13.8	0.04	0.04	0.06	0.02	0									n.d.								
	6 Apr.	82	16.1	16.1	19.7	12.0	0.04	0.04	0.08	0.01	0									n.d.								
	14 Apr.	64	16.1	16.2	19.4	11.6	0.05	0.05	0.10	0.02	0									n.d.								
	20 Apr.	2	18.4	18.4	18.6	18.2	0.06	0.06	0.06	0.06	9	19.6	19.5	21.5	17.9	0.08	0.08	0.12	0.06	0								
	27 Apr.	0									17	21.7	21.7	23.3	19.1	0.13	0.13	0.17	0.07	0								
	2 May	29	18.2	18.2	23.1	14.2	0.08	0.07	0.17	0.02	15	21.8	21.8	26.3	17.5	0.15	0.14	0.26	0.06	0								
	18 May	164	22.6	22.7	27.2	17.9	0.19	0.18	0.33	0.09	529	23.9	23.8	31.9	17.4	0.21	0.18	0.52	0.09	41	24.5	24.3	29.0	19.2	0.26	0.25	0.41	0.09
	25 May	9	26.7	27.4	29.0	20.5	0.33	0.38	0.43	0.13	10	25.0	23.4	31.2	21.3	0.28	0.21	0.50	0.12	9	25.3	24.8	31.0	21.0	0.27	0.26	0.47	0.11
	6 Jun.	1	30.9	30.9	30.9	30.9	0.47	0.47	0.47	0.47	9	32.6	32.3	39.8	24.6	0.61	0.55	1.16	0.25	7	33.5	34.1	41.5	26.9	0.66	0.68	1.20	0.30
	22 Jun.	7	45.0	42.7	68.3	34.9	2.12	1.47	6.59	0.78	5	37.1	37.2	40.2	32.7	0.92	0.96	1.26	0.58	8	42.6	41.6	49.0	37.2	1.36	1.31	1.91	0.83
	6 Jul.	93	48.9	48.6	59.9	41.6	2.18	2.12	3.35	1.43	2	50.3	50.3	50.4	50.1	2.32	2.32	2.41	2.22	2	46.0	46.0	51.4	40.5	1.95	1.95	2.70	
	3 Aug.	5	71.7	79.3	91.2	48.5	8.20	9.70	15.34	1.94	0									0								
2012	10 Apr.	9	19.9	19.3	23.1	16.3	0.12	0.10	0.20	0.05	1	21.1	21.1	21.1	21.1	0.14	0.14	0.14	0.14	n.d.								
	17 Apr.	186	19.9	19.9	25.5	16.5	0.11	0.11	0.17	0.07	37	20.5	20.9	24.0	16.4	0.13	0.14	0.23	0.01	0								
	23 Apr.	26	21.8	21.7	27.6	19.2	0.17	0.16	0.25	0.10	351	21.0	20.9	28.8	13.6	0.13	0.13	0.41	0.05	48	21.7	21.4	25.8	18.6	0.15	0.14	0.25	0.09
	10 May	60	26.6	26.7	31.7	21.2	0.32	0.32	0.54	0.15	21	27.0	27.3	30.7	21.7	0.30	0.30	0.45	0.13	14	27.9	27.8	32.3	24.1	0.37	0.34	0.63	0.19
	22 May	3	35.8	36.7	36.8	33.8	0.75	0.76	0.79	0.71	21	31.7	30.8	41.0	25.8	0.57	0.52	1.15	0.26	11	35.6	35.8	43.9	25.0	0.87	0.83	1.46	0.29
	14 Jun.	6	38.7	37.1	43.4	35.4	1.08	0.90	1.59	0.78	2	41.4	41.4	42.1	40.7	1.34	1.34	1.34	1.33	12	45.7	45.9	64.0	33.8	1.81	1.71	4.64	0.65
	26 Jun.	8	53.0	51.8	67.9	40.3	3.01	2.53	6.20	1.18	1	50.7	50.7	50.7	50.7	1.95	1.95	1.95	1.95	9	52.3	50.6	62.0	47.8	2.62	2.30	4.11	1.88
	17 Jul.	8	56.0	55.8	63.4	50.1	3.05	2.97	4.61	2.09	3	63.9	62.5	69.7	59.6	4.69	4.46	5.77	3.83	0								

n.d.: no data

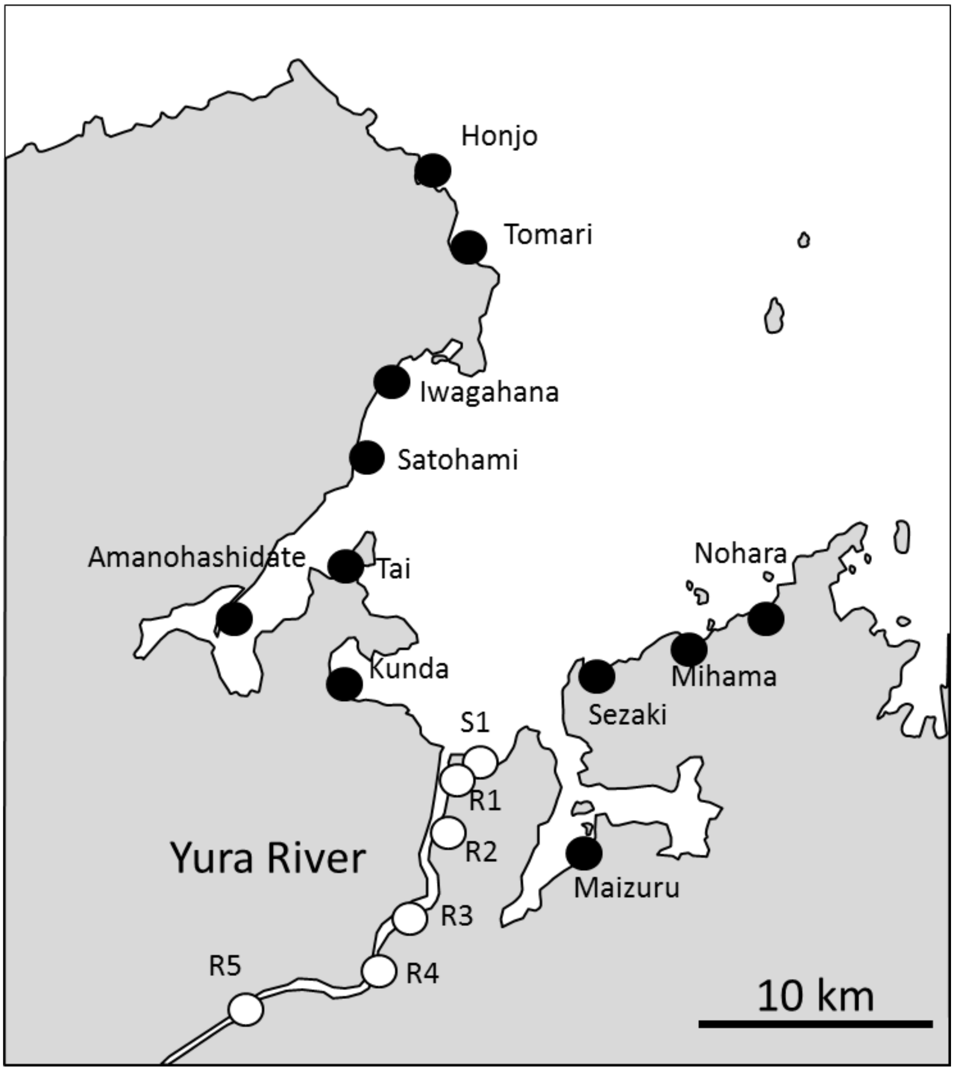

Fig. 3-1 Sampling stations around the Tango Sea. Filled circles indicate the stations of broad area sampling. Open circles shows the stations for estuarine sampling. S1 was used for both surveys.

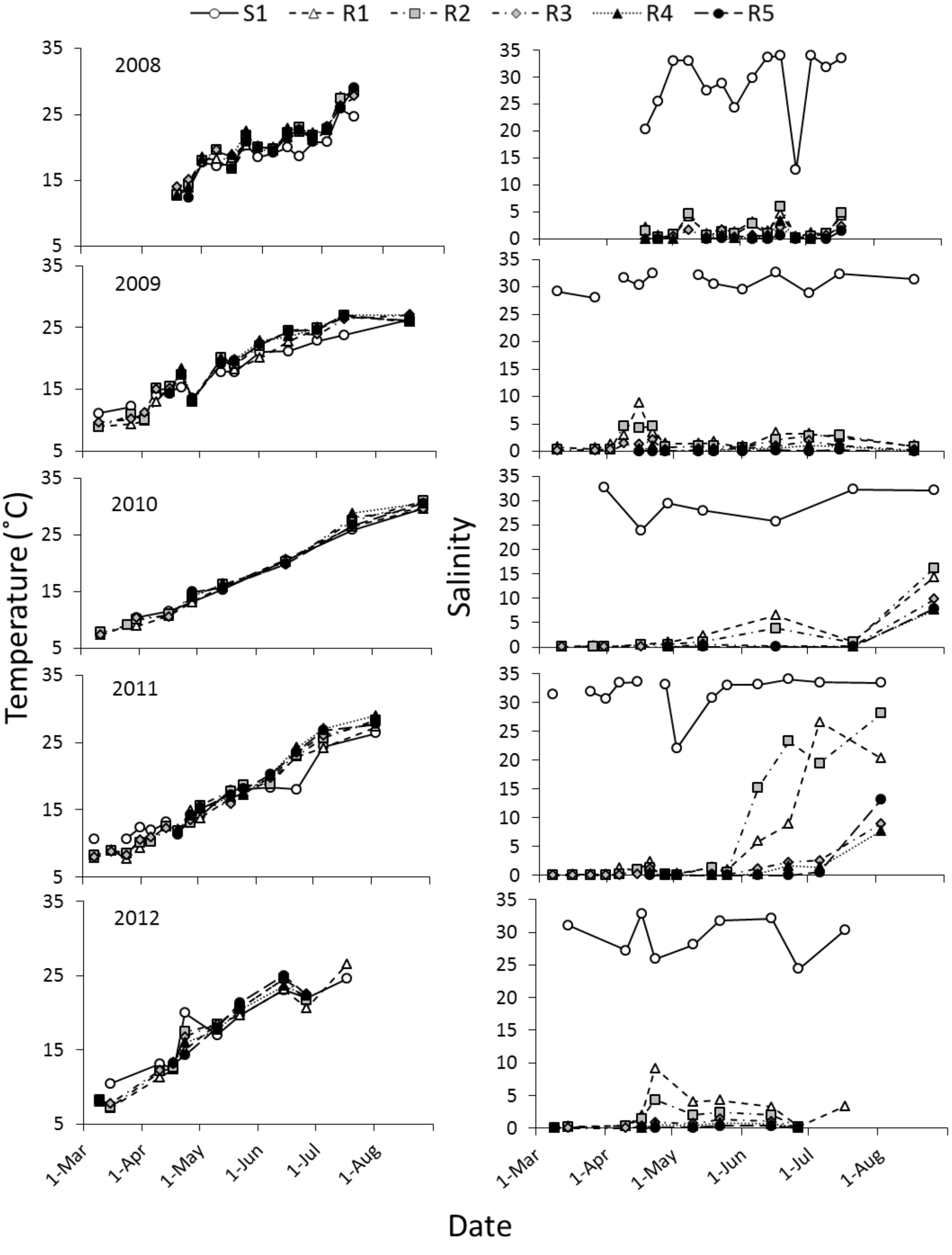

Fig. 3-2 Temperature and salinity in the Yura River estuary.

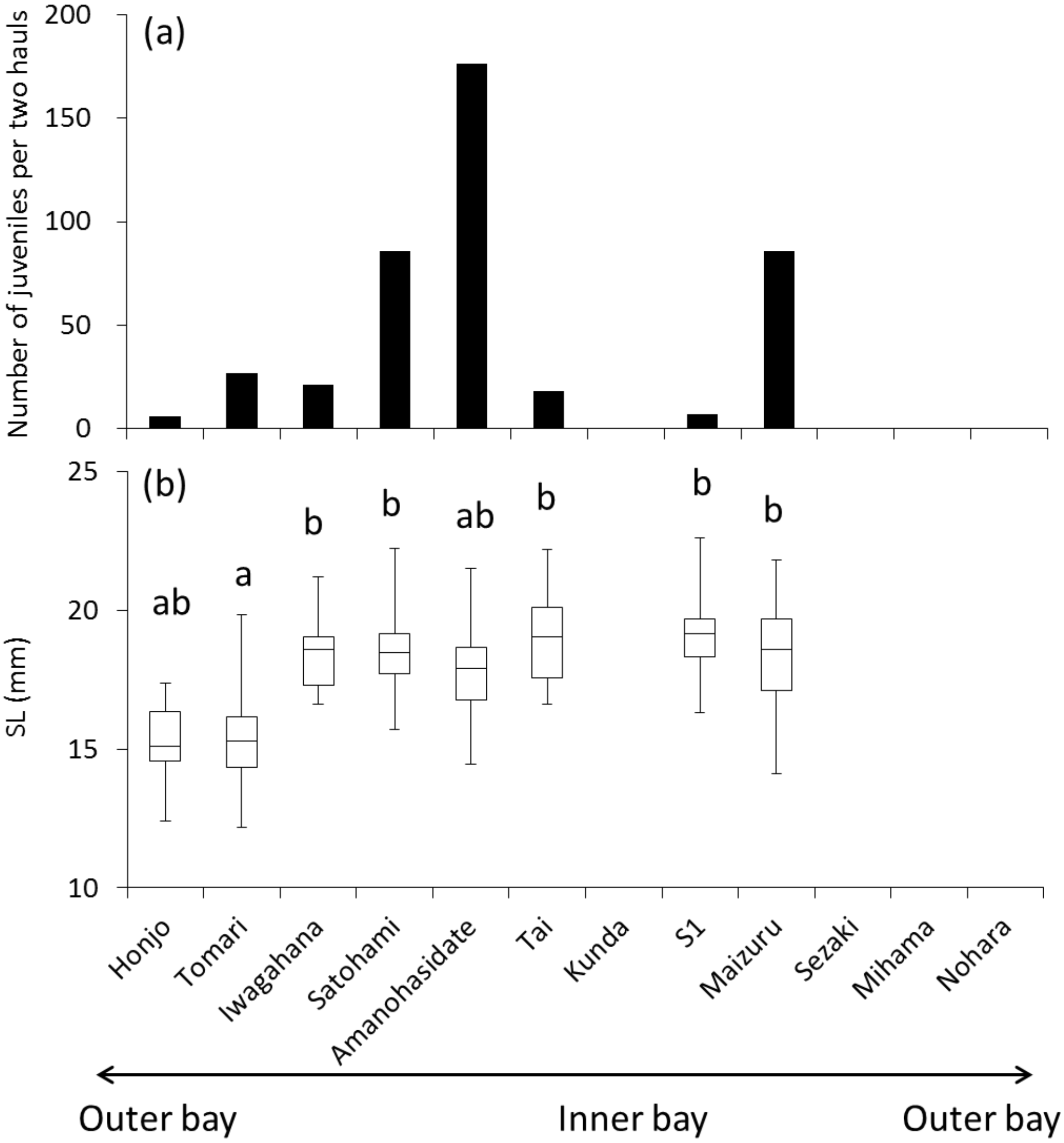

Fig. 3-3 (a) Number of individuals collected and (b) standard lengths (SL) of juveniles collected in broad area sampling in 2012. The solid line within boxplots represents the median standard length, the lower and upper boundaries of boxes represent the 25th and 75th precentiles of length and the lower and upper whiskers represent the minimum and maximum lengths. Different alphabets indicate the significant difference (Kruskal-Wallis test, followed by Sheffe's test, $P \leq 0.05$).

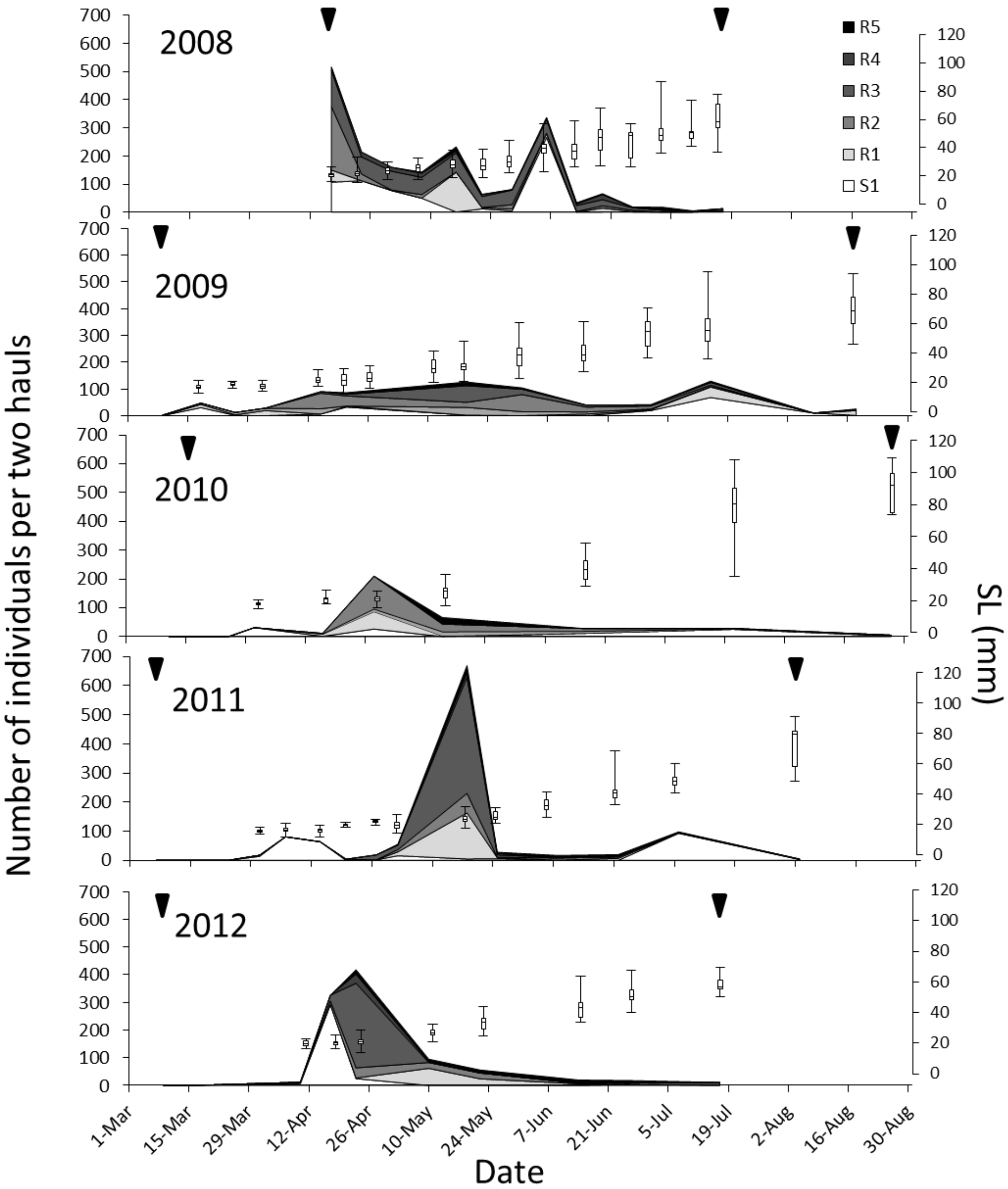

Fig. 3-4 Number of individuals collected and standard lengths (SL) of juveniles. Solid lines within boxplots represent the median SL, the lower and upper boundaries of boxes represent the 25 % and 75 % of SL, and the lower and upper whiskers represent the minimum and maximum SL. Triangles show the start and end of sampling periods.

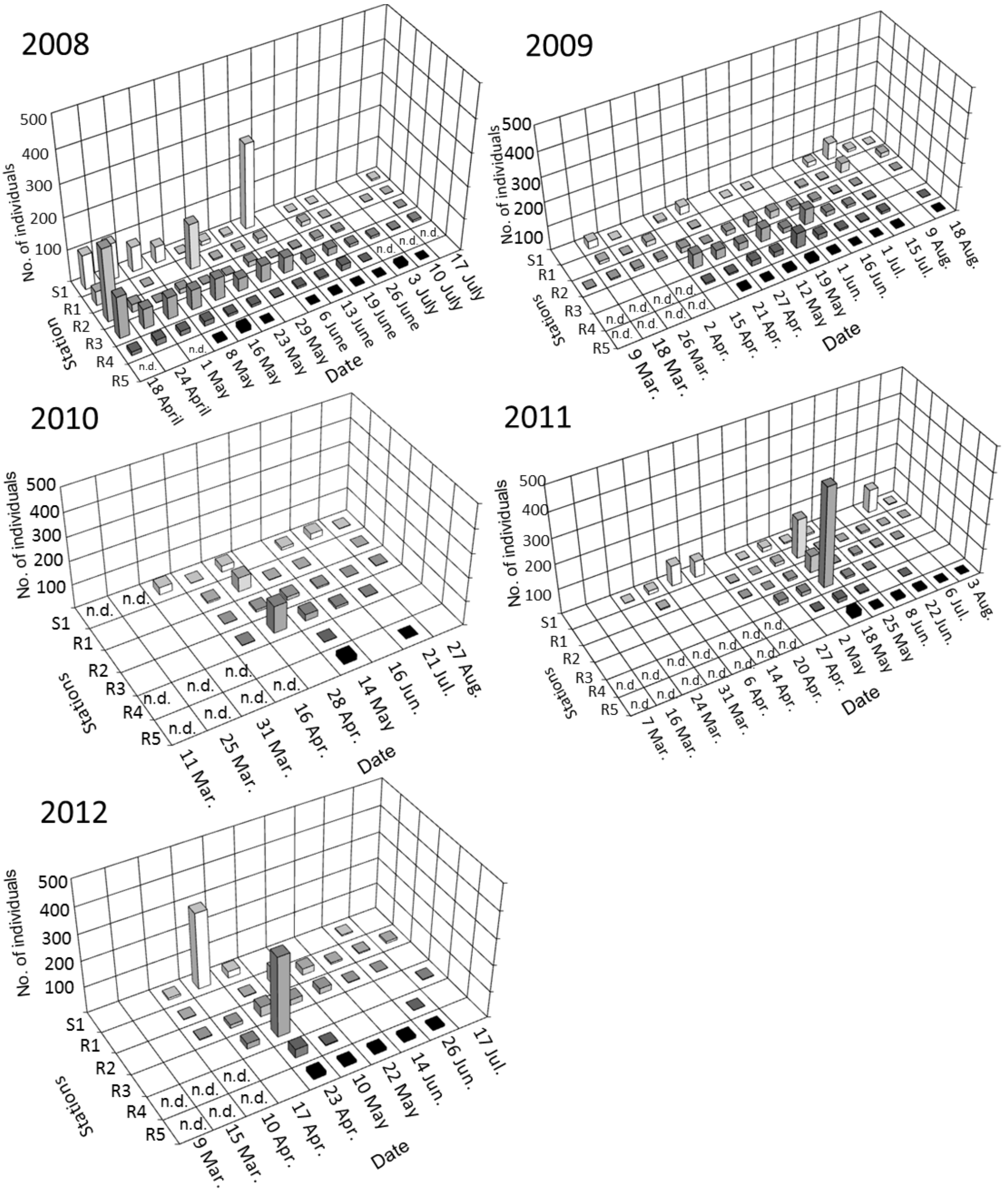

Fig. 3-5 Number of temperate seabass juveniles collected at each station. n.d. means that seines were not conducted at the station on the date.

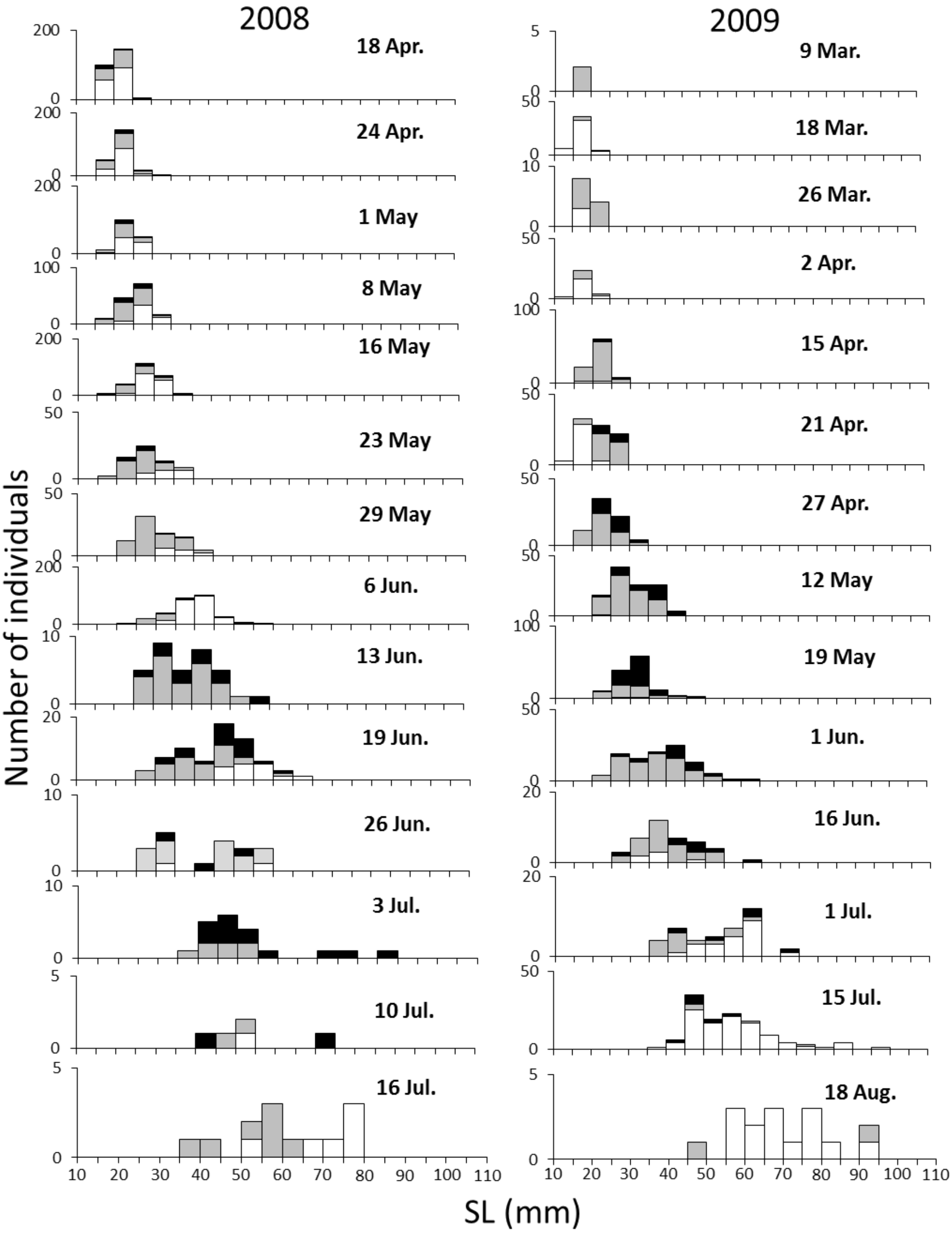

Fig. 3-6 Standard lengths (SL) of juvenile temperate seabass. White, gray and black bars mean juveniles in S1 and R1, R2 and R3, and R4 and R5, respectively based on the distance from the river mouth, salinity and prey environments (see Chapter 4).

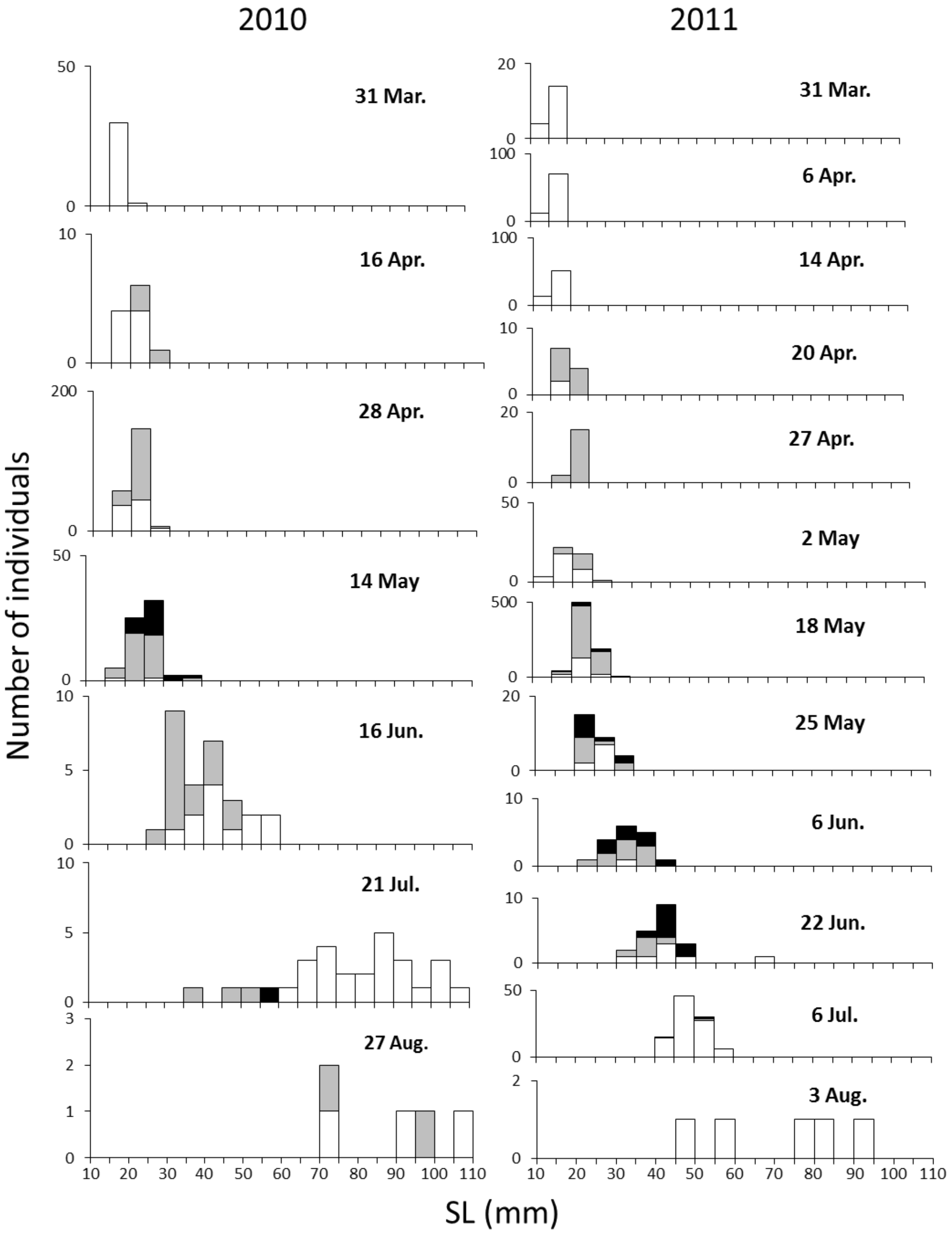

Fig. 3-6 Continued.

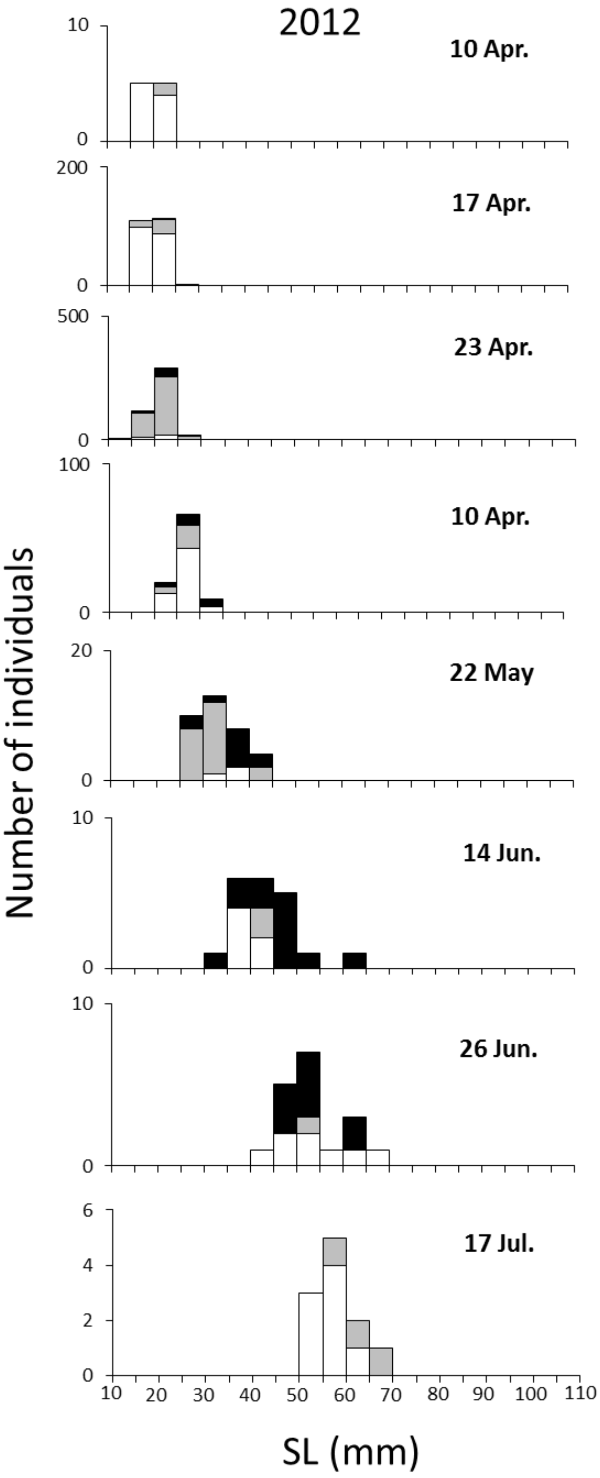

Fig. 3-6 Continued.

Chapter 4

River ascending mechanisms of juvenile temperate seabass in the stratified Yura River estuary

Introduction

Estuaries are characterized by their high productivity and many animals utilize them as nurseries (Beck et al., 2001). Success of migration into estuaries is one of the most important factors for juveniles to achieve good survivals (Beck et al., 2001). Estuaries, in which hydrodynamics is strongly affected by river flows and tidal conditions, are characterized by its high time-spatial complexity of the hydrology (Kasai et al., 2010). This complexity would affect the migration of juveniles that utilize estuaries as nurseries. Environmental conditions would control migration ecologies of juveniles through two different ways. First, hydrological conditions affect the movements of juveniles directly. Especially, juveniles should overcome the river flow regardless of their poor swimming ability. Larvae of some species of fish use tidal currents to overcome this difficulty. They distribute surface or middle layers to migrate onshore and upstream with onshore flood tidal currents. They move to bottom layer and reside there during ebb tide to avoid offshore currents. This mechanism is called "tidal selective transportation" (James and Robert, 1982; Gibson, 1997; Islam et al., 2007). However, in microtidal estuaries, fishes cannot use this mechanism, so that they would use another way to migrate. Saltwedge intrusion is another possible environmental factor which juveniles might use when they ascend rivers in the microtidal estuaries, because water flows upstream in the saltwedge (Dyer, 1973). This would be effective for juveniles to avoid flowing out by the river current and achieve efficient ascending to upper estuaries.

Second, many studies reported that there are various endogenous factors for starting the migration behavior of fishes (Boubée et al., 2001; Tsukamoto et al., 2009). There are mainly two distinct processes controlling migration of fish: first, the physiological developments of migratory readiness whereby the juveniles undergo physiological, morphological and behavioural changes, and second, the environmental triggers stimulate migration behaviors when endogenous conditions have been completed (Solomon, 1978; Tsukamoto et al., 2009). Temperature is one of the most important factors for initiating migration behavior of juveniles by fulfilling these endogenous conditions (Uchida et al., 1990; Benoît et al., 2000; Zydlewski et al., 2005; Jansen and Gislason, 2011). In the case of smolt fishes, seasonal increases in daylength and temperature are hypothesized to synchronize physiological and behavioral changes necessary for successful migration to the sea (McCormick et al., 1998). Therefore, many studies described the relationship between temperature and the timing of migration in the field. The cumulative temperature has been often used as the indicator of starting fish migration for several kinds of fish (Nakamura and Kasuya, 2004; Zydlewski et al., 2005). However, the endogenous processes stop below a certain temperature, called “base temperature” (Kaeriyama, 1989; Trudgill et al., 2005). The difference between observed temperature and base temperature (effective temperature) is more meaningful to consider the effects of temperature on the biological processes. Effective cumulative temperature thus should be used as the indicator of the various biological processes (Kaeriyama, 1989; Trudgill et al., 2005).

Juvenile temperate seabass ascend rivers at the size of ca. 20 mm standard length (Chapter 3; Matsumiya et al., 1982). This fish use tidal selective transportation to ascend macrotidal estuaries such as the Chikugo River estuary (Ohta, 2004; Islam et al., 2007). However, river ascending mechanisms is unknown in the microtidal estuaries such as the Yura River estuary. Saltwedge intrusion is possibly an important hydrological event for river ascending in this estuary Hypothesis in this chapter is that juvenile uses the saltwedge intrusion for ascending the Yura River estuary. In addition, the relationship between effective cumulative temperature and timing of river ascending was estimated to confirm that temperature is also important factor for deciding the timing of river ascending.

Materials and methods

Field sampling

Samplings were conducted at the stations of estuarine samplings (Fig. 4-1). Stations were divided into three groups; coastal area (S1 and R1), lower estuary (R2 and R3) and upper estuary (R4 and R5) for simplification.

Conductivity data loggers (INFINITY-CT A7CT-USB, JFE ADOVANTEC) were set in the bottom layer of the river to monitor the change of bottom salinity with the saltwedge intrusion. The loggers were set at the stations 0, 6 and 11 km from the river mouth (Fig. 4-1). The loggers were set from February to May every year. However, in 2012 no logger at 0 km was set. The data logger at 6 km upstream was lost because of a flood event in May 2011. Salinity was recorded every 10 minutes.

Laboratory analysis

Standard length (SL: mm) was measured for every individual. Individuals for otolith analyses were randomly selected from each sampling station on 18 March and 15 April 2009, 28 April 2010, 18 May 2011 and 23 April 2012. Otoliths (lapillus) were removed from those samples. Otoliths were embedded in epoxy resin on glass slides and polished with fine sandpaper until the core clearly appeared. Lapilli were used in this study because they were subject to fewer sub-daily increments and peripheral primordia than sagittae for seabass juveniles of ca. 20 to 30 mm SL (Fujita, 2004; Suzuki et al., 2008a; Islam et al., 2009). Daily rings of otoliths were counted and each increment widths were measured using a video monitor and an otolith reading system (ARP/W, Ratoc System Engineering). Age of temperate seabass juveniles was estimated by adding 4 to the increment counts, as the first daily increment is deposited at day 4 (the first feeding date) in the lapilli of this species (Suzuki et al., 2008a).

Environmental data

Daily mean discharge data of the Yura River from March to May in 2009-2012 (measured in Fukuchiyama, 37 km upstream from the river mouth; Fig. 4-1a) were obtained from Ministry of Land, Infrastructure, Transport and Tourism. As representative of the temperature in the Tango Sea, daily temperature data in the Tango Sea at the depth of 12 m in Miyazu (Fig. 4-1b) were obtained from Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Center. Daily mean sea water level data in the same period in the Maizuru port (Fig. 4-1b) were gained from Japan Meteolorogical Agency.

Data analysis

The distance of saltwedge intrusion in the Yura River estuary was estimated from the daily sea level at Maizuru and river discharge at Fukuchiyama using the equation from Kasai et al. (2010). The distance of saltwedge intrusion was defined here as the distance from the river mouth to the tip of the salt wedge, in which salinity is 5 at the bottom (Kasai et al., 2010). The distance from river mouth to the most upstream station in which juveniles were collected is defined as juvenile river ascending distance. These two distances were compared.

SL - daily age linear relationships were determined for every year. The ages of every individual in each year were estimated by using these relationships and SL data. Individuals with the SL that is out of the age range of samples for otolith analyses were eliminated from this estimation because of the uncertainty in age estimations. Hatch dates were estimated from estimated age and collected date for each individual. Individuals were categorized into some cohorts with 10 days duration. The cohorts including more than 5 individuals were selected for further analyses.

River ascending index on i th sampling day (A_i) were determined as follows;

$$A_i = N_i - N_{i-1} ,$$

where N_i is the total number of individuals collected in the lower and upper estuary on the i th sampling day. To compare this index among all cohorts, it was standardized as

$$\%A_i = \frac{100A_i}{\sum A_i},$$

and subsequently cumulated as follows;

$$F_i = \sum_1^i \%A_i.$$

The low of effective cumulative temperature is described as follows (Kaeriyama, 1989; Trudgill et al., 2005);

$$k = D(T - t),$$

where k (C°-days) is an effective cumulative temperature. D (days) is period that a biological process takes to complete, T (C°) is mean temperature during a biological process and t (C°) is designated as an estimated base temperature. In this study, the juvenile ascent is considered as a biological process. Here, D is the period that each cohort takes to start ascending the river (equal to the mean daily age of each cohort at the day of ascending the river) and T is mean temperature that juveniles experienced in the sea during the period between mean hatch date of the cohort and the day of ascending the river. The day of ascending the river is estimated by following two ways; first days that individuals started to be collected in the lower or upper estuary (first ascending day) and at the days that most of individuals ascend, which is defined as the day that $\%A_i$ exceeded 50 (main ascending day). Both two days were determined for each cohort. Parameters k and t were estimated by a linearizing transformation for the variable D resulting in the equation

$$\frac{1}{D} = -\frac{t}{k} + \frac{T}{k} .$$

t and k are constants and estimated from the linear regression of T and $1/D$. t and k were estimated for both first river ascending days and main river ascending days. F_i and effective cumulative temperatures were compared to detect the relationship between river ascending behavior and temperature.

Results

Saltewedge intrusion dynamics and juvenile river ascending

The fluctuation pattern of river discharge in spring changes year-to-year (Fig. 4-2). River discharge in 2009 was low throughout spring season except for a flood event in March. In 2010, there were many flood events from March to the end of April, and subsequently river flow decreased in May. However, the river discharge was low during May except for a flood event at the end of the month. The river discharge was low until April and then two heavy floods (over 1000 m^3s^{-1}) occurred in the middle and late May 2011. In 2012, river flow was high until mid-April, but low from the late April.

Salinity in bottom layer changed according to the fluctuation of the river discharge (Fig. 4-3). In 2009, bottom salinity started to increase at 6 km upstream since beginnig of March. Then the saltwedge reached 11 km upstream from the beginning of April which is in good agreement with low discharge after April. In 2010, saltwedge ascended the river up to 6 km upstream from the end of April when the river discharge decreased. Saltwedge then reached 11 km upstream in the beginning of May. In 2011, salinity around the river mouth increased from April, and then saltwedge reached 11 km upstream in the middle of April and mid-May, followed by the flash out by the large floods. Bottom salinity at 6 km upstream began to rise from the beginning of April 2012. Saltwedge reached to 11 km upstream in the middle of April.

Timings of juvenile movement from the coastal area to the lower estuary and the lower estuary to the upper estuary corresponded to the saltwedge intrusion into the Yura River estuary (Fig. 4-3). For example, in 2009, juvenile distributions were restricted in the lower estuary during March and beginning of April, when saltwedge intruded until 6.5 km upstream. Juveniles then reached the upper estuary from mid-April, corresponding to the rise of bottom salinity at 11 km upstream (Fig. 4-3). These correspondences were observed in all years. In April 2011, however, no juveniles appeared in the middle and upper estuary until later-April even though saltwedge already intruded around the river mouth and almost reached 11 km upstream (Fig. 4-3). Comparison between estimated saltwedge intrusion distance and juvenile ascending distance showed few juveniles ascended further than the saltwedge intrusion (Fig. 4-4). Juveniles went beyond the saltwedge only on 15 April 2009 and 18 May 2011.

Temperature and timings of river ascending of juveniles

Temperature in Miyazu was generally high in 2009 and low in 2010 and 2011 (Fig. 4-5). Temperature decreased from December to March and lowest temperature was recorded in March in every year. Then temperature started to increase from the end of March.

Using the Age-SL relationships for each year (Table 4-1), SL data was converted to daily age data. Hatch date distributed mainly from the mid-January to mid-February (Fig. 4-6). The peak was in the end of January in 2009, 2010 and 2012, while the mid-February in 2011. Samples were categorized into some cohorts (Fig. 4-6). $\%A_i$ changed with time comprised of mainly two phases (Fig. 4-7); subtle ascent ($\%A_i$ was mostly lower than 30%) followed by mass ascent ($\%A_i$ > 50 %). $\%A_i$ of different cohort showed different timing of surge; earlier cohorts ascended earlier (Fig. 4-7). The first ascending days ranged from 9 March (2009) to 18 May (2011) among cohorts.

Main river ascending days were considerably different from 10 April (2012) to 18 May (2011). Mean temperatures they experienced until the first ascending days ranged from 11.0 to 12.7 ˚C (Fig. 4-8), showing significant correlation between $1/D$ and T ($P \leq 0.05$), while no significant relationship was obtained for the main river ascending days ($P > 0.05$, Fig. 4-8). Base temperature (t) and effective cumulative temperature (k) were estimated as 5.0 ˚C and 514.1 ˚C-days for the first ascending day. Temperature at the first ascending days was not ascertaining value, but various ranged from 11.7 to 16.1 ˚C (Fig. 4-9). However, all cohorts in all four years showed similar pattern of F_i trajectories against effective cumulative temperature (Fig. 4-9). Most of all cohorts started to ascend the river at the ca. 500 degree-days.

Discussion

Juveniles changed their distribution in the Yura River according to the change of saltwedge intruding distances (Fig. 4-3). Distances of juvenile river ascending were within the estimated distances of saltwedge intrusion except for 15 April 2009 and 18 May 2011 (Fig. 4-4). Although estimated distances of saltwedge intrusion on 15 April 2009 was 9.3 km, saltwater was observed by a conductivity logger at 11 km upstream where is the most upstream station juveniles were collected on that date (Fig. 4-3). This indicates that juvenile distribution on this date was still below the distance of saltewdge intrusions. On the other hand, both estimated distance of saltwedge intrusion and bottom conductivity logger indicated saltwedge remained around 11 km upstream, while juveniles went further on 18 May 2011. Only larger individuals (> 23 mm SL) reached to 15 km upstream station (R5), while smaller ones (< 23 mm SL) remained at 11 km upstream station (R4) on 18 May 2011 (Fuji, unpublished data). This would mean that only larger juveniles have enough osmoregulation and swimming ability to ascend the river against freshwater flow. Given the information that most of juveniles ascend the river with the size smaller than 23 mm SL (Chapter 6), early juvenile temperate seabass utilized the saltwedge intrusion to ascend the Yura River estuary. These results indicate that juvenile temperate seabass utilized the saltwedge intrusion for ascending the Yura River estuary. In the Chikugo River estuary, which is characterized by its large tidal amplitude, juveniles of temperate seabass use tidal selective transportation to ascend the river (Islam et al., 2007; Ohta, 2004). Not only temperate seabass but also many fish species utilize the tidal currents for migration in their early life stage because their swimming abilities are not enough to move against water currents (Gibson, 1997; James and Robert, 1982; Islam et al., 2007). However, in the Yura River estuary, there is no strong tidal current because of small tidal amplitude (Kasai et al., 2010). This means that juveniles cannot use the tidal selective transportation in this area. The temperate seabass juveniles are small when they ascend the river (ca. 20 mm SL; Chapters 3 and 6). Generally speaking, small juveniles have little ability to swim. For example, juvenile red seabream *Pagrus major* at the size of 20 mm SL can swim at 0.18 ms^{-1} at a maximum (Yano and Ogawa, 1981). Surface water at the Yura River mouth flows downstream at the speed of 0.22 ms^{-1} in summer, the lowest river discharge season in a year (Yamazaki et al., 2005). It is considered that this current speed even increases in winter and spring when the river discharge is higher than summer because of snow melting (Fig. 1-2, Kasai et al., 2010). This means that it is difficult for juvenile seabass to ascend the river against the surface water current. In addition, osmoregulation ability of small juveniles is still not completed. Hirai (2002) reported that direct transportation of juvenile temperate seabass at the size of smaller 20 mm SL from seawater to freshwater condition killed them, while juveniles survived against the gradual decrease of salinity. The salinity of surface water in spring drastically changes from ca. 30 to almost 0 within small spatial range (ca. 1 km) around the Yura River mouth (Kasai et al., 2010). On the other hand, there is stable broad brackish layer between saltwedge and surface layer in the Yura River estuary in which juveniles can adjust them to lower salinity (Kasai et al., 2010). In addition, water flows upstream in the bottom layer when saltwedge intrudes (Dyer, 1973). Therefore, it is efficient for juveniles to use the saltwedge intrusion to ascend the microtidal estuary. On the other hands, this also means that when saltwedge does not intrude into the river, few juveniles can enter the river. Shoji et al. (2006a) considered that high river flow had the potential to decrease the probability of immigration of juvenile seabass into the river by increasing juvenile seaward dispersion. Shoji and Tanaka (2006b) also argued this fault of ascending would lead to higher mortality, because there are more predators in the high salinity environment, e.g., jelly fishes and arrow-worms. This would mean annual variation of saltwedge intrusion affect the recruitment of temperate seabass in the Tanog Sea. Further study is necessary to confirm this possibility.

Juveniles in 2011 did not ascend the river until mid-April even though saltwedge intruded in the river (Figs. 4-3 and 4-4). This means that saltwedge intrusion is one of the necessary conditions to ascend the river. Saltwedge intrusion would be like an opening gate: juveniles can enter the estuary only when the gate opens. However, it does not mean that juveniles always ascend the river when saltwedge intrudes. They must be ready to ascend rivers; filling the three necessary conditions, i.e. body development, endocrinological condition, and psychological processes (Tsukamoto et al., 2009).

This study found that not the threshold temperature but the effective cumulative temperature was the meaningful indicator of initiating the river ascending (Fig. 4-9). Some previous papers reported that there are temperature thresholds for initiating the fish migration (Kusuda, 1963, Solomon, 1978). On the other hand, cumulative temperature is known to be good index for predicting timings of migration for some fishes (Bohlin et al., 1993; Nakamura and Kasuya, 2004; Zydlewski et al., 2005; Hoffman et al., 2008). This study advocates the latter studies. Former studies did not consider the effects of hatch dates and only focused on the first ascending day in a year. This study showed many cohorts ascended the river in various timings (Fig. 4-7). This means that the temperatures when they started ascending are different among the cohorts and there should be no threshold of temperature initiating migration behavior (Fig. 4-9).

Tsukamoto et al. (2009) considered that fish start to migrate by receiving a trigger from particular endogenous or exogenous factors after filling three necessary conditions; age or body size, endocrinological condition and physiological process. Higher temperature would accelerate juvenile migration by meeting these three necessary conditions for starting migration. For example, high temperature often leads to short periods of metamorphosis (body development) in larvae of many marine fish species (Benoît et al., 2000). Completion of metamorphosis of seabass larvae and juveniles corresponds to the complement of osmoregulation, which is necessary for diadromous migrations (Hirai, 2002). This means that larvae can complete the preparation for osmoregulation in younger age under higher temperature. This enables them to ascend the river in younger age (Fig. 4-8a). In addition, higher temperature could also affect the physiological and psychological conditions of fish and accelerate the starting migration which leading to migrating behaviors (Uchida et al., 1990; McCormick et al., 1996). After filling these three conditions, particular stimulations would induce the migration behavior of juveniles. Rainfall and the following high turbidity are possible triggers for starting migration for some fishes (Boubée et al., 2001; Iwata et al., 2003). In the case of catadromous ayu, freshwater fall is the important stimulation to induce the river ascending behavior (Uchida et al., 1990). Being exposed to river plume in the coastal area is one of the potential triggers for juvenile temperate seabass to start river ascending behavior, because juvenile temperate seabass starts to change the structure of gills to adjust to lower salinity water after they experienced lower salinity water (Hirai et al., 1999). In addition, river plume would be the important directing post from the coastal area to the estuaries (Vinagre et al., 2007). This means that juveniles distributed near the river mouth would be easier to ascend the river. On the other hand, cumulative temperature was unrelated to the timing of main river ascending (Fig. 4-8b). Main river ascending of most cohorts occurred after the flood events (Figs. 4-2 and 4-7). Therefore, vast of lower salinity water by flood events might stimulate much more juveniles distributed not only around the Yura River mouth but also the other coastal areas resulting in main river ascending of juveniles.

Table 4-1 Regressions for stardard length (SL,mm) and age (day) for juveniles collected in the Yura River estuary from 2009 to 2012. All *P*-vaules for each regression were <0.001.

Year	Age-SL regression	R^2	n
2009	Age = 4.68SL − 15.99	0.76	115
2010	Age = 4.14SL − 3.54	0.62	33
2011	Age = 3.43SL + 14.63	0.46	30
2012	Age = 2.63SL + 35.90	0.51	26

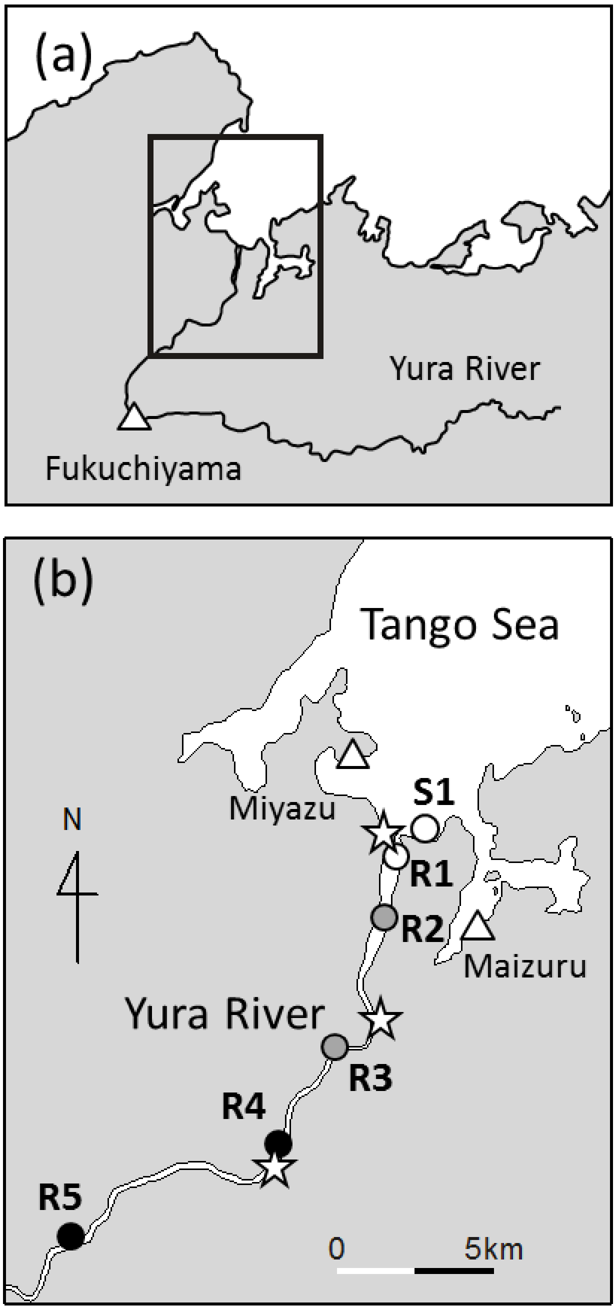

Fig. 4-1 Sampling stations along the Yura River estuary. Sampling stations were divided into three groups; coastal area indicated by open circles, lower estuary indicated by gray circles and upper estuary indicated by filled circles. Points that salinity loggers were set are indicated by stars.

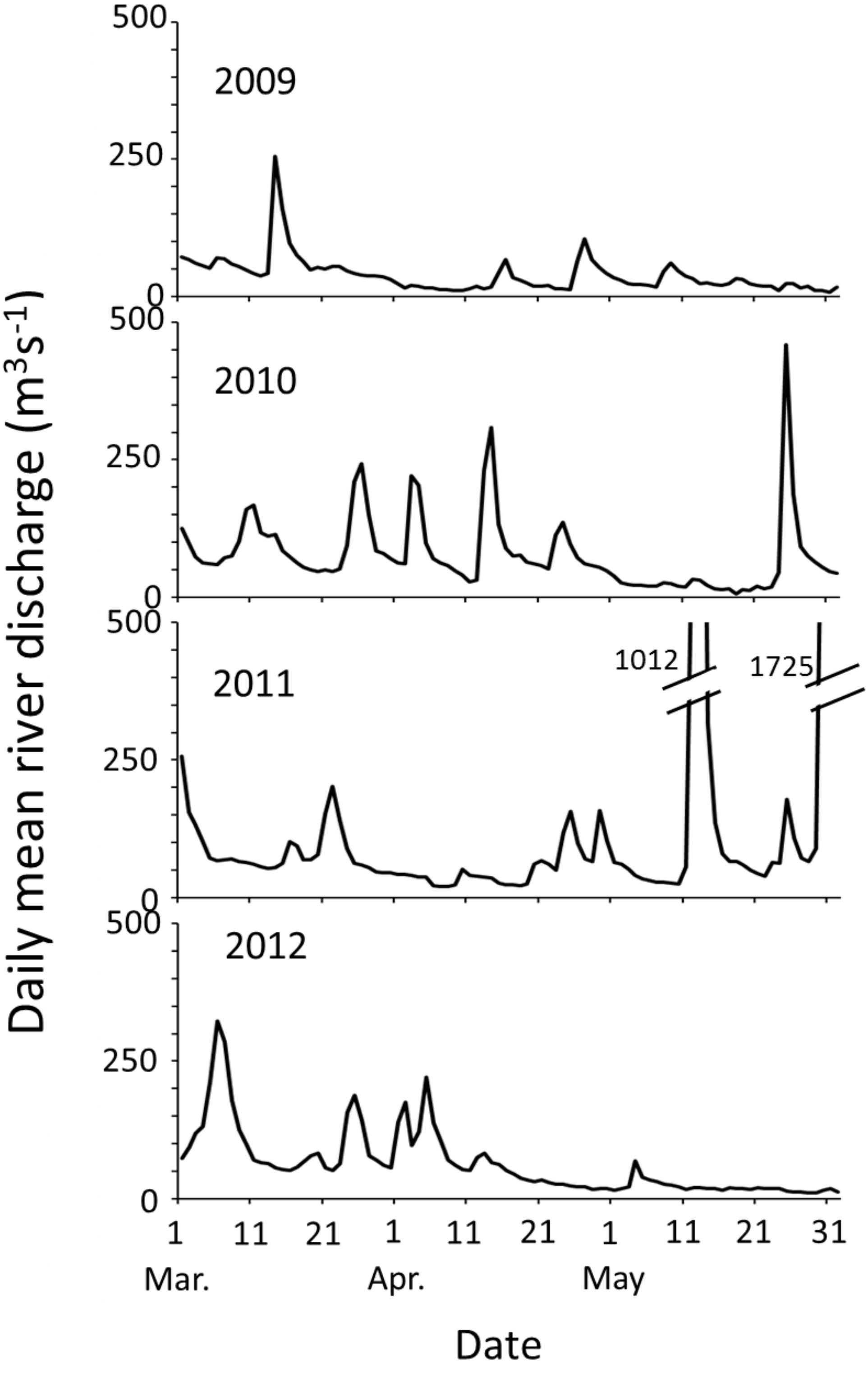

Fig. 4-2 Daily Yura River discharge from March to May in four years.

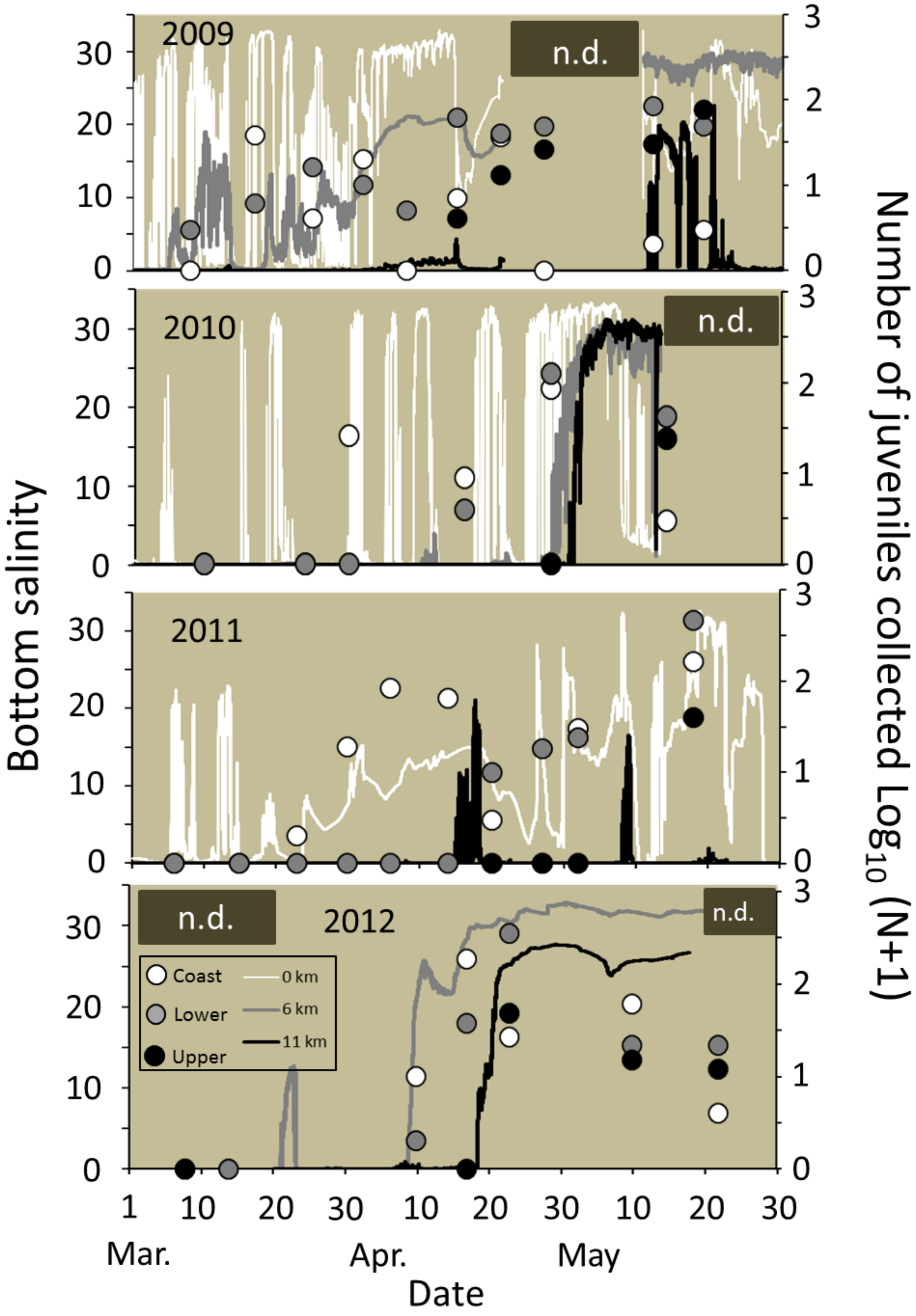

Fig. 4-3 Bottom salinity measured by salinity loggers and total number of juvenile temperate seabass collected in each area. n.d. means no salinity data.

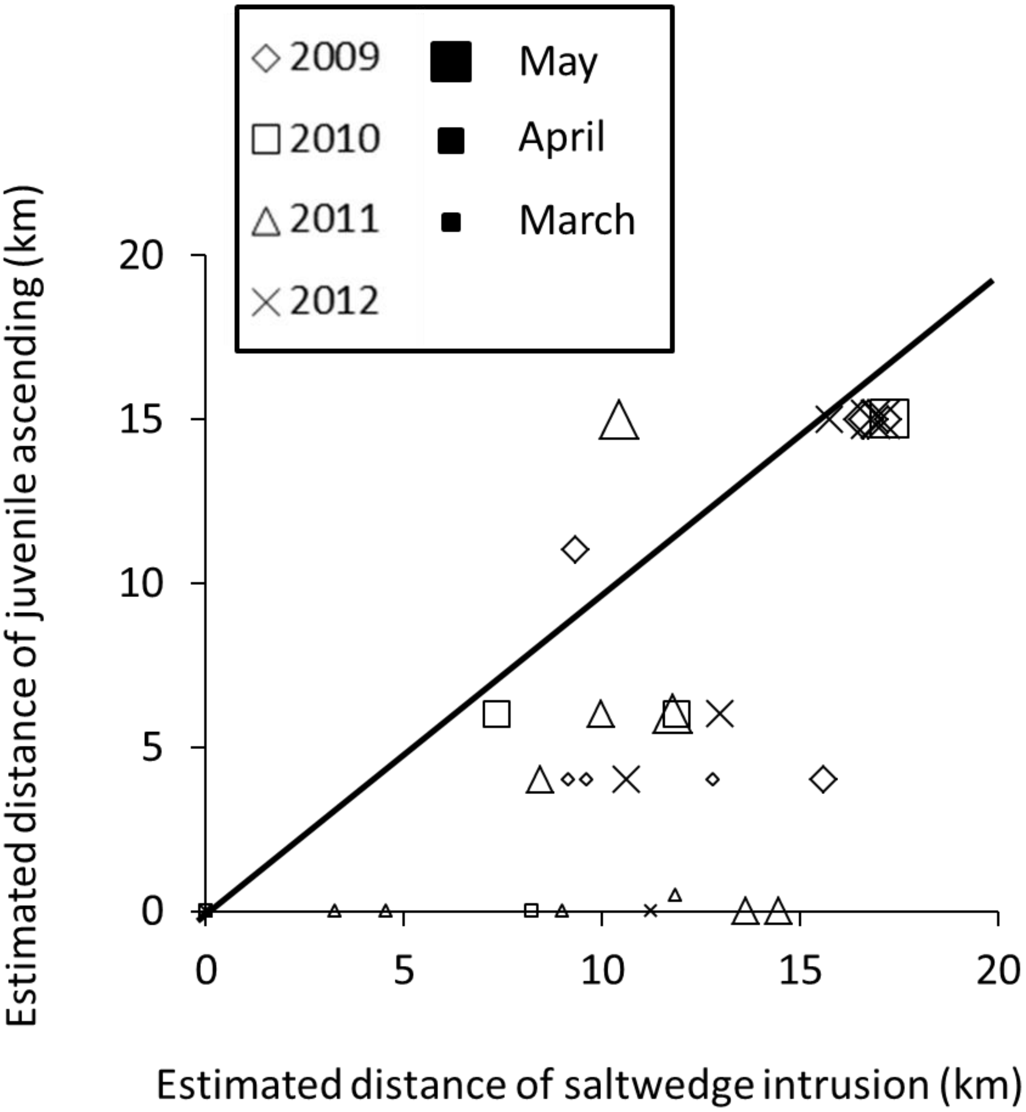

Fig. 4-4 Relationship between estimated distance of saltwedge intrusion and estimated distance of juvenile ascending. A line shows y = x. Larger symbols indicate later samples.

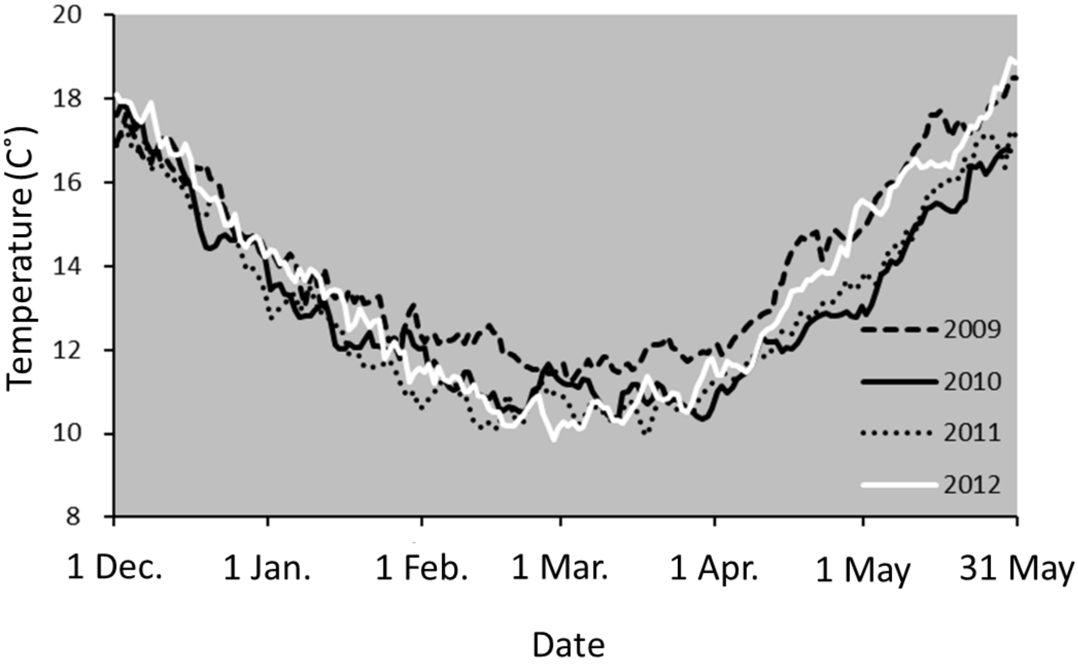

Fig. 4-5 Daily temperature observed at 12 m depth in Miyazu.

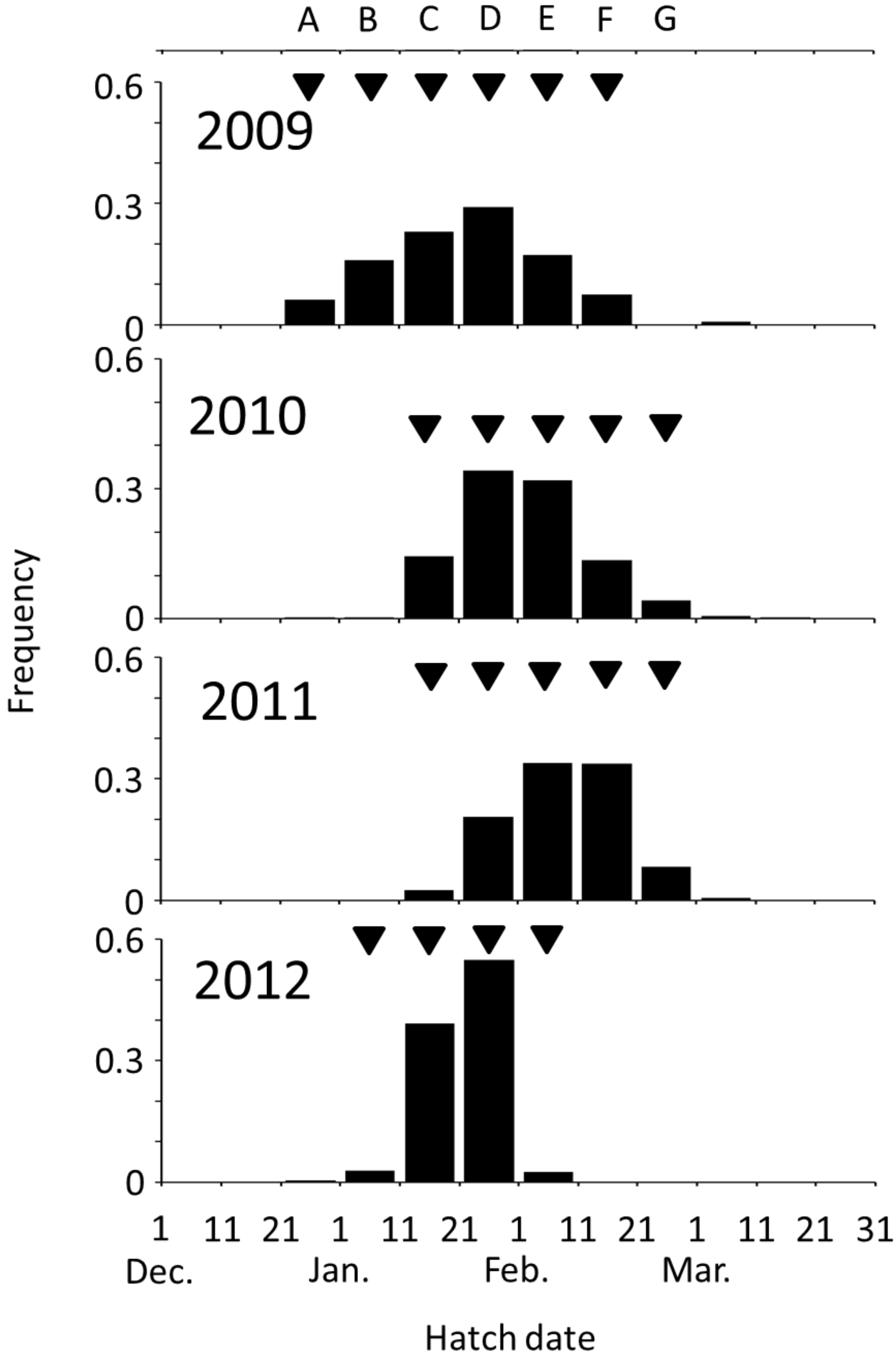

Fig. 4-6 Hatch date distributions of juvenile temperate seabass. Alphabet characters indicate the cohorts. Triangles indicate cohorts used for further analysis.

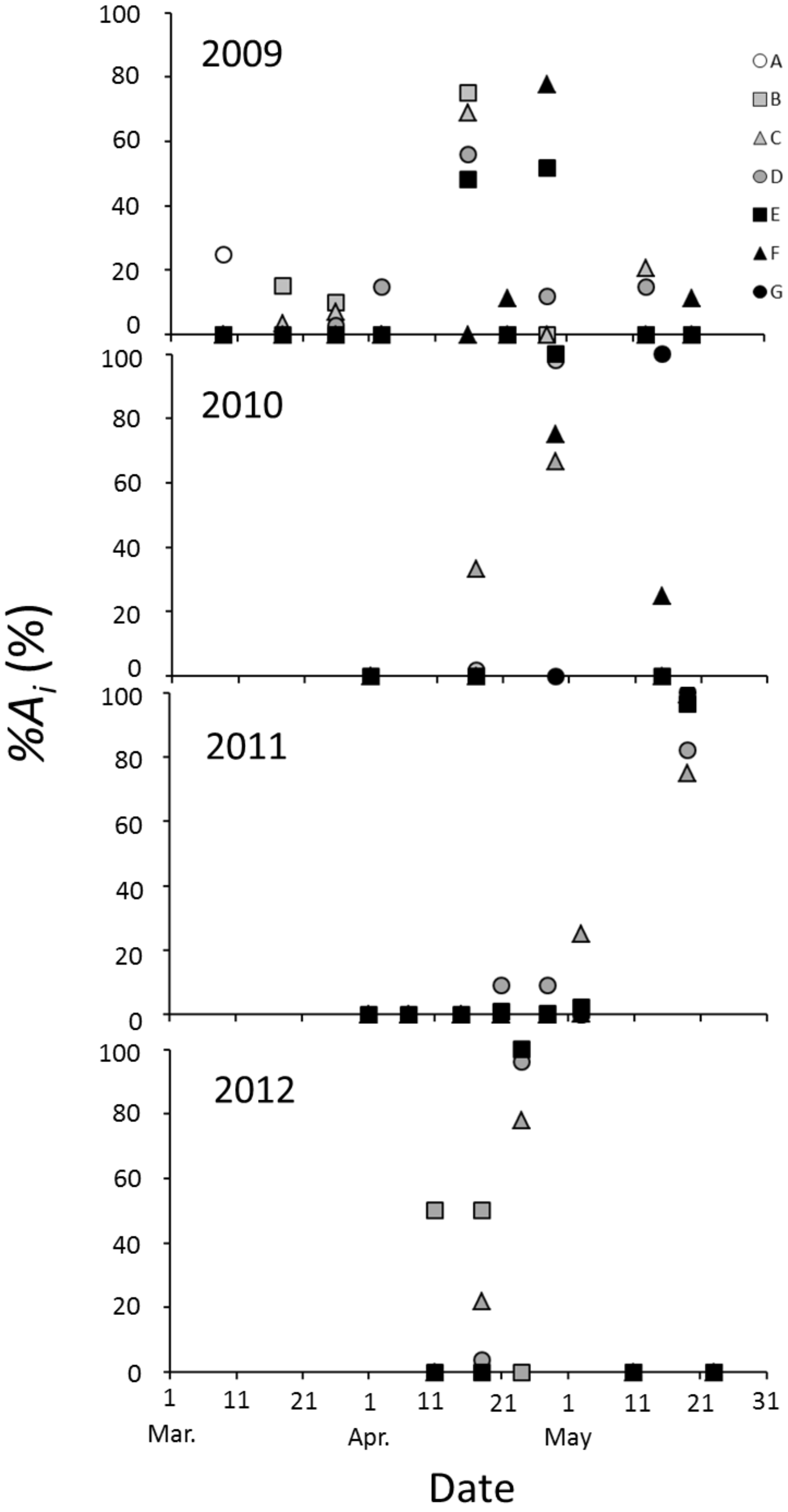

Fig. 4-7 River ascending index (%A_i) of juvenile for each cohort. Alphabets of legends coincide with name of cohorts indicated in Fig. 4-6.

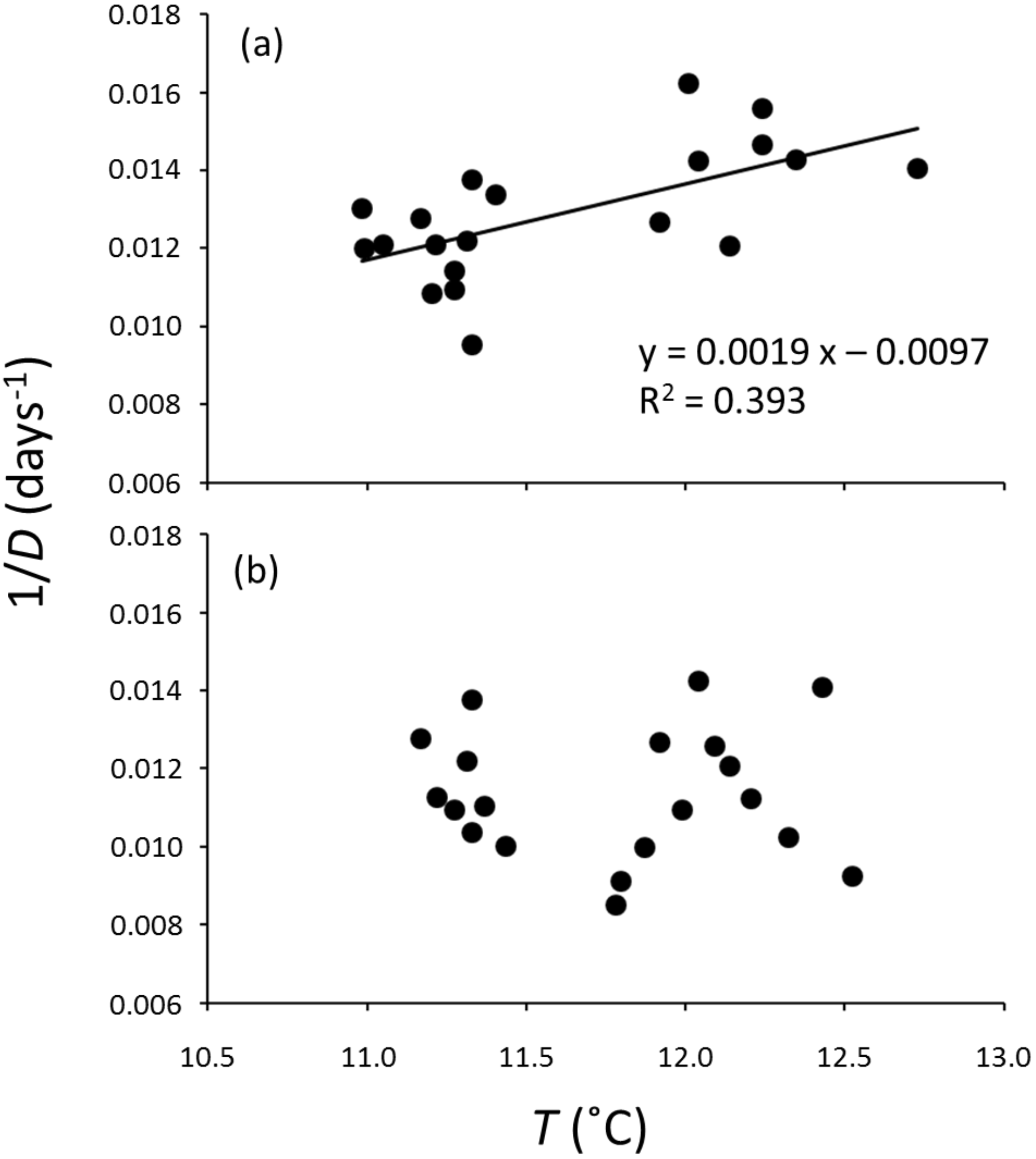

Fig. 4-8 (a) Relationship between inverses of daily ages at first river ascending days (D) of juveniles and mean experienced temperature (T : ˚C) until ascending. (b) Relationship between inverses of daily ages at main river ascending days and mean experienced temperature until main ascending days.

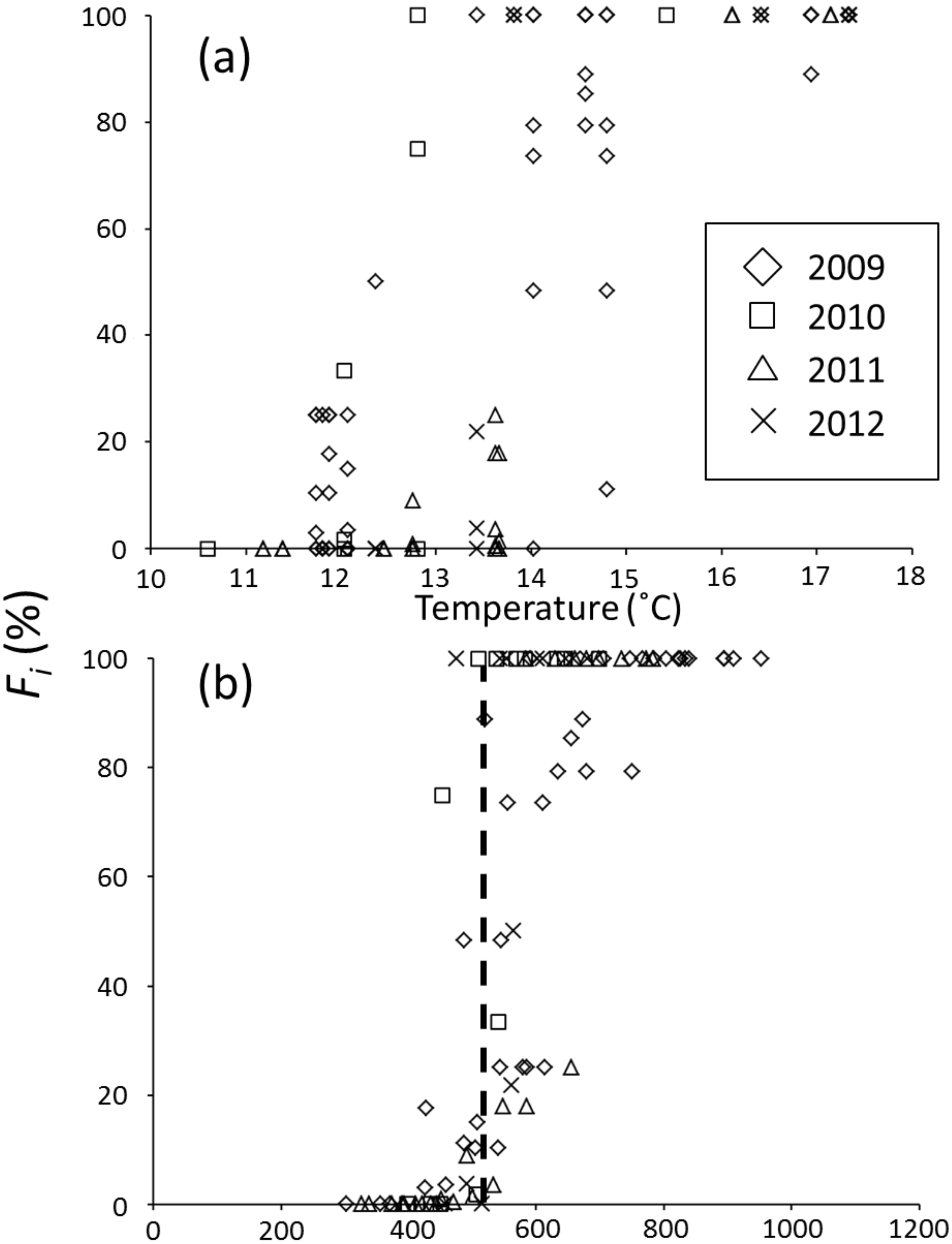

Fig. 4-9 Relationships between cumulative river ascending index (F_i) and (a) temperature and (b) effective cumulative temperature. Broken line indicates the effective cumulative temperature estimated for the first ascending days (514 ˚C-days).

Chapter 5

Feeding ecology of juvenile temperate seabass in the Yura River estuary

Introduction

Knowledge of the foraging ecology of fishes is fundamental for the management and conservation of their populations and habitats. The factors that influence the acquisition and assimilation of food can have significant consequences for the condition, growth, survival and recruitment of fishes (Nunn et al., 2011). It is considered that the intra- and/or inter-specific competition for prey items is important in juvenile stage for recruitment of fishes because the nurseries and the amount of available prey items are often limited (van der Veer et al., 2000; Shoji and Tanaka, 2008). Sometimes prey abundance limits the growth of juveniles in the nursery area (Fujii and Noguchi, 1996). Therefore, abundance of prey items has been widely used as an index of quality of nurseries (Beck et al., 2001). It is thus necessary to investigate the feeding ecology of juveniles and prey environment in the nurseries.

Not only densities but also size distributions of the preys could affect feeding conditions, and consequent growth and survival of fishes (Nunn et al., 2011). There is the optimal size of prey items for each species (Werner and Mittelbach, 1981). The optimal prey size often shifts to larger sizes with the growth of juveniles to take energy efficiently (Hart and Connellan, 1984). Therefore, the size composition of ambient prey items could affect the growth and survival of juveniles (Hart and Connellan, 1984; Pazzia et al., 2002).

Estuaries are considered as important nurseries for many fishes because of high productivity of prey organisms (North and Houde, 2003; Elliott et al., 2007). High abundance of prey items in estuaries would support the good growth and survival of juveniles (Yamashita et al., 2001). North and Houde (2003) showed that of copepods and larvae of white perch *Morone americana* and striped bass *Morone saxatilis* aggregated around estuarine turbidity maximum (ETM). They suggested the importance of retention within the ETM for these larvae to meet high density of prey items. It is also well known that many fishes utilize ETM during their larval and juvenile stages to achieve good feeding condition in the Chikugo River estuary, Japan (Islam and Tanaka, 2006). However, no ETM is formed in the Yura River estuary because of its small tidal currents (Kasai et al., 2010). This implies that the prey environment for temprate seabass is considerably different between the Chikugo River estuary and the Yura River estuary. However, few studies have been conducted for the prey environment and feeding ecology of juvenile temperate seabass in the Yura River estuary.

In this chapter, the prey distributions and the size of prey items were investigated to elucidate the prey environment and feeding ecology of juvenile temperate seabass in the Yura River estuary. The abundance and size of prey items in stomachs of juvenile temperate seabass were also surveyed to reveal their feeding ecology.

Materials and methods

Field sampling

Juvenile temperate seabass was collected at the stations of the estuarine sampling following the way indicated in Chapter 3. In addition, prey items were collected by a sledge net (net mouth 0.4 m high and 0.6 m wide, mesh size 0.33 mm). The sledge net was not used in 2008. No towing of sledge net was conducted at station R4 because of the difficulty of sampling. The sledge net was towed 19 m of along the shore line. The juveniles and prey items collected were frozen by the dry ice immediately after the collection. Collected samples were transported to the laboratory and kept in a freezer until further analyses.

Laboratory analysis

The food organisms collected by the sledge net were identified to the possible lowest taxonomic level. Mysids, which are the most important prey for juvenile temperate seabass (see Results), were identified to the species level. Density was calculated as the number of each major taxon per swept area. Body lengths of ambient mysids collected by the sledge net were measured by an ocular micrometer to the nearest 0.1 mm in April and May 2009. When more than 50 mysids were obtained, 50 individuals were randomly extracted from the sample and analyzed.

The standard length (SL: mm) and body weight (BW: mg) of juveniles were measured. The seeabass stomachs were extracted from ca. 15 juveniles of each sampling station, and dissected under a stereomicroscope. The ratio of empty gut was calculated as the percentage of the number of fish with empty stomach in relation to the total number analysed. Stomach contents were classified into major taxa and mysids were identified to the level of species. The body lengths of prey items in the stomach were measured by an ocular micrometer to the nearest 0.1 mm. The composition of each prey item was evaluated by calculating the percentage numerical composition ($\%N_i$), percentage frequency of occurrence ($\%F_i$) and percentage of wet weight composition ($\%W_i$) as follows:

$$\%N_i = \frac{N_i}{\sum N_i} \times 100,$$

where N_i is the number of prey i species,

$$\%F_i = \frac{F_i}{F} \times 100,$$

where F_i and F are the number of fish fed on prey i species and total number of fish that had stomach content on each prey, respectively, and

$$\%W_i = \frac{W_i}{\sum W_i} \times 100,$$

where W_i is the wet weight of prey item i species.

The contribution of each prey item to the diet was determined using the index of relative importance (IRI_i) as

$$IRI_i = (\%N_i + \%W_i) \times \%F_i.$$

The IRI_i was standardized to $\%IRI_i$ as

$$\%IRI_i = \frac{IRI_i}{\sum IRI_i} \times 100.$$

Stomach contents index (*SCI*) was calculated for each individual as follows:

$$SCI = \frac{SW}{BW} \times 100,$$

where *SW* is the total wet weight of stomach contents for each individual. Index of mean prey weight fed by juveniles (*IW*) was calculated for each juvenile as follows;

$$IW = \mathrm{Log}\left(\frac{SW}{SN}\right),$$

where *SN* means the total number of prey items per fish.

According to the environmental condition, ambient prey items and stomach contents of juveniles, sampling stations were classified into three groups; coastal area (S1 and R1), lower estuary (R2 and R3) and upper estuary (R4 and R5, Fig. 4-1). *SCI* and *IW* were analyzed following this classification. See “Results” for detail.

Results

Ambient prey items

Mysids distributed widely in the Yura River estuary and adjacent coastal area, although the species compositions were different among stations (Table 5-1). Mysids comprised of mainly three species, *Archaeomysis vulgaris*, *Nipponomysis toriumii* and *Orientomysis japonica* at S1 in April. Especially, *A. vulgaris* dominated in all 4 years. Only *A. vulgaris* appeared at S1 in May. *A. vulgaris* occurred also at R1 except for April and May 2009 and May 2012. Only one species, *Neomysis awatchsensis* was dominant at estuarine sites (R2, R3 and R5). The densities of total mysids were highest at R2 or R3 in most cases except for April in 2010 and 2011 (Fig. 5-1 and Table 5-1). The abundance of copepods was highest at S1 in April, while highest at R2 or R3 in May in all four years (Fig. 5-1). The size range of ambient mysids varied from 0.7 mm to 12.7 mm (Fig. 5-2). The larger size classes were occupied by *A. vulgaris* (mean±standard deviation: 7.3±2.6 mm) at S1 in April. On the other hand, *N. toriumii* comprised of small size classes (3.0±1.2 mm, Fig. 5-2). All size classes are comprised of by *N. awatchensis* from R1 to R5 both in April and May. Mean body lengths and standard deviations (SD) of *N. awatchensis* were 4.9±2.4 mm and 4.0±1.5 mm at R2 and R5 in April, respectively. The size of *A. vulgaris* was 4.8±2.6 mm at S1 in May. The mean body lengths of *N. awatchensis* were 4.8±3.0 mm, 3.9±2.0 mm, 6.8±1.7 mm, 4.8 ±2.1 mm at R1, R2, R3 and R5, respectively.

Feeding habits of juvenile temperate seabass

The main prey items were copepods and/or mysids but not consistent among stations and years in April (Fig. 5-3). On the other hand, mysids were the main prey items at all stations in May. The feeding habits changed from copepods to mysids with growth of juvenile temperate seabass (Fig. 5-4). The main foods were copepods for juvenile smaller than 25 mm SL. The importance of mysids as prey item drastically increased as juveniles grow larger than 25 mm SL. The maximum size of prey item fed by juveniles increased from ca. 15 mm to 25 mm SL and then stagnated (Fig. 5-5). The main small prey items were copepods ranged from 0.3 to 2.0 mm (Fig. 5-5). Prey items larger than 2.0 mm were mainly composed of mysids. Average sizes of prey items fed by juveniles of each size class of 2.5 mm interval also increased with juvenile size (Fig. 5-6a). The number of prey items per fish (feeding intensity) increased with juvenile size from 15 mm to 20 mm SL then decreased after 20 mm SL (Fig. 5-6b). *SCI* increased with growth of fish (Fig. 5-6c). The mysids *A. vulgaris*, *N. toriumii* and *O. japonica* were observed in the stomach of juveniles at both S1 and R1 (Tables 5-2, 5-3 and 5-4). However, $\%N_i$ and $\%F_i$ of *A. vulgaris* were considerably lower than the other species regardless of its high density in the field (Tables 5-1 and 5-2). The species of mysids which were fed by juveniles at S1 was similar to those at R1 (Tables 5-2, 5-3 and 5-4). Given these characteristics of feeding habits, ambient mysids species (Table 5-1) and environmental conditions (Chapter 3), the stations were divided into three groups; coastal area (S1 and R1), lower estuary (R2 and R3) and upper estuary (R4 and R5). Further analysis was conducted according to this classification.

SCI was lowest in the coastal area and highest in the upper estuary both in April and May every year (Fig. 5-7). In most cases, *SCI* in the upper estuary were significantly higher than that in the other areas ($P \leq 0.05$, ANOVA followed by Tukey's test). Percentages of empty stomach showed no consistent tendency (Fig. 5-7). The mean prey biomass fed by juveniles (*IW*) increased with growth of juvenile (Fig. 5-8a). As the index for the prey size selectivity of juveniles, *IW'* was defined as the residuals from the logarithmic function derived from data in Fig. 5-8a. *IW'* showed increasing tendency from coastal area to upper estuary (Fig. 5-8b). Averaged *IW'* was significantly higher in the upper estuary than the coastal area (ANOVA followed by Tukey's test, $P = 0.05$). Mean *SCI* for each area showed significant positive relationship with *IW'* ($p \leq 0.01$, Fig. 5-8c). Maximum sizes of preyed mysids were always higher in the middle and upper estuary than in the lower estuary except for juveniles smaller than 20 mm SL (Fig. 5-9). Juveniles larger than 20 mm SL fed on significantly larger mysids in the upper estuary than that in the other areas ($P \leq 0.05$, Kruskal-Wallis test followed by Sheffe's test; Fig. 5-9).

Discussion

Copepods and mysids were the major prey items for juveniles smaller and larger than 25 mm SL, respectively in the Yura River estuary (Fig. 5-4). In most cases, smaller juvenile temperate seabass (< 25 mm SL) mainly feeds on small prey items, especially copepods and/or cladocerans in estuaries and coastal area (Fujita et al., 1988; Iwamoto et al., 2010; Suzuki et al., 2008b; Hayashi and Kiyono, 1978). A part of juveniles on this stage already start to feed on larger preys such as mysids (Fujita et al., 2007; Hayashi and Kiyono, 1978). The importance of mysids as foods of larger juveniles (> 25 mm SL) has also been reported in other fields in Japan (Fujita et al., 2007; Hayashi and Kiyono, 1978; Honda et al., 1997; Yamazaki, 2002). The main prey item of temperate seabass was copepods until 40 mm SL in the Chikugo River estuary (Suzuki et al., 2008b). However, the species composition of copepods in the stomachs changes from smaller to larger ones with immigration of juveniles into the Chikugo river estuary at the size around 20 mm SL (Islam et al., 2011). Nip et al. (2003) reported that temperate seabass of 11-20 mm body length (BL) fed on copepods and cladocerans, shifting to larger ones, e.g., decapods and amphipods at ca. 20 mm BL in the Tolo harbor, Hong Kong. Therefore, the various shifts of feeding habits at the beginning of the juvenile stage in various fields could be summarized as the increase of sizes of prey items with growth of juveniles.

Ontogenetic shift of prey size is reported for juveniles of many fish species. It frequently coincides with the body development (Yube et al., 2006; Nunn et al., 2011). As Shirota (1978) and Nip et al. (2003) reported, the shit of prey size of juvenile temperate seabass could be related to metamorphosis and increase in the mouth gape of fish. Tamura et al. (2013) reported that temperate seabass completed the juvenile swimming and feeding mode at 20 mm BL and this completion of metamorphosis would be important for the shift of feeding habits. The timing that juveniles start to eat the larger prey, mysids in this study, coincided with the length of completion of metamorphosis reported in Tamura et al. (2013). The swimming ability would be necessary for juveniles to capture larger and active prey items such as mysids (Nunn et al., 2011). The increase of the maximum food sizes between 15 mm to 25 mm SL would be caused by increase of gape size of juveniles. The maximum size of foods then stagnated because the size reached the maximum size of mysids in the Yura River estuary (Figs. 5-2 and 5-5).

This study indicated juveniles increased the number of prey items consumed (mainly comprised of copepods) until ca. 22 mm SL to sustain their feeding conditions (Fig. 5-6). The decrease of number of preys after 22 mm SL coincided with the shift of main food item from copepods to mysids and increase of mean prey size (Figs. 5-5 and 5-6). This also coincided with the shift of main food from copepods to mysids. As the results, *SCI* increased with growth of juveniles (Figs. 5-6 and 5-7a). These results would mean that juveniles larger than 22 mm SL could not maintain their feeding conditions (indicated as *SCI*) by having only smaller prey items such as copepods and thus they shift their main foods to larger ones (mysids). This result suggests the importance of mysids as prey items in this field. On the other hand, the main food item is copepods and the feeding intensity of juveniles consistently increased until at least ca. 30 mm SL in the Chikugo River estuary (Islam et al., 2011). The high density of larger copepods (*Sinocalanus siinensis* with the size of ca. 2 mm; Hibino et al., 1999) in the ETM of Chikugo River estuary would enable juveniles to achieve good feeding condition by just increasing feeding intensity on copepods.

Many studies showed that the ontogenetic shift of prey size often corresponds to the shifts in habitat use, as also shown in this study (Yamada et al., 1998; Arrhenius 1996; Ghan and Sprules, 1993; Pittman and McAlpine, 2001; Tomiyama and Omori, 2008; Nunn et al., 2011). It is considered that the ontogenetic habitat shift is related to minimization of the ratio of mortality risk to growth rate (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000). The prey shift to larger size would enable juveniles to grow faster, because it decreases the amount of time spent capturing unit abundance of prey (Kislalioglu and Gibson, 1976; Hart and Connellan, 1984; Olson, 1996; Pazzia et al., 2002; Sherwood et al., 2002; Yube et al, 2006). In addition, temperate seabass would be exposed to large predators e.g., flathead *Platycephalus* sp., black sea bream *Acanthopagrus schlegelii* and Japanese flounder *Paralichthys olivaceus,* in the deeper area of the coastal area, where settled larvae resided just before the juvenile stage (Fuji, unpublished data). Therefore, habitat shift to shallower area in larval-juvenile stage would be important for minimize the ratio between mortality and growth.

The main mysid species collected at S1 by the sledge net was *A. vulgaris* (Table 5-1). However, temperate seabass at S1 rarely fed on *A. vulgaris* in spite of its high abundance in the environment (Fig. 5-1; Table 5-2). The negative selectivity on *A. vulgaris* could be explained by its diel behavior rhythm. *A. kokuboi,* which is similar species to *A. vulgaris*, is known to show a diurnal rhythm. They bury their body into sands during the daytime (Takahashi and Kawaguchi, 1997). The temperate seabass juveniles feed on their prey items in the morning and there would be a gap with appearance time of *A. vulgaris* in the water column (Hayashi and Kiyono, 1978; Hibino et al., 2006). Yamamoto et al. (2004) reported juvenile Japanese flounder fed rarely *Iiella oshimai,* which buried their body into sand in daytime, despite of its abundance in ambient environment in the Hiuchinada, Seto Island Sea. On the other hand, *O. japonica, N. toriumii* and *N. awatchensis* are epifaunal (Akiyama S, personal communication; Toda et al., 1982). This difference in the life style of mysids would lead to the juvenile prey selectivity. The total densities of mysids except for *A. vulgaris* were always highest at R2 or R3 (Fig. 5-1). The size compositions of mysids except for *A. vulgaris* were also significantly larger at R2 and R5 than S1 in April (Kruskal-Wallis test followed by Scheffe's test, $P \leq 0.05$). Few mysids except for *A. vulgaris* distributed at S1 in May. These results would mean that prey environments is better in the estuary than the coastal area.

More abundant and larger prey items in the estuary would lead to better feeding condition in the estuary. There was a positive relationship between *SCI* and mean prey sizes (Fig. 5-8c). This indicates that juveniles improve their feeding condition by increasing the size of prey items. The maximum sizes of preyed mysids in the coastal area were generally smaller than those in the other areas (Fig. 5-9), reflecting the smaller ambient mysids in the coastal area (Fig. 5-2). Mean size of prey items fed by juveniles were also smaller in the coastal area (Fig. 5-8b). Therefore *SCI* in the coastal area were always lower than the other areas (Fig. 5-7). Similar pattern of prey size, abundance and feeding condition of juvenile temperate seabas was observed also in the Chikugo River estuary (Islam et al., 2006). It would be disadvantage for fish when it could not shift to larger prey items with their growth (Sherwood et al., 2002; Keeley and Grant, 2001). For example, lake trout *Salvelinus namaycush* ordinary becomes piscivorous from zooplanktonivorous with their growth. However in the lake with no small fish as prey items lake trout cannot shift their feeding habits to larger preys (Pazzia et al., 2002). They reported that trout juveniles in the lake with no prey fish grew worse than those in the lake with fish preys. Similar patterns of prey environments, feeding habits and growth were also reported for many salmonid fishes (Keeley and Grant, 2001) and juvenile seabass *L. latus* (Yube et al., 2006).

Generally speaking, density-dependent survival mechanisms are dominant after settlement stage of larvae (van der Veer et al., 2000; Shoji and Tanaka, 2008). Larvae and juveniles of coastal fishes distribute in restricted areas after planktonic stage and thus they start to share the limited prey items (van der Veer et al., 2000). Higher abundance of prey items can support more juveniles. The density of main prey items was generally higher in the lower estuary than the other areas in the Yura River estuary (Fig. 5-1). The abundances of juveniles were also higher in middle estuary than the other areas (Chapter 3). The *SCI* in the middle estuary were as much as or higher than *SCI* in the coastal area (Fig. 5-7). The ratios of empty stomach were moderate in the lower estuary (Fig. 5-7). These results indicate that high density of prey items would support high density of juveniles in the middle estuary. This means that lower estuarine habitat has larger carrying capacity than the coastal area. This also implies that the estuary could produce more juveniles per unit area than the coastal area.

It was clear from Figs. 5-8 and 5-9 that juveniles in the upper estuary fed on larger prey items than the other areas. This led to high *SCI* in the upper estuary (Figs. 5-7). This cannot be explained by the abundance and size of prey items in the fields because prey density was higher in the middle estuary and size of mysids showed no difference between the two areas (Figs 5-1 and 5-2). Therefore, the size selectivity of juveniles on prey items could differ between the upper estuary and other areas. One possible factor to affect the prey selectivity of juveniles is metabolism. Kerr and Secor (2009) reported that different contingents in one population of white perch (migrants to brackish area and residents in freshwater area) showed different energetic tactics that significantly influence the scope for growth. They found that migrant contingent showed higher consumption and growth rates than residents. Morinville and Rasmussen (2003) also showed similar pattern of contingents and metabolism for brook trout *Salvelinus fontinalis*. This kind of difference in metabolism may affect the energetic bottlenecks for growth of juveniles and ontogenetic niche shift of prey sizes (Sherwood et al., 2002). At least, the lower and upper estuary can supply larger prey items for migrant juveniles to shift to larger preys and achieve higher *SCI* than the coastal area.

Table 5-1 Density of food organisms collected by a sledge net (ind. m^{-2})

Year	Prey organims		April					May				
			Station					Station				
			S1	R1	R2	R3	R5	S1	R1	R2	R3	R5
2009	Copepoda total		1763.2	2.7	1.3	3.9	6.1	13.5	13.0	88.4	0.0	1.5
		Calanoida	1763.2	2.2	1.0	3.1	4.0	13.5	12.5	0.0	3.1	0.0
		Cyclopoida	0.0	0.5	0.2	0.8	1.2	0.0	0.5	0.0	0.8	0.0
		Harpacticoida	0.0	0.0	0.1	0.0	0.9	0.0	0.0	0.0	0.0	0.0
	Mysidacea total		25.1	0.0	45.6	4.8	2.1	26.8	4.0	114.2	7.3	5.1
		Archeomysis vulgaris	8.9	0.0	0.0	0.0	0.0	26.8	0.0	0.0	0.0	0.0
		Nipponomysis toriumii	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Orientomysis japonica	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Neomysis awatschensis	0.0	0.0	45.6	4.8	2.1	0.0	4.0	114.2	7.3	5.1
		Paracanthomysis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Amphipoda		11.0	0.6	0.0	0.0	0.3	289.5	0.2	6.0	0.1	0.1
	Chironomid larvae		0.0	0.1	0.1	1.1	1.1	0.0	0.0	0.0	1.3	0.7
	Tanaidacea		0.0	0.0	0.1	0.0	0.1	0.0	0.4	0.2	0.2	0.1
	Insect larvae		0.0	0.0	0.0	0.4	0.8	0.0	0.0	0.0	0.1	0.1
	Cladocera		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cumacea		0.5	0.0	0.0	0.1	0.0	0.0	0.0	0.2	0.0	0.0
	Corophiidea		0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Isopoda		0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
	Decapoda		0.4	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0

Table 5-1 Continued

Year	Prey organims		April					May				
			Station					Station				
			S1	R1	R2	R3	R5	S1	R1	R2	R3	R5
2010	Copepoda total		18.1	0.3	0.4	5.6	0.4	0.4	0.3	3.7	30.6	2.9
		Calanoida	4.5	0.2	0.4	0.0	0.0	0.1	0.2	0.4	30.3	0.1
		Cyclopoida	12.6	0.0	0.0	4.7	0.4	0.1	0.0	0.0	0.3	2.8
		Harpacticoida	1.0	0.1	0.0	0.9	0.0	0.2	0.1	0.0	0.0	0.0
	Mysidacea total		81.1	6.7	11.7	33.0	8.2	1.6	11.5	67.8	301.1	35.0
		Archeomysis vulgaris	65.2	0.1	0.0	0.0	0.0	1.6	0.1	0.0	0.0	0.0
		Nipponomysis toriumii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Orientomysis japonica	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Neomysis awatschensis	0.1	6.7	11.7	33.0	8.2	0.0	11.3	67.8	301.1	35.0
		Paracanthomysis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Amphipoda		11.0	6.7	0.1	0.0	0.3	84.8	0.8	1.0	8.5	0.7
	Chironomid larvae		0.0	0.1	0.0	11.1	14.9	0.0	0.0	0.0	4.2	1.7
	Tanaidacea		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1
	Insect larvae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4
	Cladocera		0.0	0.0	0.0	1.8	0.9	0.0	0.0	0.0	0.0	1.8
	Cumacea		0.0	0.0	0.0	0.0	0.0	1.5	0.2	0.0	0.0	0.0
	Corophiidea		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Isopoda		0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
	Decapoda		0.1	0.0	0.0	0.0	0.0	0.1	3.6	1.5	0.0	0.1

Table 5-1 Continued

Year	Prey organims		April					May				
			Station					Station				
			S1	R1	R2	R3	R5	S1	R1	R2	R3	R5
2011	Copepoda total		48.0	6.4	12.3	11.1	5.6	1.8	1.5	4.7	59.6	0.3
		Calanoida	0.0	0.0	10.8	11.1	0.6	0.9	1.5	3.5	48.0	0.3
		Cyclopoida	48.0	6.4	1.5	0.0	4.4	0.9	0.0	1.2	9.4	0.0
		Harpacticoida	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	2.3	0.0
	Mysidacea total		363.7	1.8	44.2	243.9	4.1	66.4	22.8	4.1	62.0	0.9
		Archeomysis vulgaris	342.7	1.8	0.0	0.0	0.0	66.4	0.9	0.0	0.0	0.0
		Nipponomysis toriumii	21.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Orientomysis japonica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Neomysis awatschensis	0.0	0.0	44.2	243.9	4.1	0.0	21.9	4.1	62.0	0.9
		Paracanthomysis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Amphipoda		65.5	4.1	1.8	0.6	0.3	7.6	0.6	0.3	0.0	0.0
	Chironomid larvae		0.0	0.0	0.0	0.6	1.2	0.0	0.0	0.0	3.5	0.6
	Tanaidacea		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Insect larvae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
	Cladocera		0.0	0.0	0.3	0.0	0.6	0.0	0.0	0.0	2.3	0.0
	Cumacea		10.5	0.0	0.0	0.0	0.0	8.5	0.0	0.3	0.0	0.0
	Corophiidea		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Isopoda		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Decapoda		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5-1 Continued

Year	Prey organims		April					May				
			Station					Station				
			S1	R1	R2	R3	R5	S1	R1	R2	R3	R5
2012	Copepoda total		5.0	0.1	29.8	7.6	6.4	3.9	1.6	41.2	76.0	0.6
		Calanoida	4.7	0.0	26.9	4.1	0.0	2.3	1.3	41.2	73.5	0.0
		Cyclopoida	0.3	0.1	0.0	3.5	5.8	1.6	0.1	0.0	2.5	0.6
		Harpacticoida	0.0	0.0	2.9	0.0	0.6	0.0	0.1	0.0	0.0	0.0
	Mysidacea total		6.1	5.0	69.0	64.9	0.0	4.1	3.8	53.5	73.2	1.8
		Archeomysis vulgaris	4.7	0.1	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0
		Nipponomysis toriumii	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Orientomysis japonica	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Neomysis awatschensis	0.0	4.8	69.0	64.9	0.0	0.0	3.8	53.5	73.2	1.8
		Paracanthomysis spp.	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
	Amphipoda		9.4	0.1	1.2	0.0	1.8	13.2	0.4	6.7	1.6	0.1
	Chironomid larvae		0.0	0.0	0.0	8.2	43.9	0.0	0.0	0.6	3.4	2.6
	Tanaidacea		0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.6	0.1	0.0
	Insect larvae		0.0	0.0	0.0	0.6	0.6	0.0	0.0	0.0	0.0	2.2
	Cladocera		0.0	0.0	0.0	0.0	1.2	0.0	0.1	0.0	0.0	1.5
	Cumacea		0.3	0.0	0.0	0.0	0.0	6.7	0.0	0.3	0.0	0.0
	Corophiidea		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Isopoda		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Decapoda		0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0

Table 5-2 %N_i of stomach contents of temperater seabass

Year	Month	Station	Mysids					Copepoda				Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaeta	Fish	Others
			Neomysis awatchensis	*Archaeomysis vulgaris*	*Nipponomysis toriumii*	*Orientomysis japonicus*	Total	Calanoida	Cycloopoida	Harpacticoida	Total						Chironomid larvae	Other insects			
2008	April	S1	0.0	0.0	2.6	40.3	42.9	0.0	0.0	13.0	13.0	0.0	0.0	0.0	6.5	0.0	0.0	0.0	0.0	0.0	37.7
		R1	0.0	0.0	0.0	0.0	0.0	28.1	6.3	53.1	87.5	9.4	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0
		R2	3.0	0.0	0.0	0.0	3.0	1.3	66.6	4.0	71.9	21.9	0.0	0.0	0.2	0.0	2.6	0.0	0.2	0.0	0.0
		R3	29.0	0.0	0.0	0.0	29.0	2.7	31.3	1.3	35.3	13.4	0.0	0.0	0.0	0.0	21.9	0.4	0.0	0.0	0.0
		R4	21.1	0.0	0.0	0.0	21.1	0.0	15.8	0.0	15.8	30.4	0.0	0.0	0.0	0.0	32.7	0.0	0.0	0.0	0.0
		R5																			
	May	S1	0.0	0.0	0.0	94.3	94.3	0.0	0.9	0.0	0.9	0.4	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.4
		R1																			
		R2	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	23.2	0.0	0.0	0.0	23.2	0.0	66.2	0.0	66.2	0.0	0.0	2.1	0.0	0.0	7.0	1.4	0.0	0.0	0.0
		R4	63.9	0.0	0.0	0.0	63.9	0.0	23.0	0.0	23.0	0.0	0.0	1.6	0.0	0.0	6.6	1.6	0.0	0.0	3.3
		R5	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2009	April	S1	0.0	0.0	0.0	0.2	0.9	98.1	0.0	0.2	98.3	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.4
		R1																			
		R2	12.0	0.0	0.0	0.0	12.0	24.1	3.6	59.0	86.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
		R3	24.4	0.0	0.0	0.0	24.4	18.0	48.8	1.9	68.7	6.4	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
		R4	4.1	0.0	0.0	0.0	4.1	59.1	36.4	0.0	95.5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
		R5																			
	May	S1	0.0	25.0	0.0	0.0	50.0	0.0	25.0	25.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1																			
		R2	11.1	0.0	0.0	0.0	11.1	78.0	0.0	4.2	82.1	4.9	0.0	0.7	0.5	0.0	0.5	0.0	0.0	0.0	0.0
		R3	4.1	0.0	0.0	0.0	4.1	86.1	0.6	0.2	86.9	7.1	0.0	0.1	0.1	0.0	1.4	0.1	0.0	0.2	0.0
		R4	7.9	0.0	0.0	0.0	7.9	91.9	0.0	0.0	91.9	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
		R5	95.5	0.0	0.0	0.0	95.5	0.0	1.5	0.0	1.5	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	1.5	0.0

Table 5-2 Continued

Year	Month	Station	Mysids					Copepoda				Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaeta	Fish	Others
			Neomysis awatchensis	*Archaeomysis vulgaris*	*Nipponomysis toriumii*	*Orientomysis japonicus*	Total	Calanoida	Cycloopoida	Harpacticoida	Total						Chironomid larvae	Other insects			
2010	April	S1	0.0	1.3	11.8	0.0	13.2	19.7	0.0	65.8	85.5	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
		R1	0.0	1.1	0.0	0.0	1.1	45.0	0.3	51.5	96.8	0.0	1.9	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
		R2	0.4	0.0	0.0	0.0	0.4	75.9	0.0	23.7	99.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	0.2	0.0	0.0	0.0	0.2	88.3	0.5	10.6	99.5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
		R4																			
		R5																			
	May	S1																			
		R1	0.0	9.5	4.8	9.5	23.8	0.0	0.0	71.4	71.4	0.0	0.0	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0
		R2	75.0	0.0	0.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	16.4	0.0	0.0	0.0	16.4	14.6	5.5	0.4	20.4	62.8	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
		R4	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R5	66.7	0.0	0.0	0.0	66.7	10.6	21.2	0.0	31.8	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
2011	May	S1	0.0	0.0	33.3	41.7	75.0	8.3	0.0	0.0	8.3	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0
		R1	0.2	0.2	0.3	0.0	0.7	84.8	4.8	9.5	99.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1
		R2	32.0	0.0	0.0	0.0	32.0	46.0	2.0	20.0	68.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	2.1	0.0	0.0	0.0	2.1	89.9	0.6	7.2	97.7	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
		R4	43.5	0.0	0.0	0.0	43.5	2.2	13.0	0.0	15.2	0.0	0.0	0.0	0.0	17.4	19.6	4.3	0.0	0.0	0.0
		R5	81.1	0.0	0.0	0.0	32.6	0.0	5.4	0.0	5.4	0.0	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	0.0
2012	April	S1	0.0	0.0	5.3	84.2	89.5	10.5	0.0	0.0	10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1																			0.0
		R2	2.7	0.0	0.0	0.0	2.7	37.2	0.3	59.4	97.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	1.5	0.0	0.0	0.0	1.5	67.1	0.0	31.5	98.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R4	0.6	0.0	0.0	0.0	0.6	75.3	1.8	21.7	98.8	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
		R5	20.0	0.0	0.0	0.0	20.0	0.0	20.0	10.0	30.0	0.0	0.0	0.0	0.0	0.0	20.0	30.0	0.0	0.0	0.0
	May	S1																			0.0
		R1	57.6	12.1	0.0	9.1	78.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.2	0.0	0.0	0.0	0.0	0.0	0.0
		R2	98.8	0.0	0.0	0.0	98.8	1.2	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3																			0.0
		R4	4.8	0.0	0.0	0.0	4.8	78.6	2.4	11.9	92.9	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0
		R5	9.0	0.0	0.0	0.0	9.0	60.3	10.3	0.0	70.5	0.0	0.0	0.0	0.0	0.0	10.3	3.8	0.0	6.4	0.0

Table 5-3 %F_i of stomach contents of temperate seabass

Year	Month	Station	Mysids					Copepoda				Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaeta	Fish	Others
			Neomysis awatchensis	*Archaeomysis vulgaris*	*Nipponomysis toriumii*	*Orientomysis japonicus*	Total	Calanoida	Cycloopoida	Harpacticoida	Total						Chironomid larvae	Other insects			
2008	April	S1	0.0	0.0	7.7	53.8	53.8	0.0	0.0	23.1	23.1	0.0	0.0	0.0	15.4	0.0	0.0	0.0	0.0	0.0	42.3
		R1	0.0	0.0	0.0	0.0	0.0	41.7	16.7	58.3	83.3	16.7	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.0	0.0
		R2	4.0	0.0	0.0	0.0	4.0	20.0	80.0	28.0	92.0	76.0	0.0	0.0	4.0	0.0	28.0	4.0	0.0	0.0	4.0
		R3	73.1	0.0	0.0	0.0	76.9	23.1	69.2	7.7	76.9	38.5	0.0	0.0	0.0	0.0	61.5	3.8	0.0	0.0	0.0
		R4	56.3	0.0	0.0	0.0	56.3	0.0	50.0	0.0	50.0	37.5	0.0	0.0	0.0	0.0	62.5	0.0	0.0	0.0	0.0
		R5																			
	May	S1	0.0	0.0	0.0	92.6	92.6	0.0	7.4	0.0	7.4	3.7	0.0	0.0	18.5	0.0	0.0	0.0	0.0	0.0	3.7
		R1																			
		R2	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	50.0	0.0	0.0	0.0	50.0	0.0	60.0	0.0	60.0	0.0	0.0	6.7	0.0	0.0	23.3	6.7	0.0	0.0	0.0
		R4	60.9	0.0	0.0	0.0	60.9	0.0	26.1	0.0	26.1	0.0	0.0	4.3	0.0	0.0	13.0	4.3	0.0	0.0	8.7
		R5	75.0	0.0	0.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2009	April	S1	0.0	0.0	0.0	5.9	29.4	64.7	0.0	5.9	70.6	0.0	0.0	0.0	5.9	0.0	0.0	0.0	5.9	0.0	11.8
		R1																			
		R2	20.0	0.0	0.0	0.0	20.0	40.0	5.0	25.0	65.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0
		R3	69.2	0.0	0.0	0.0	69.2	48.7	25.6	15.4	61.5	12.8	0.0	0.0	0.0	0.0	5.1	0.0	0.0	0.0	0.0
		R4	33.3	0.0	0.0	0.0	33.3	83.3	83.3	0.0	83.3	0.0	0.0	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0
		R5																			
	May	S1	0.0	50.0	0.0	0.0	100.0	0.0	50.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1																			
		R2	70.0	0.0	0.0	0.0	70.0	90.0	0.0	15.0	90.0	25.0	0.0	20.0	15.0	0.0	15.0	0.0	0.0	0.0	0.0
		R3	78.9	0.0	0.0	0.0	78.9	89.5	10.5	5.3	89.5	36.8	0.0	5.3	5.3	0.0	15.8	5.3	0.0	10.5	0.0
		R4	85.0	0.0	0.0	0.0	85.0	55.0	0.0	0.0	55.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0
		R5	100.0	0.0	0.0	0.0	100.0	0.0	7.1	0.0	7.1	0.0	0.0	0.0	0.0	0.0	7.1	0.0	0.0	7.1	0.0

Table 5-3 Continued

Year	Month	Station	Mysids					Copepoda				Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaeta	Fish	Others
			Neomysis awatchensis	*Archaeomysis vulgaris*	*Nipponomysis toriumii*	*Orientomysis japonicus*	Total	Calanoida	Cycloopoida	Harpacticoida	Total						Chironomid larvae	Other insects			
2010	April	S1	0.0	7.7	46.2	0.0	46.2	23.1	0.0	69.2	69.2	0.0	0.0	0.0	7.7	0.0	0.0	0.0	0.0	0.0	0.0
		R1	0.0	20.0	0.0	0.0	20.0	80.0	6.7	86.7	93.3	0.0	6.7	0.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0
		R2	11.1	0.0	0.0	0.0	11.1	88.9	0.0	66.7	88.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	6.7	0.0	0.0	0.0	6.7	100.0	6.7	46.7	100.0	0.0	0.0	0.0	0.0	0.0	13.3	0.0	0.0	0.0	0.0
		R4																			
		R5																			
	May	S1																			
		R1	0.0	50.0	50.0	50.0	50.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
		R2	16.7	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	53.3	0.0	0.0	0.0	53.3	26.7	26.7	6.7	46.7	26.7	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0
		R4	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R5	86.7	0.0	0.0	0.0	86.7	13.3	33.3	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0
2011	May	S1	0.0	0.0	60.0	40.0	60.0	20.0	0.0	0.0	20.0	0.0	0.0	0.0	40.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1	13.3	6.7	6.7	0.0	20.0	93.3	46.7	86.7	93.3	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0	6.7
		R2	53.3	0.0	0.0	0.0	53.3	46.7	6.7	13.3	46.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	26.7	0.0	0.0	0.0	26.7	73.3	20.0	46.7	73.3	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0
		R4	66.7	0.0	0.0	0.0	66.7	13.3	26.7	0.0	33.3	0.0	0.0	0.0	0.0	6.7	40.0	26.7	0.0	0.0	0.0
		R5	60.0	0.0	0.0	0.0	60.0	0.0	20.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	6.7	6.7	0.0	0.0	0.0
2012	April	S1	0.0	0.0	9.1	36.4	45.5	18.2	0.0	0.0	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1																			
		R2	26.7	0.0	0.0	0.0	26.7	53.3	6.7	73.3	80.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	18.8	0.0	0.0	0.0	18.8	68.8	0.0	62.5	75.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R4	10.0	0.0	0.0	0.0	10.0	90.0	50.0	80.0	90.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0
		R5	50.0	0.0	0.0	0.0	50.0	0.0	25.0	25.0	25.0	0.0	0.0	0.0	0.0	0.0	25.0	50.0	0.0	0.0	0.0
	May	S1																			
		R1	84.6	15.4	0.0	15.4	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.5	0.0	0.0	0.0	0.0	0.0	0.0
		R2	100.0	0.0	0.0	0.0	100.0	7.1	0.0	0.0	7.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3																			
		R4	66.7	0.0	0.0	0.0	66.7	66.7	33.3	66.7	66.7	0.0	0.0	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0
		R5	36.4	0.0	0.0	0.0	36.4	18.2	9.1	0.0	18.2	0.0	0.0	0.0	0.0	0.0	36.4	18.2	0.0	36.4	0.0

Table 5-4 %W_i of stomach contents of temperate seabass

Year	Month	Station	Mysids	Copepods	Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaetes	Fish	Others
										Chironomid larvae	Other insects			
2008	April	S1	91.1	2.5	0.0	0.0	0.0	6.5	0.0	0.0	0.0	0.0	0.0	0.0
		R1	0.0	79.2	1.9	0.0	0.0	0.0	0.0	18.9	0.0	0.0	0.0	0.0
		R2	0.0	69.8	10.0	0.0	0.0	0.2	0.0	17.3	2.7	0.0	0.0	0.0
		R3	87.9	4.3	0.1	0.0	0.0	0.0	0.0	7.0	0.6	0.0	0.0	0.0
		R4	81.3	0.7	1.7	0.0	0.0	0.0	0.0	16.3	0.0	0.0	0.0	0.0
		R5												
	May	S1	95.7	0.1	0.2	0.0	0.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0
		R1												
		R2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	87.3	2.1	0.0	0.0	1.7	0.0	0.0	4.6	4.3	0.0	0.0	0.0
		R4	97.1	0.5	0.0	0.0	0.5	0.0	0.0	0.3	0.9	0.0	0.0	0.7
		R5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2009	April	S1	1.5	98.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2
		R1												
		R2	91.8	7.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
		R3	93.4	6.3	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
		R4	68.5	31.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
		R5												
	May	S1	98.2	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1												
		R2	87.5	11.7	0.1	0.0	0.3	0.2	0.0	0.1	0.0	0.0	0.0	0.0
		R3	58.1	33.1	0.6	0.0	0.0	0.1	0.0	0.7	0.1	0.0	7.4	0.0
		R4	89.6	10.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R5	99.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0

Table 5-4 Continued

Year	Month	Station	Mysids	Copepods	Cladocera	Decapoda	Tanaidacea	Amphipoda	Isopoda	Insects		Polychaetes	Fish	Others
										Chironomid larvae	Other insects			
2010	April	S1	47.3	46.9	0.0	0.0	0.0	5.8	0.0	0.0	0.0	0.0	0.0	0.0
		R1	18.2	79.9	0.0	1.6	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
		R2	0.2	99.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	0.4	98.9	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
		R4												
		R5												
	May	S1												
		R1	89.0	3.4	0.0	0.0	0.0	7.6	0.0	0.0	0.0	0.0	0.0	0.0
		R2	89.5	0.0	0.0	0.0	10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	90.2	6.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R4	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R5	99.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
2011	May	S1	96.1	0.0	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0
		R1	51.5	48.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
		R2	98.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	86.6	13.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
		R4	94.4	0.3	0.0	0.0	0.0	0.0	1.6	1.0	2.7	0.0	0.0	0.0
		R5	99.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
2012	April	S1	99.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R1												
		R2	40.3	59.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3	68.4	31.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R4	15.0	83.9	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0
		R5	76.3	7.9	0.0	0.0	0.0	0.0	0.0	2.3	13.5	0.0	0.0	0.0
	May	S1												
		R1	95.4	0.0	0.0	0.0	0.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0
		R2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		R3												
		R4	60.4	39.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
		R5	69.4	5.3	0.0	0.0	0.0	0.0	0.0	1.8	1.5	0.0	22.0	0.0

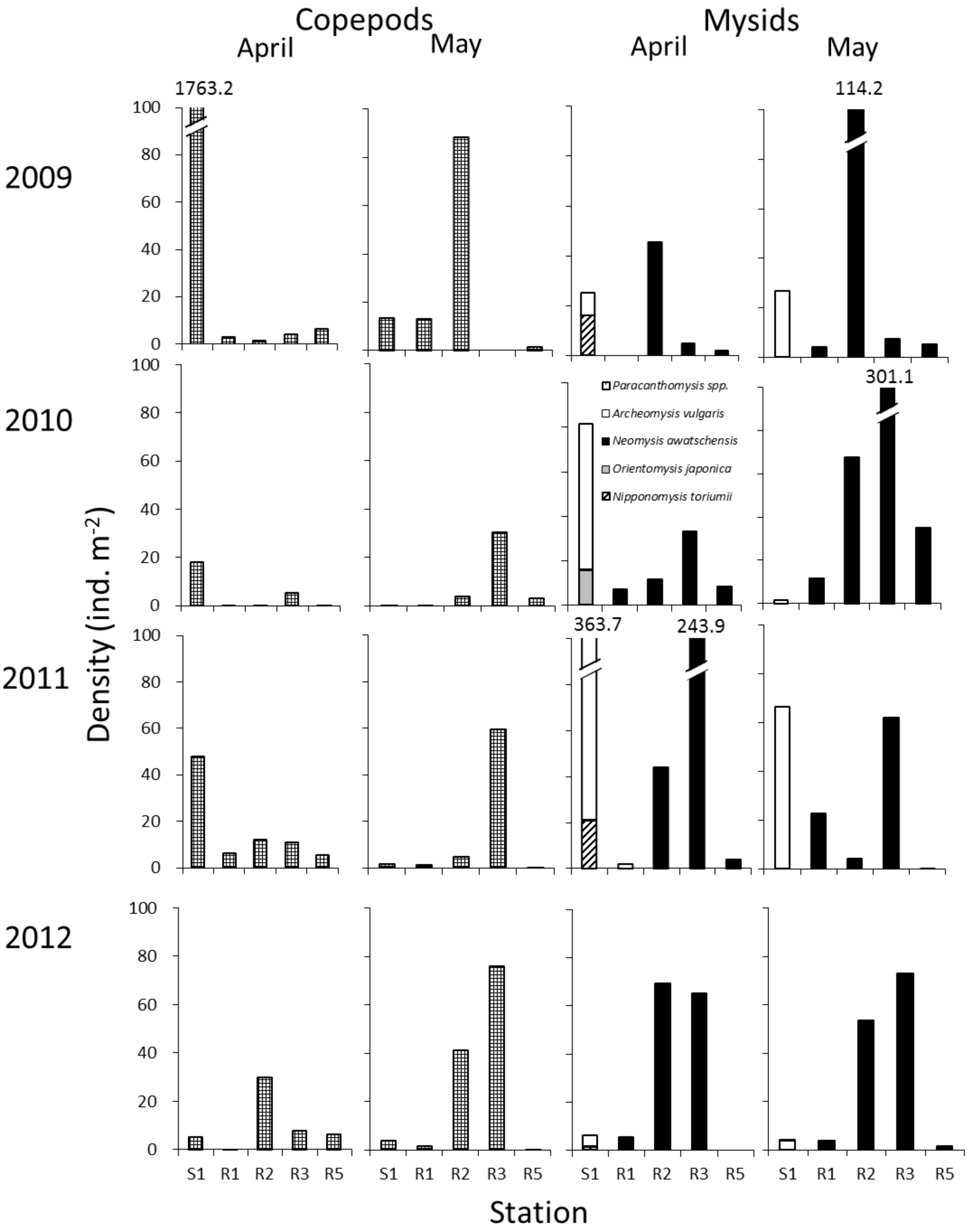

Fig. 5-1 Densities of copepods and mysids collected by the sledge net.

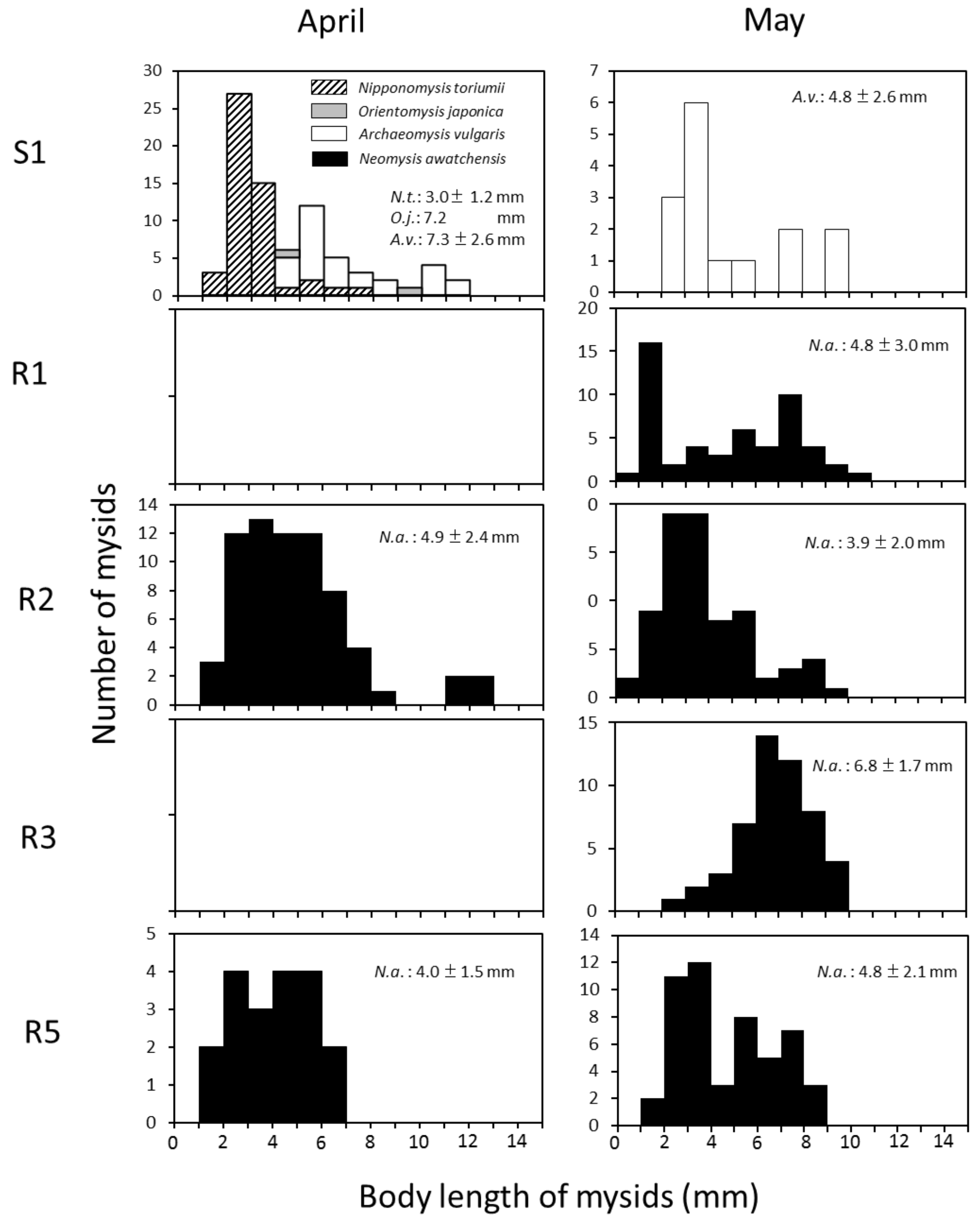

Fig. 5-2 Body lengths of mysids collected by a sledge net on 21 April and 12 May 2009. Mean values ± standard deviations are indicated in each figure.

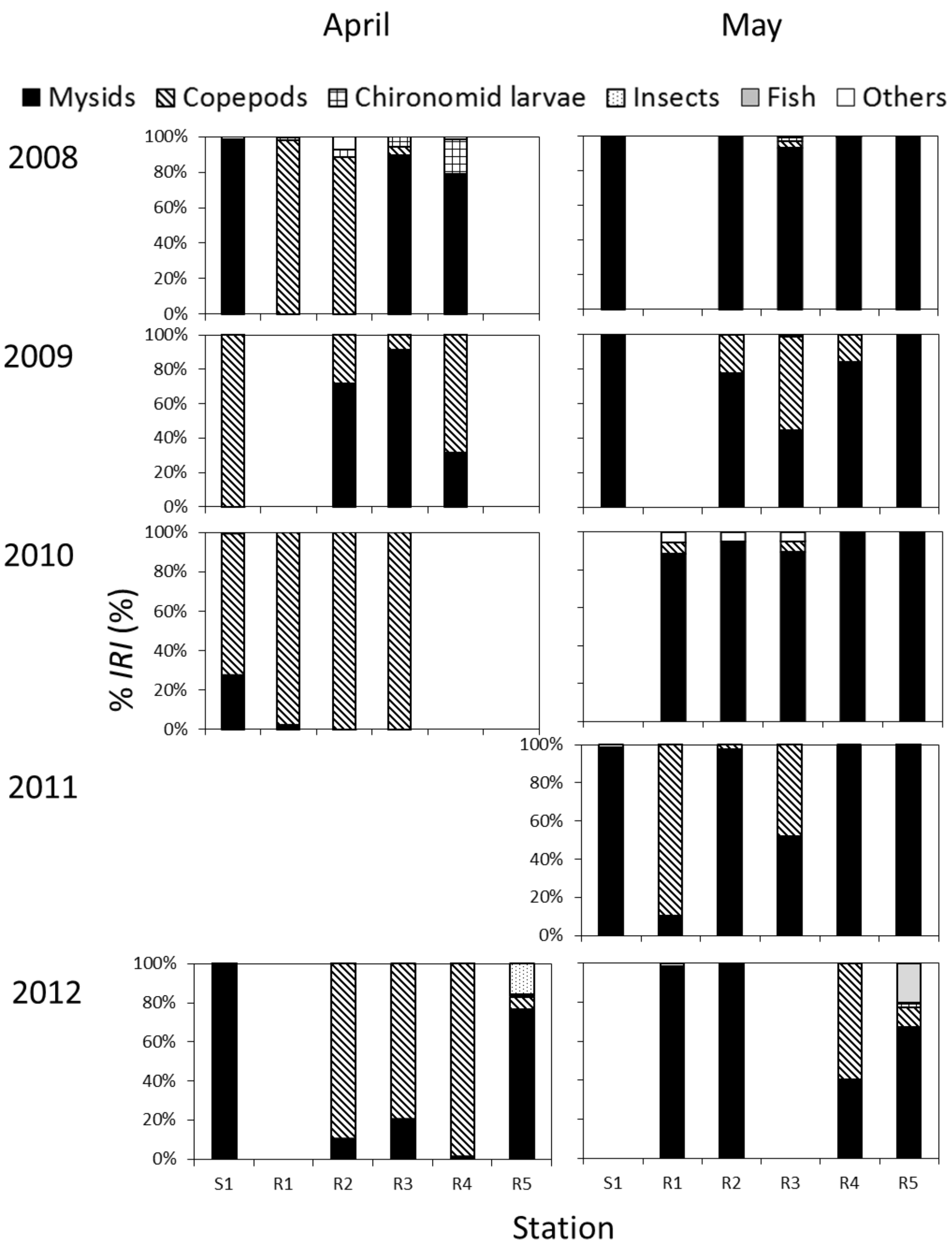

Fig. 5-3 Percentage of index of relative importance (%*IRI*) of juvenile temperate seabass.

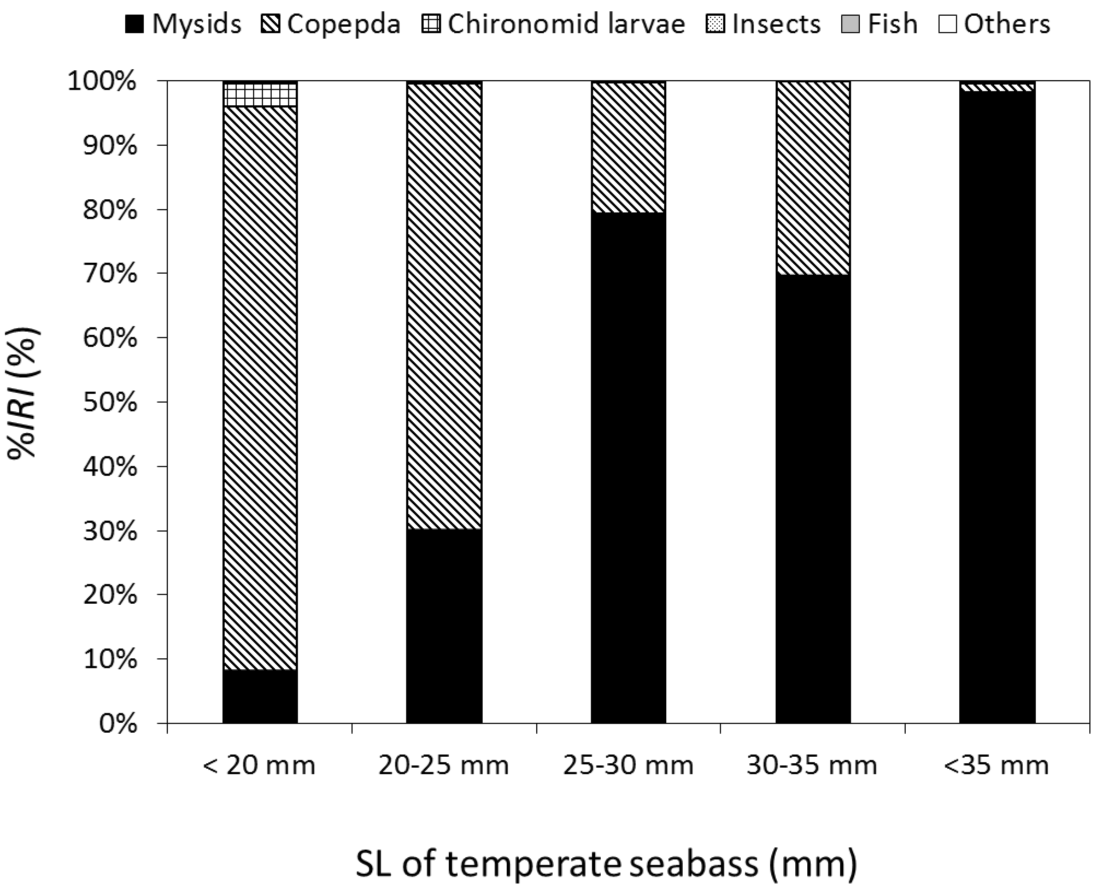

Fig. 5-4 Percentage of index of relative importance (%*IRI*) by the standard length (SL) of juvenile temperate seabass.

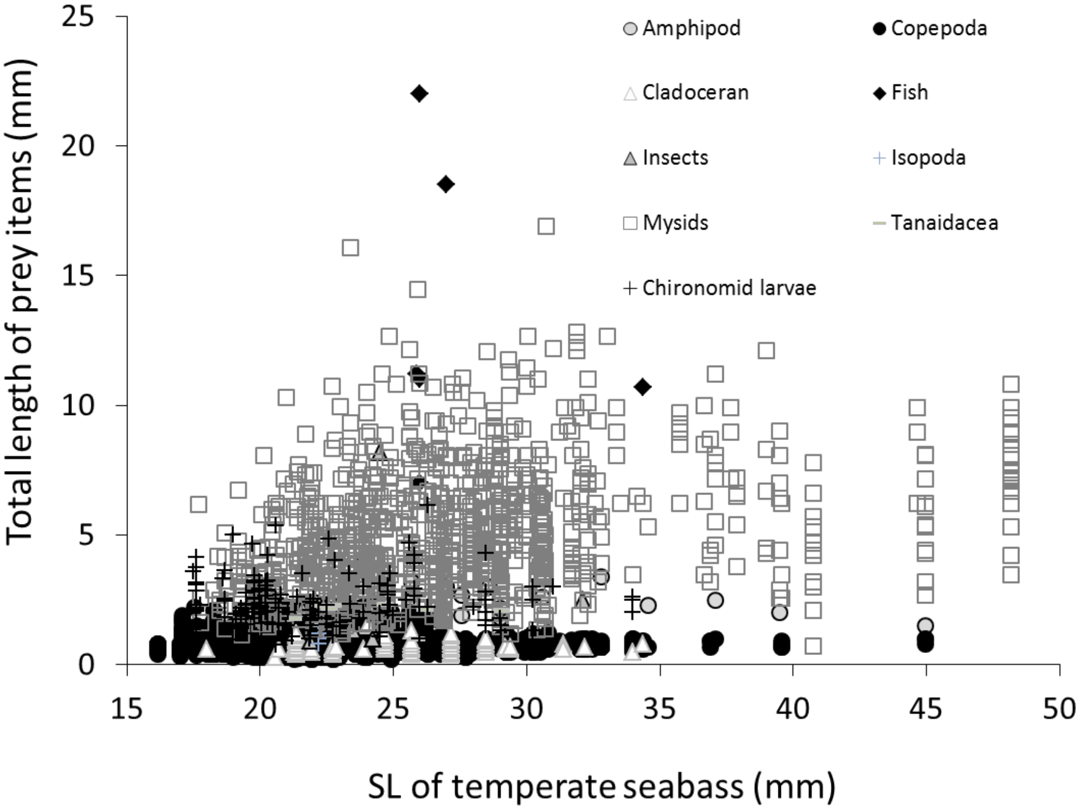

Fig. 5-5 The relationship between predator size (standard length, SL) and prey size.

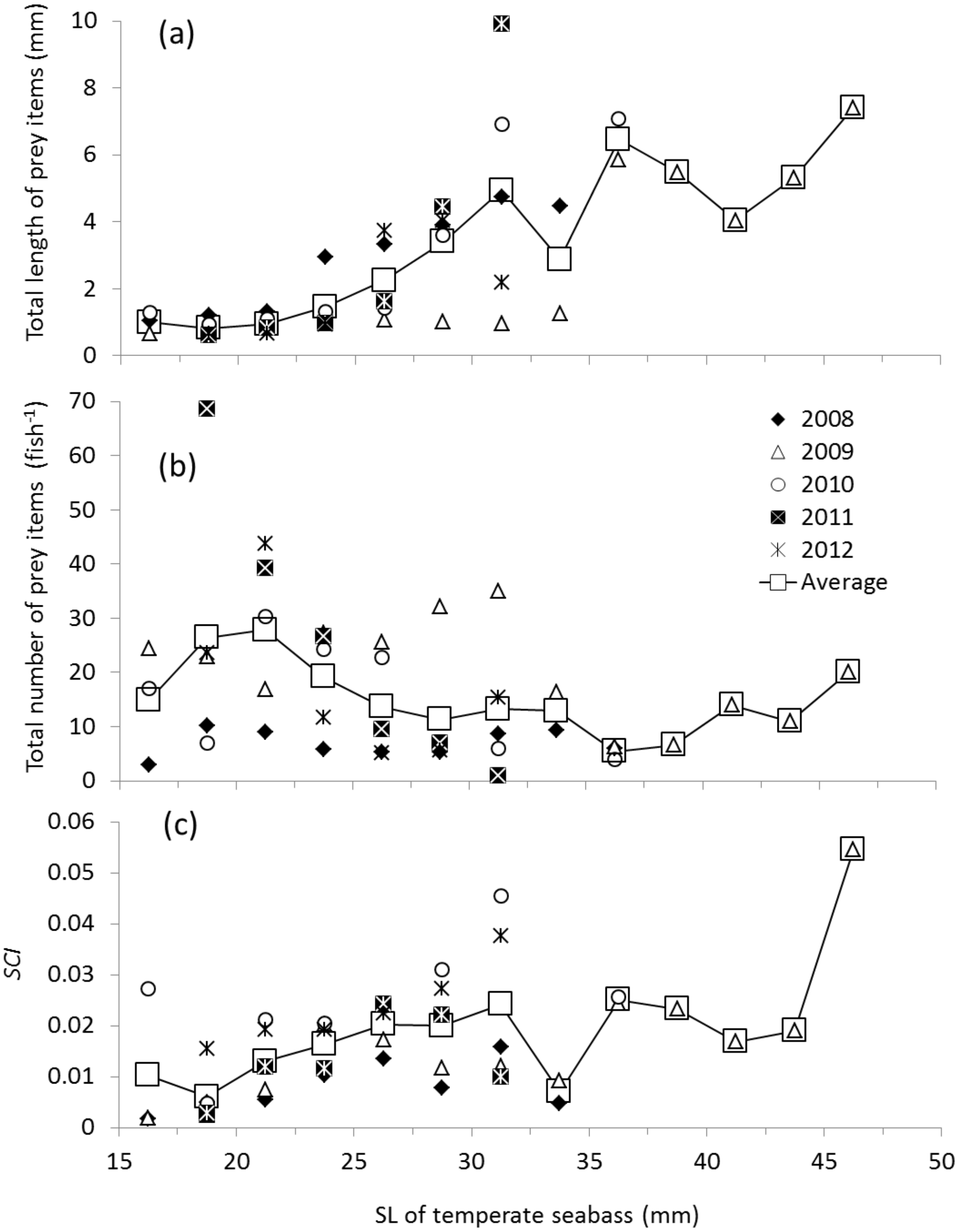

Fig. 5-6 The relationships between standard length (SL) of temperate seabass and (a) mean prey size (b) mean total number of prey items and (c) mean *SCI* for each year.

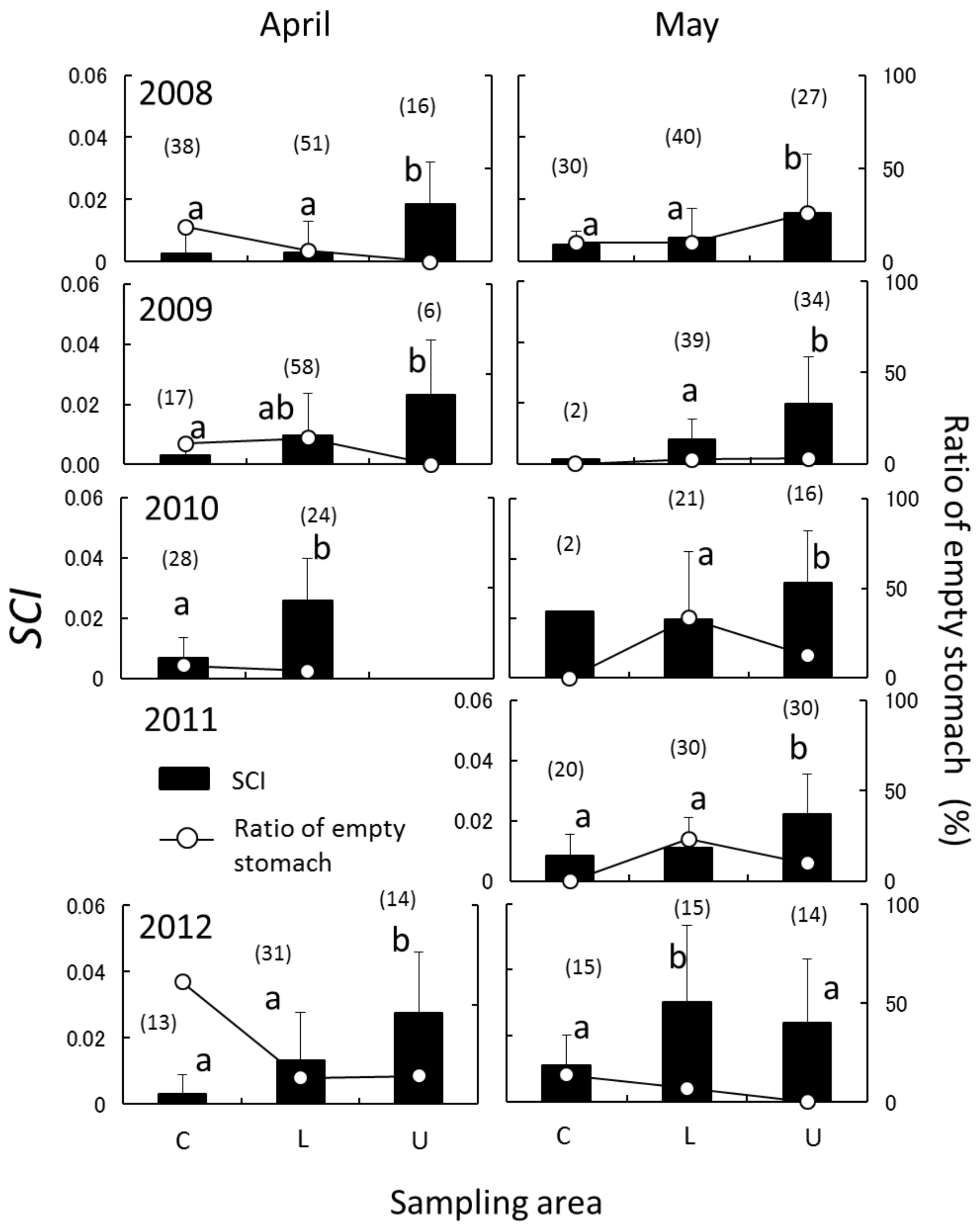

Fig. 5-7 Mean stomach content index (*SCI*) and ratios of empty stomach of temperate seabss in coastal area (C), lower estuary (L) and upper estuary (U). Different alphabets indicate the significant difference ($P \leq 0.05$). Numbers in parentheses are the number of juveniles analyzed.

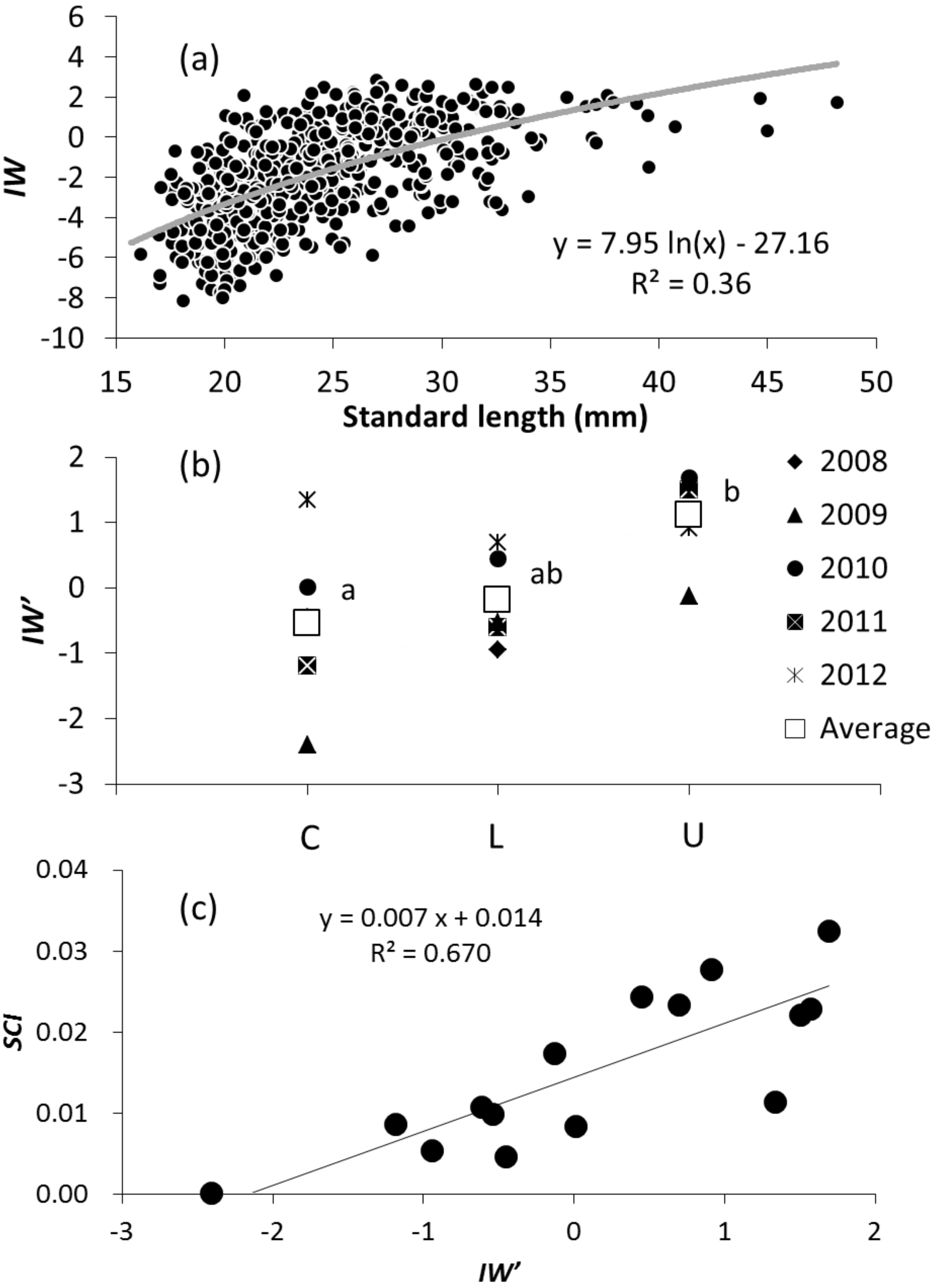

Fig. 5-8 (a) The relationship between standard length and *IW* (b) mean *IW'* in the coastal area (C), lower estuary (L) and upper estuary (U) and (c) relationship between *IW'* and *SCI.* Different alphabets in (b) indicate the significant difference (ANOVA followed by Tukey tests, $P \leq 0.05$).

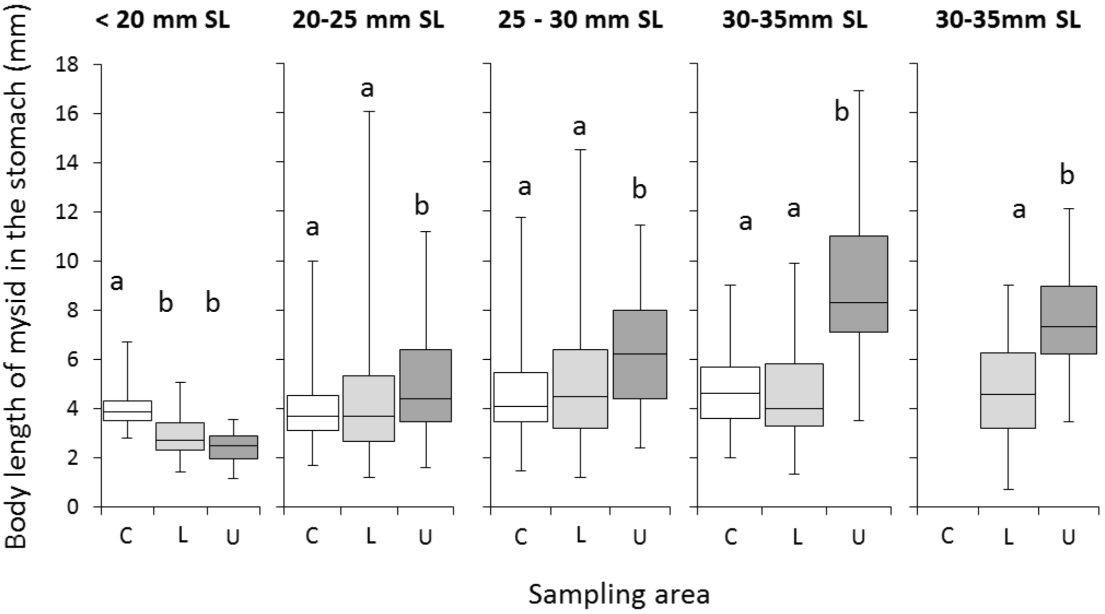

Fig. 5-9 Body length of mysids fed by temperate seabass of each size class in the coastal area (C), lower estuary (L) and upper estuary (U). Different alphabets indicate the significant difference (Kruskal-Wallis tests followed by Scheffe's tests, $P \leq 0.05$).

Chapter 6

Migration ecology of juvenile temperate seabass: a carbon stable isotope approach

Introduction

A large number of early juvenile temperate seabass distributed in the freshwater zone as well as in the coastal zone (Chapter 3). It was also observed that mysids were the most important food items in both zones (Chapter 5). However, details of the pattern of migration between these two zones, e.g., duration of residence in the estuary, remain unknown. The duration of the juvenile residence in the estuary is important information for further analysis about growth, survival and their contribution to adult population.

Stable isotope ratios have often been used to examine the feeding habits of animals, because predators reflect the ratios of their prey items (DeNiro and Epstein, 1978; Minagawa and Wada, 1984). From the relationship between prey items and predators, in recent years, stable isotopes have also been applied successfully in studies tracking fish migration (Hobson, 1999). Organisms moving between isotopically distinct food webs can retain information of a previous feeding location for periods that depend on the elemental half-life (the time taken for the stable isotope ratios of animal tissues to change by half) in their tissues (Hobson, 1999; Suzuki et al., 2008a). Since stable isotope ratios gradually approach that of the new prey items, it is possible to determine the residence time in the new feeding location using the half-life. In aquatic ecosystems the respective organic sources along salinity gradients tend to have distinctive values of the stable carbon isotope ratio ($\delta^{13}C$) (Fry and Sherr, 1984; Suzuki et al., 2008b). $\delta^{13}C$ is therefore useful to characterize fish migration between high salinity and low salinity areas.

The objectives of this study are to determine details of the migration pattern of *L. japonicus* juveniles between the coastal area and the Yura River by using $\delta^{13}C$. First, $\delta^{13}C$ of juveniles and mysids, which are the most important prey item for juveniles (Chapter 5), were examined along the salinity gradient. The ranges on which $\delta^{13}C$ of juveniles should converge during their long residence in the river and the surf zone were calculated from $\delta^{13}C$ of mysids in the river and surf zone, respectively. Finally the seasonal migration dynamics of juveniles were determined comparing the observed $\delta^{13}C$ of juveniles and expected $\delta^{13}C$ ranges.

Materials and methods

Samplings were conducted at the stations of estuarine samplings following the methods in Chapter 3 from April to July 2008 (Fig. 3-1). Gill nets were also used to collect larger juveniles in July. The standard length (SL; mm) and wet body weight (BW; mg) of samples were measured.

The trophic enrichment value and the half-life of tissues are necessary to use stable isotope ratios for characterizing the migration of fish. Since the values for *L. japonicus* juveniles are already known (Suzuki et al., 2005), $\delta^{13}C$ can be used as a tracer of migration of the *L. japonicus* juveniles between the Yura River and the adjacent surf zone, if $\delta^{13}C$ of the prey items have distinct values between these two zones. For stable isotope analysis, lateral white muscle anterior to the dorsal fin was excised from 10 randomly selected juveniles from each sampling station on every sampling day. Mysids are the most important dietary item for juvenile *L. japonicus* in the Yura River estuary (Chapter 5). Therefore, undigested mysids were picked out from the stomachs of juveniles for the stable isotope analysis of prey items. Fish tissues and mysids were dried at 60 °C for 24 h. No lipid extraction for fish samples and acidification for mysids samples were conducted because the previously estimated trophic enrichment and half-life were detected by experiments without these treatments (Suzuki et al., 2005). Some smaller mysids were pooled to obtain sufficient material for isotope analysis. Larger mysids and all juveniles were analyzed individually. Carbon stable isotope ratios were determined using a stable isotope ratio mass spectrometer (Delta S, Finnigan MAT) in continuous-flow mode, equipped with an elemental analyzer (EA1108, Fisons Instrument). Stable isotope ratios were described as parts per thousand (‰) deviations from the international standard using:

$$\delta^{13}C = 1000(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}},$$

where R is $^{13}C^{12}C^{-1}$. Pee Dee Belemnite was used as the standard and DL-alanine as a secondary standard to verify the accuracy of the stable isotope analyzes. Standard deviations for the secondary standard were < 0.15 ‰.

R2, R3, R4 and R5 were assigned to the estuary (ES) and R1 and S1 to the coastal area (CA) by characteristics of $\delta^{13}C$ of prey items (see Results). The ranges on which $\delta^{13}C$ of juveniles should converge during their long residence in respective zones (hereafter, expected range) were estimated to discuss the migration of fish. Small juveniles (≤ 25 mm SL) were considered separately from larger juveniles (> 25 mm SL), because they would have recently migrated from the more offshore areas to the coastal area (Islam et al., 2010) and reflect the feeding habits in their pelagic larval stage in the offshore areas. In light of the larval signature of $\delta^{13}C$, the expected range of CA for smaller fish was estimated based on $\delta^{13}C$ of juveniles at S1 as follows: the regression formula was calculated between SL and $\delta^{13}C$ of juveniles of ≤ 25 mm SL at S1, then the range was defined as that value ± 0.5 ‰. For the larger juveniles (> 25 mm SL), the expected ranges were estimated by adding trophic enrichment (2.0 ± 0.5 ‰; Suzuki et al., 2005) to the mean $\delta^{13}C$ values of mysids in ES and CA. $\delta^{13}C$ of mysids in CA did not fluctuate through the sampling period, thus the expected range in CA was calculated from the mean $\delta^{13}C$ of mysids in all months. On the contrary, $\delta^{13}C$ of mysids in ES became more depleted during the sampling period. Therefore the expected ranges in ES were separately calculated from $\delta^{13}C$ of mysids in each month. To discuss the migration between CA and ES, fish were assigned to the marine (MA) signal group, the upper estuary (UE) signal group or the transient (TS) signal group, using their individual $\delta^{13}C$ values and the expected ranges in both areas. Juveniles were categorized into three groups (Fig. 6-1); fish with a $\delta^{13}C$ equal to or higher than the expected range of CA were identified as the MA signal group. Fish with a $\delta^{13}C$ equal to or lower than the expected range of ES were assigned to the UE signal group. Individuals with intermediate $\delta^{13}C$ values between these expected ranges were assigned to the TS signal group. Following migration, the $\delta^{13}C$ value of fish tissues should converge on a value reflecting the new diet after a long residence time (> 20 days, Suzuki et al., 2005). The expected changes in $\delta^{13}C$ with their migration are schematically shown in Fig. 5-1. If juveniles migrate from CA to ES, $\delta^{13}C$ of juveniles are expected to shift from the MA signal to the UE signal through the TS signal during their residence in ES. On the other hand, if juveniles migrate seaward from ES, their signal will change from the UE or the TS signal to the MA signal. Individuals that remain in CA would show consistent $\delta^{13}C$ with their growth.

To estimate a composition of each migration group (i.e. MA, TS and UE signal groups) for all individuals sampled in ES on each sampling day, migration group composition at all stations in ES was summed up in proportion to numbers of individuals sampled at respective stations. In the same way, standard length composition was estimated on each sampling day. The number and size of individuals in ES with MA signal ("river ascending individuals", see Chapter 7) were analyzed to examine the detailed aspects of the upstream migration.

Results

$\delta^{13}C$ of mysids can be divided into two groups; CA and ES (Fig. 6-2). $\delta^{13}C$ of mysids in ES became depleted from ca. -21 ‰ in April to ca. -25 ‰ in July. On the contrary, $\delta^{13}C$ of mysids in CA remained enriched at ca. -20 ‰ throughout the sampling period (Fig. 6-2).

Figure 6-3 shows the relationship between SL and δ^{13}C of all sizes of juveniles. δ^{13}C of juveniles in CA were enriched and there was no significant relation between SL and δ^{13}C (ANCOVA, $R^2 = 0.005$, $n = 133$, $P > 0.05$), while those in ES became increasingly depleted with their growth and showed significantly negative correlation (ANCOVA, slope = -0.080; $R^2 = 0.41$, $n = 312$, $P < 0.05$). δ^{13}C values of individuals smaller and larger than 25 mm SL are given in Figs. 6-4 and 6-5, respectively. Small juveniles (≤ 25 mm SL) in CA indicated a positive relationship between SL and δ^{13}C (Fig. 6-4). Most small juveniles in ES also showed a similar pattern. A distinct expected range of ES could not be set for small fish (≤ 25 mm SL) because the expected range in CA for smaller juveniles was depleted and overlapped with that of ES in April and May (Fig. 6-4). Therefore, all individuals with lower δ^{13}C than the expected range of CA were assigned to the UE signal group (Fig. 6-4). For large juveniles (> 25 mm SL), the expected ranges were separately calculated from δ^{13}C of mysids in ES and CA (Fig. 6-5). δ^{13}C of most juveniles in ES changed in response to the changes of expected ranges in ES. However, all juveniles larger than 70 mm SL in ES had enriched δ^{13}C and were outside the expected range of ES (Fig. 6-5).

Individuals were assigned to the MA, UE or TS signal group based on their δ^{13}C values (Fig. 6-6). Most juveniles in ES had the MA signal, although some juveniles had the UE signal in April and early May. There were some juveniles with the MA signal in ES from mid-May to early June, but juveniles mainly had the TS or the UE signal. After mid-June, all juveniles in ES were assigned to the TS or the UE group. In contrast, all juveniles in CA were assigned to the MA group in April and May (Fig. 6-6). In June, a small fraction of juveniles at R1 had the TS signal. More than half of juveniles in the CA indicated the TS signal in July.

Size of river ascending individuals ranged from 17 to 50 mm SL with a peak of 19 to 22 mm SL (Fig. 6-7a). Most of individuals ascended the river with size ranged within 15-30 mm SL. This size was steady until 8 May, then increased with time after mid-May (Fig. 6-7b). Most juveniles started to migrate upstream with the size of ≤ 25 mm SL until 8 May, while the size range shifted to > 25 mm SL after 16 May. The abundance of river ascending juveniles gradually decreased with time from April to mid-May, and juveniles rarely migrated upstream of the river in June (Fig. 6-7c).

Discussion

$\delta^{13}C$ of prey items

The different trends in δ^{13}C of mysids between the two areas (Fig. 6-2) agreed with the trend of δ^{13}C of particulate organic matter (POM) in the same field and year with this study (Antonio et al., 2010); δ^{13}C of POM in the river became depleted from ca. -24 ‰ in spring to ca.-29 ‰ in summer, while δ^{13}C of POM in CA showed a constant value (ca. -22 ‰) from spring to summer. The mysid in ES was *Neomysis awatschensis* (Chapter 5), which in the eutrophic lake Kasumigaura, Japan has been shown to consume POM (reported as *Neomysis intermedia*, Toda and Wada, 1990). Therefore, the change in δ^{13}C of mysids in ES would come from the change in their foods.

Prey items sampled from fish stomach were used in this study to characterize food webs in CA and ES and to predict muscle signals. Since δ^{13}C of mysids from the stomach and the environment in R2 showed no difference (Fuji, unpublished data), it is accepted to use the stomach contents to assess the base line for migration. In addition, the species of mysids in the stomachs of juveniles were clearly different between ES and CA (Chapter 5). This indicated the representativeness of stomach contents as the baseline of migration in each zones. Additional benefit from using stomach contents was that the right prey items were analyzed with certainty (Guelinckx et al., 2006). These facts suggest that using stomach contents is the useful tool for analyzing the fish migration in the Yura River estuary.

Migration of juvenile in the Yura River estuary revealed by $\delta^{13}C$

A positive relationship between SL and $\delta^{13}C$ in small juveniles (≤ 25 mm SL; Fig. 6-4) would not be caused by the migration between CA and ES, but by the onshore migration from the pelagic zone in their larval stage. France (1995) reported a higher $\delta^{13}C$ signature in the benthic food web than that in the pelagic food web. $\delta^{13}C$ of red drum *Sciaenops ocellatus* shifted to a higher value after migration from the pelagic to the benthic habitat (Herzka et al., 2002).

The $\delta^{13}C$ values of mysids were considerably different between ES and CA, permitting us to use $\delta^{13}C$ as a tracer to examine the migration dynamics of juvenile *L. japonicus* (Fig. 6-2). In fact, the $\delta^{13}C$ trends in juveniles were significantly different between ES and CA (Fig. 6-3) and corresponded with the changes in $\delta^{13}C$ ranges expected by that of mysids in each zone (Fig. 6-5).

This study can successfully divide the individuals into three groups; the MA, TS and UE signal groups. Given the expected shift of signals during migration between CA and ES (Fig. 6-1), fish in ES with the MA signal indicate upstream migration. On the contrary, individuals in CA with the TS or the UE signal indicate seaward migration. Fish with the MA signal in ES were observed from April to mid-June, suggesting that juveniles continued to ascend the river until mid-June (Fig. 6-7). Individuals with the MA signal appear at R5 in May, suggesting that some juveniles ascended the river until 15 km upstream within several days. The abundance of river ascending juveniles drastically decreased from April to early May and was low after mid-May (Fig. 6-7c). In July, approximately half of the juveniles in ES had the TS signal; juveniles smaller than 70 mm SL with the TS signal indicated a $\delta^{13}C$ value close to the expected range of ES (Fig. 6-5), indicating that they had inhabited ES for more than 20 days (half-life, Suzuki et al., 2005). These juveniles would have ascended the river in June. All individuals larger than 70 mm SL in ES also had the TS signal (Fig. 6-5). Juveniles in the upper Chikugo River estuary began to expand their own home ranges to the lower estuary, and their $\delta^{13}C$ signal became enriched toward the convergence range of the high salinity area (Suzuki et al., 2008b). Larger juveniles in the Yura River estuary may also expand their home range and change their food.

In CA, all juveniles had the MA signal in April and May (Fig. 6-6), indicating that there were many juveniles that remained in CA in April and May. In June and July, $\delta^{13}C$ values of some fish in CA were considerably depleted in comparison with the expected range of CA and close to that of ES (Fig. 6-5), indicating that they had resided in ES for a certain period and recently moved to CA. It is therefore considered that some juveniles in ES migrated seaward from June. Together with larger juveniles with the TS signal in ES in July, this migration would be a part of the expansion of their home range from ES to CA. It would be a good approach to analyze $\delta^{13}C$ of the liver in addition to the muscle tissue to confirm this hypothesis, because the liver shows a more rapid rate of change in relation to changes in food associated with the migration (Suzuki et al., 2005; Suzuki et al., 2008b).

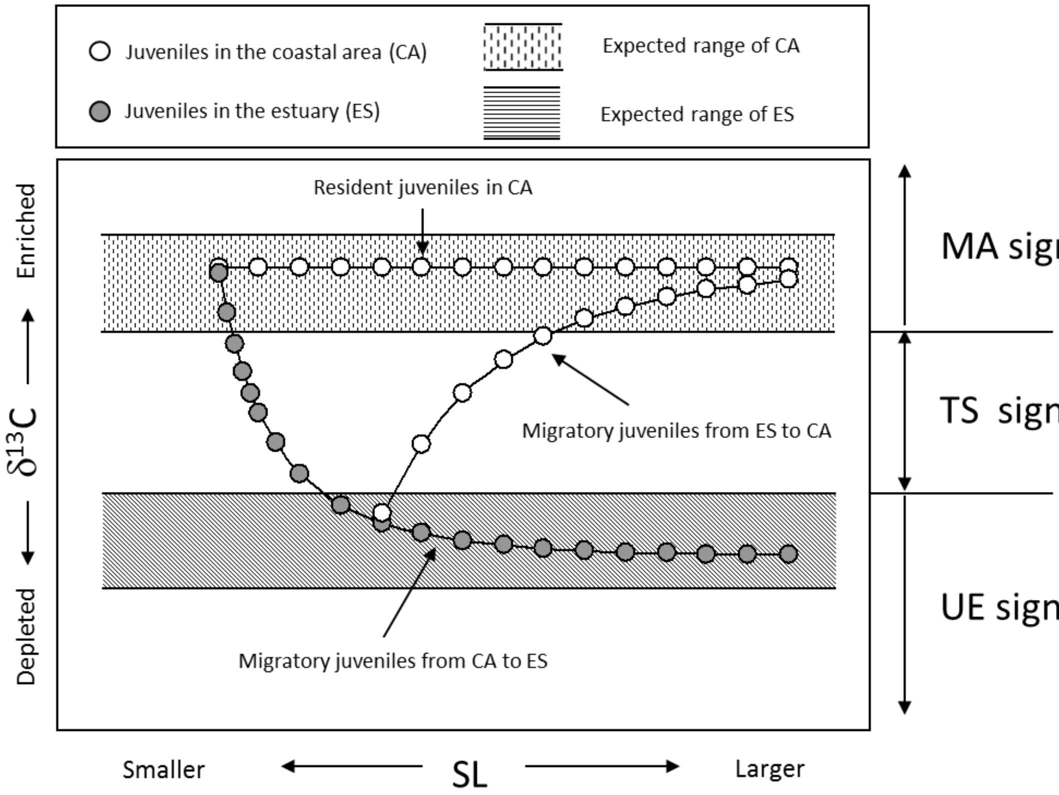

Fig. 6-1 Schematic representation of δ^{13}C change exhibited by *Lateolabrax japonicus* juveniles caught in the coastal area (CA) and the estuary (ES) in each migration pattern: reside in CA, migrate to ES, and migrate seaward from CA. Dotted area and hatched area show the expected range (see "Materials and methods") of CA and ES, respectively.

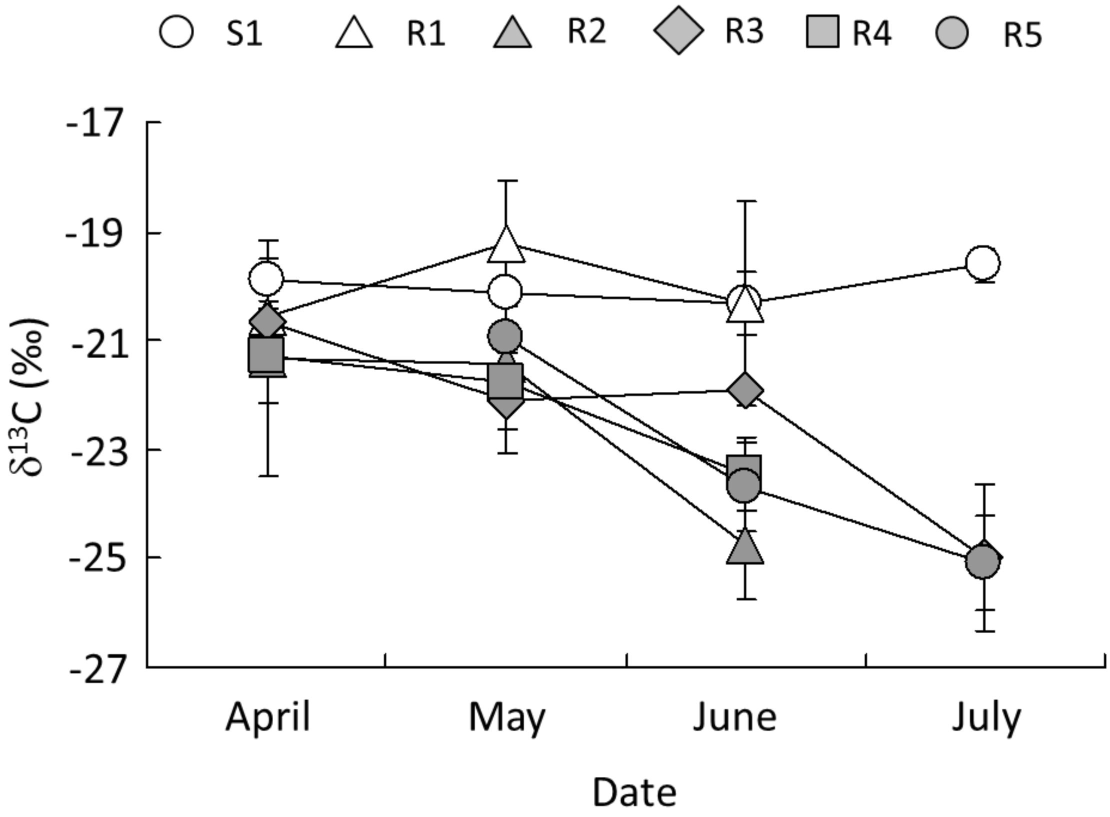

Fig. 6-2 Monthly changes in δ^{13}C of mysids in 2008. Error bars indicate standard deviations. Open and shaded symbols represent the coastal area (CA) and the estuary (ES), respectively.

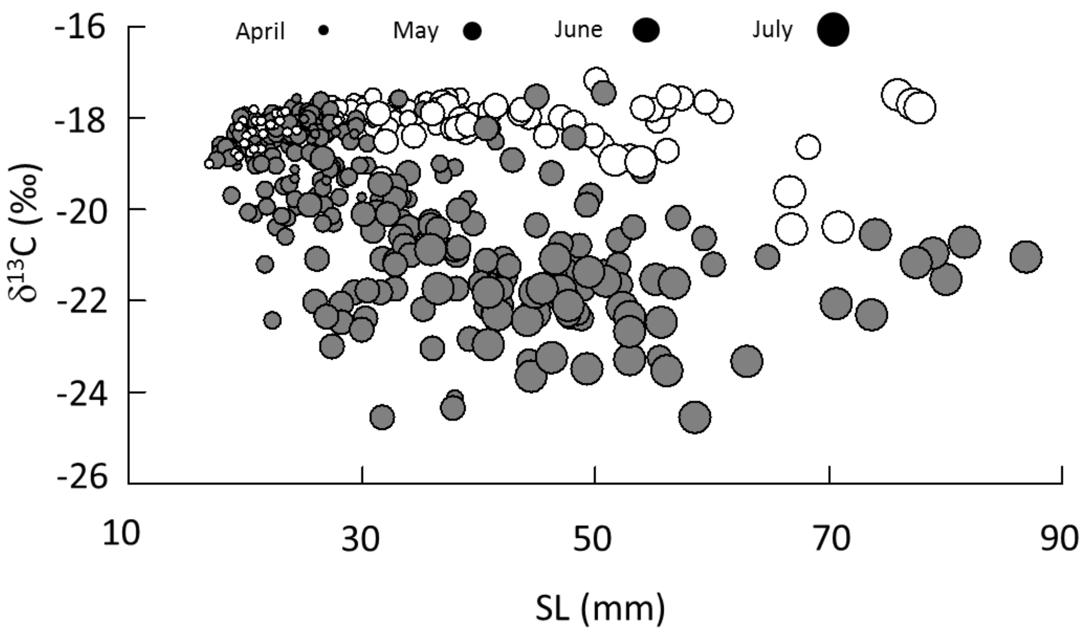

Fig. 6-3 Relationship between δ^{13}C of the muscle tissue and standard lengths (SL) of *Lateolabrax japonicus* collected in the coastal area (CA; open circles) and the estuary (ES; closed circles) in 2008. The size of plots indicates the season juveniles collected.

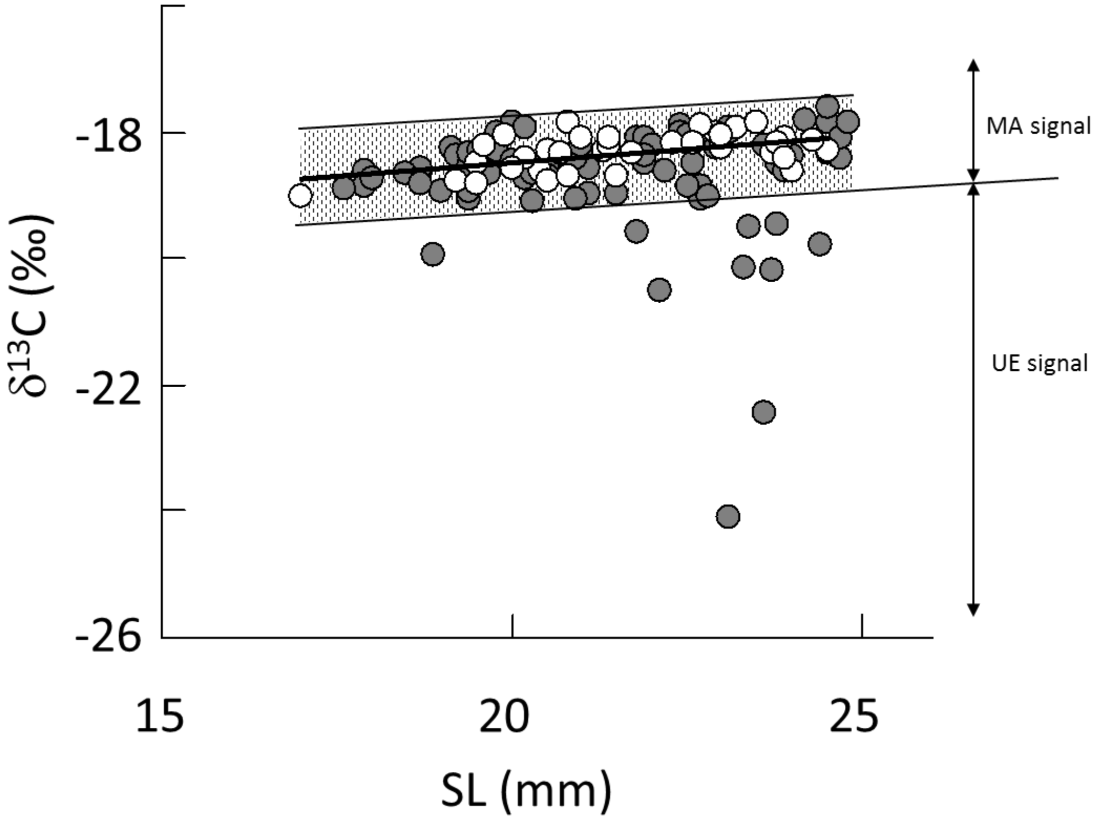

Fig. 6-4 Relationship between muscle δ^{13}C and standard lengths (SL) of *Lateolabrax japonicus* smaller than 25 mm SL caught in the coastal area (CA; open circles) and the estuary (ES; closed circles) in 2008. Dotted area indicates δ^{13}C range on which muscle δ^{13}C values should converge in CA. This range was calculated as follows; the regression formula was calculated between SL and δ^{13}C of juveniles of ≤ 25 mm SL at S1 (δ^{13}C = 0.08SL – 20.18; $R^2 = 0.28$, n = 20, $P \leq 0.05$) then the range was defined as that value ± 0.5 ‰.

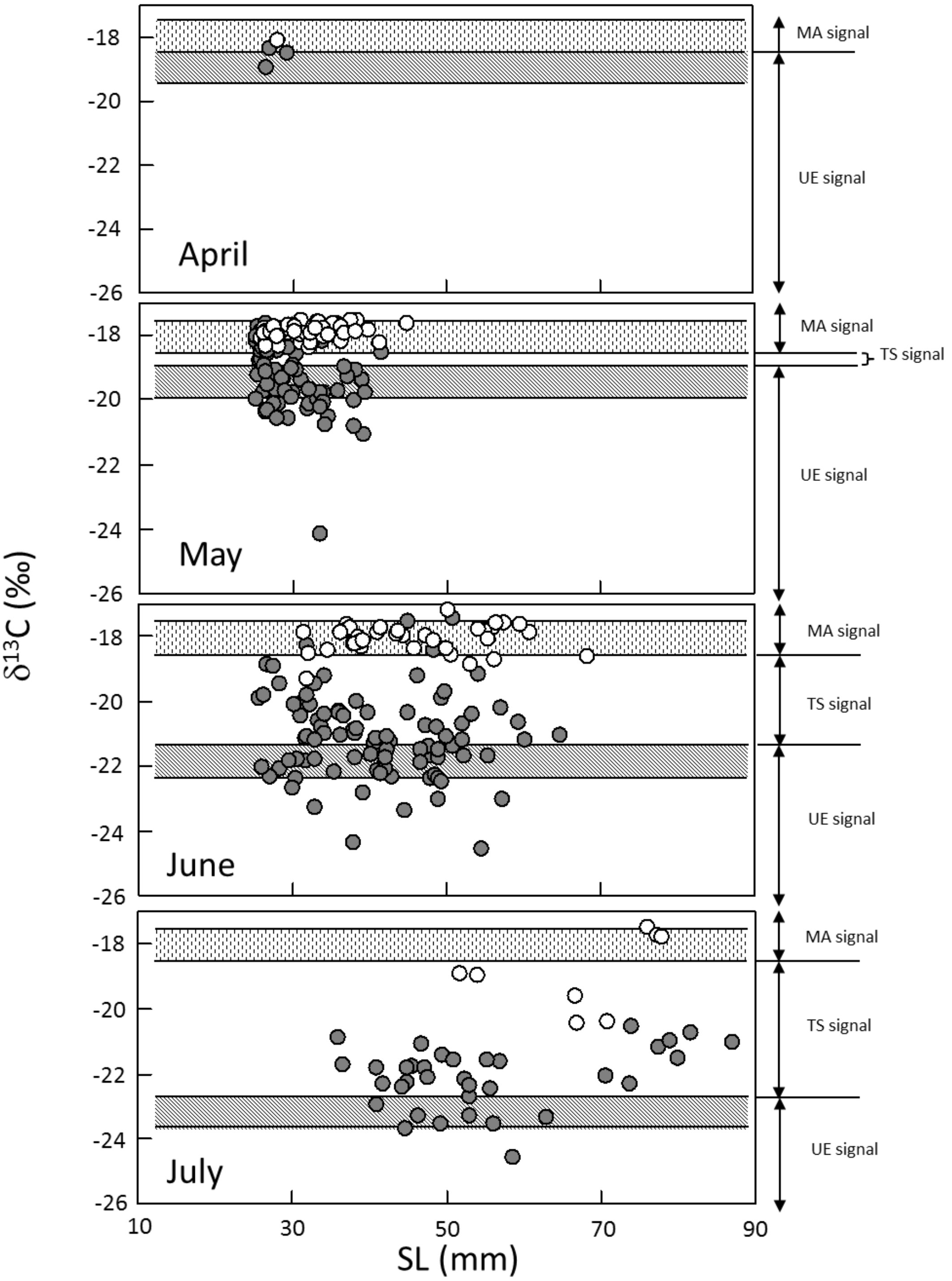

Fig. 6-5 Relationship between δ13C of muscle tissues and standard lengths (SL) of *Lateolabrax japonicus* larger than 25 mm SL caught in the coastal area (CA: open circles) and the estuary (ES: closed circles) in each month 2008.

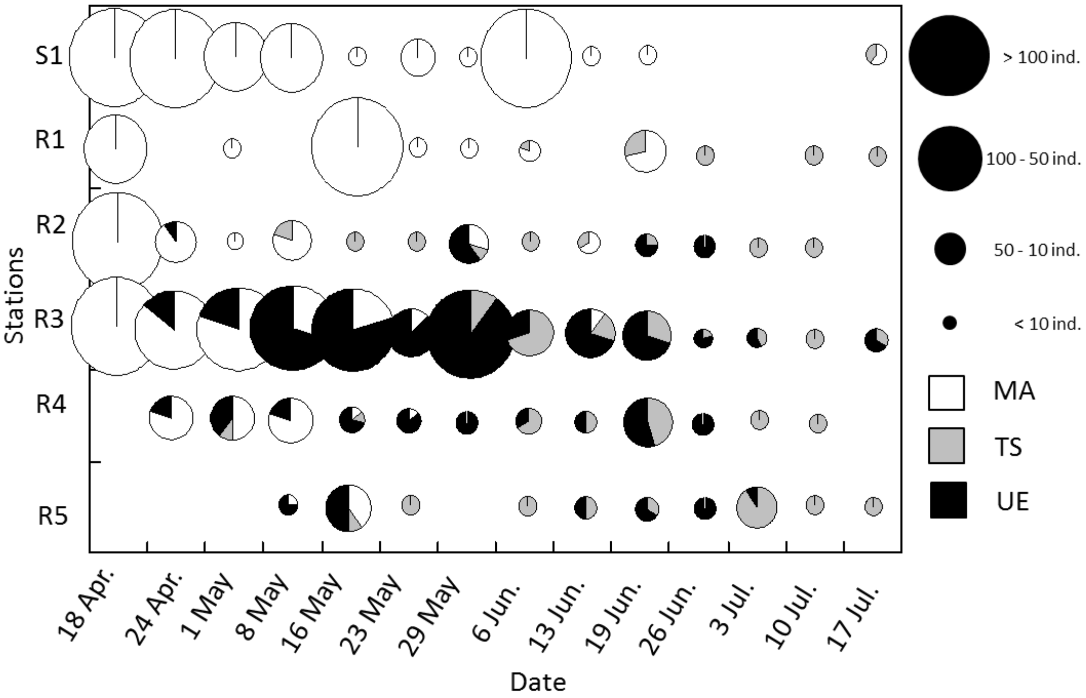

Fig. 6-6 Seasonal and spatial variation in migration groups, identified as the marine (MA), transient (TS), or upper estuary (UE) signal groups and the abundance of *Lateolabrax japonicus* in 2008.

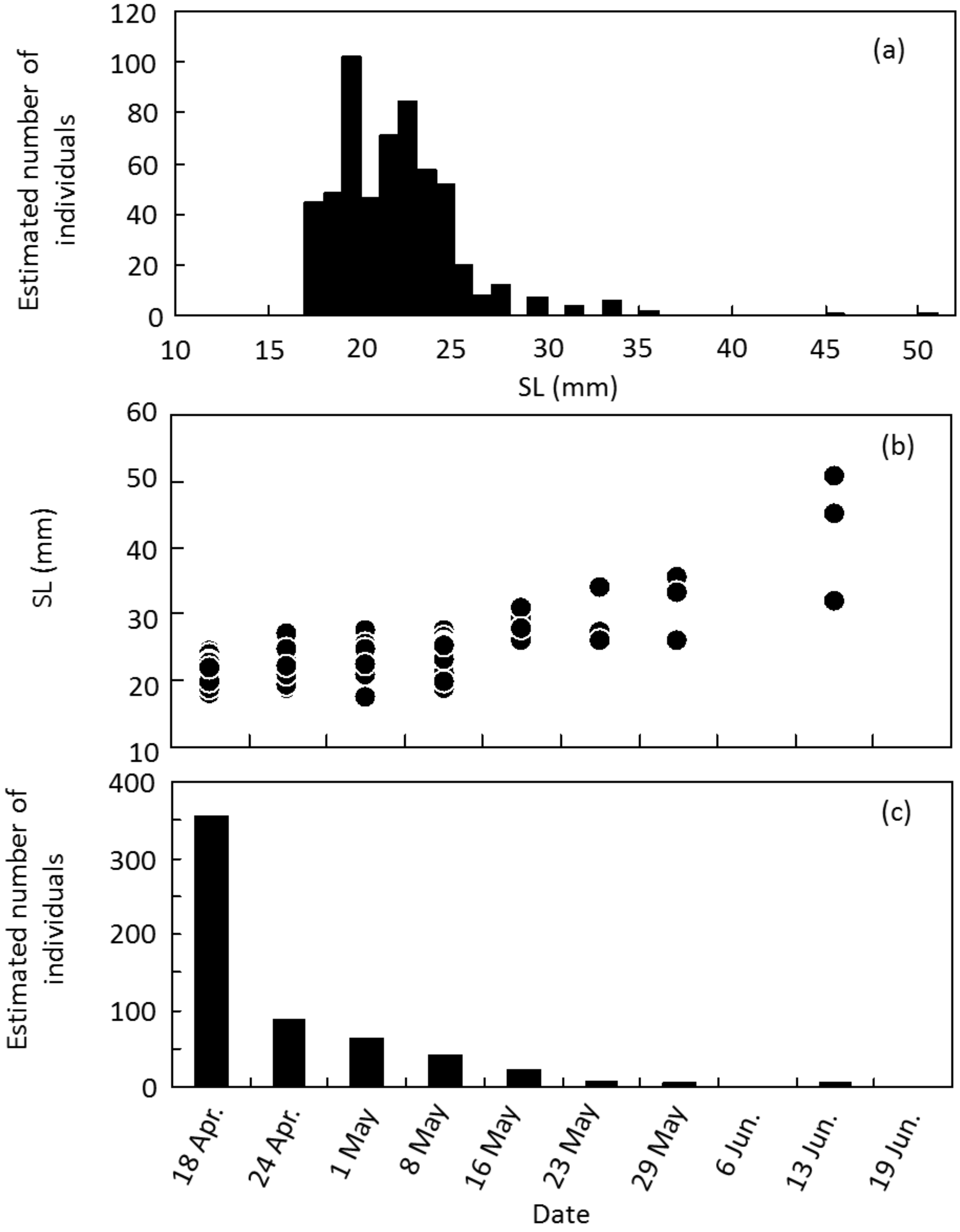

Fig. 6-7 (a) Size distribution of river ascending individuals. (b) Temporal change in standard lengths (SL) of river ascending individuals. Plots show the data of each juvenile. (c) Estimated number of river ascending individuals on each sampling day in 2008.

Chapter 7

Growth and migration patterns of juvenile temperate seabass in the Yura River estuary - combination of stable isotope ratio and otolith microstructure analyses

Introduction

Partial migration is the divergence of population into migratory and resident contingents (Jonsson and Jonsson, 1993). Juvenile temperate seabass also shows this migration pattern (Chapter 6). It is important to know the relationship between vital rates (e.g. growth, survival, etc.) and migratory behaviors to understand this migration ecology. In some fishes, larval growth is one of the most important factors for deciding the migration routes of juveniles. For example, white perch *Morone americana* spawn in the tidal freshwater area and larvae reside there. A part of the population of juveniles remains in the freshwater area while others migrate to brackish water. In this case, juveniles with poor growth during larval stage migrate to the brackish area (Kraus and Secor, 2004a). This migration pattern is observed in diverse range of fish species (Chapman et al., 2012).

Vital rates of juveniles can vary substantially among habitats during their juvenile stage. The variation could lead to differences in the relative contribution of the juveniles to the adult population and fluctuations of fish stocks (Houde, 1989; van der Veer et al., 2000; Beck et al., 2001). Therefore, growth rate has been used as an indicator of the quality of nurseries for juveniles (Franco et al., 2010). Understanding the relationship between migration pattern and growth of fish is requisite for management of their nurseries in order to conserve the stocks.

After onshore migration during larval stage of temperate seabass (Tanaka and Matsumiya, 1982; Islam et al., 2010), juvenile shows partial migration; a part of individuals migrate to the river, while others reside in the coastal area (Chapters 3 and 6). However, the growth rate and body condition of each juvenile migratory group is unknown. It is thus meaningful to estimate growth before and after the divergence of the two groups in order to understand the factors that affect the migratory pathway and the importance of the estuary as a nursery area.

Proportionality between otolith size and somatic growth has been well established for many fishes (Campana, 1990). This relationship has allowed the use of increment widths to estimate past growth rates (Campana, 1990). Therefore, combining the analysis of stable isotope ratio (Chapter 6) with that of otolith microstructure would allow us to determine if specific growth patterns are associated with particular migration strategies (Herzka, 2005).

The objective of this chapter is to clarify the relationship between migration pattern and growth of *L. japonicus* juveniles from the coastal area to the Yura River. First, juveniles were classified into four groups using the $\delta^{13}C$ of fish according to Chapter 6. Second, the growth of juveniles was evaluated using growth and body condition analysis. $\delta^{13}C$ values and otolith microstructure were then compared. Finally, relationship between the environmental factors and growth is discussed.

Materials and methods

Field sampling

Samplings were conducted at the stations of estuarine samplings following the methods in Chapter 3 from April to July 2008 (Fig. 3-1).

Laboratory analysis

Juvenile samples used in this chapter are common to those in Chapter 6. The $\delta^{13}C$ of juveniles were analyzed following the way of Chapter 6. To examine the relationship between migration patterns and condition coefficients and growth, individuals were classified into four groups based on their $\delta^{13}C$ signals (MA, TS and ES in Chapter 6) and sampling zones (ES or CA, Table 7-1); i.e. surf zone individuals, river ascending individuals, short-term resident individuals and long-term resident individuals. Suzuki et al. (2005) showed that the half-life of muscle tissues of *L. japonicus* juvenile is ca. 20 days by using diet switch experiments. The time scales elapsed after immigration into ES are therefore considered to be a few days, less than a month (mainly a few weeks) and a few months for river ascending, short-term resident, and long-term resident individuals, respectively.

The standard length (SL; mm) and wet body weight (BW; mg) of temperate seabass samples were measured. As a representative of body condition, Fulton's K condition index was calculated as follows:

$$K = 100BW/SL^3.$$

Otoliths manipulation followed the method in Chapter 4. The cohorts were defined as individuals hatched within a ca. 10-day period. Each cohort was designated with an alphabetical character from A (1 to 10 Dec.) to I (20 to 28 Feb.). The relationship between SL and otolith radius (O) was established. Back-calculation of size was conducted following the method established by Sirois et al. (1998). This method was developed to avoid the effects of the variation of growth rate over time (detailed in Sirois et al., 1998). Back-calculated lengths according to this method were provided by;

$$SL_t = SL_0 + \sum_{i=1}^{t}[W_t + a(W_t - W)]\frac{SL_c - SL_0}{O_c - O_0},$$

where SL_t is SL at age t. SL_c and O_c are SL and O at capture. SL_0 and O_0 are SL and O at first feeding. W_t is the increment width at age t and W is the mean increment width. SL_0 and O_0 are used as biological intercept in this study (Campana, 1990). SL_0 is reported as 4.7 mm (Islam et al., 2009). Mean distance from the nucleus to the first daily ring was 14.2±1.0 µm, which was measured for 200 individuals. This value (14.2) was used as O_0. Values of W were calculated for each fish. a is called "growth effect" and calculated by a linear regression using each individual fish as an independent observation (n = 200):

$$S = aG + b,$$

where S is the slope of SL-O relationship for each individual. G is the absolute linear growth rate in SL. b is an estimated parameter of the linear regression. S and G are computed for each individual as;

$$S = (L_C - L_0)/(O_C - O_0),$$

and

$$G = (L_C - L_0)/(A_C - A_0).$$

A_c and A_0 are ages at capture and first feeding, respectively.

The back-calculated SL and daily growth rates were averaged for each 10 days. Given the median age at river ascending (95 days, see Results), SL and daily growth rates before days 90 were compared between individuals in the ES (river ascending, short-term resident, and long-term resident individuals; Table 7-1) and surf zone individuals in CA to detect any differences in growth before splitting into the two migration groups. In addition, SL and daily growth rates after days 90 were compared between long-term resident individuals and surf zone individuals to examine any differences in growth after migration. The Fulton's K was also compared among four migratory groups (Table 7-1).

The slopes of SL-O relationships were compared between juveniles in ES and CA by ANCOVA. All comparisons of size and growth rates were conducted by Student *t*-tests. Body conditions were compared among migratory groups by ANOVA followed by Tukey's test.

Results

Condition coefficient

Since Fulton's K changed with growth (Fig. 7-1), K' was defined as the residuals from the linear regression between SL and K for juveniles smaller than 30 mm SL, and as residuals from the mean K for juveniles larger than 30 mm SL to avoid any confounding effect of fish size. There was a significant difference among migration groups in K' ($P \leq 0.01$, Fig. 7-2). River ascending individuals indicated significantly smaller K' than surf zone and long-term resident individuals ($P \leq 0.01$). Long term resident group showed no significant difference from the surf zone individuals ($P > 0.05$).

Growth analysis by otolith microstructures

Hatch dates of juveniles were estimated from early December to mid-February with a peak at the end of January (Fig. 7-3). The hatch date composition of juveniles showed little change with time from April to May. Juveniles of cohort E, F and G were used for the growth back calculation because of their large biomass and continuous occurrence both in CA and ES for meaningful statistical analyses. In total, ages of river ascending individuals (n = 94) ranged from 70 to 131 days with a peak of 80 to 110 days during the sampling season (Fig. 7-4). The median age of river ascending juveniles was 95 days.

The relationships between O and SL were different between individuals in ES and CA (Fig. 7-5). Individuals in CA had significantly smaller otoliths than those in ES at the same body size of fish ($P \leq 0.01$). A positive linear relationship was found between S and G (Fig. 7-6). The growth effect (a), which is described as the slope of this relationship, was estimated at 0.17.

The back-calculated growth trajectories were different between juveniles that remained in the CA and those that ascended to ES (Fig. 7-7). There were no significant differences in back-calculated growth rates between two groups under age 50 days ($P > 0.05$, Fig. 7-7a). However, over the age of 50 days, individuals in ES had significantly lower growth than juveniles in CA ($P \leq 0.01$, Fig. 7-7a). SL showed similar pattern; there was no significant difference in SL under 60 days after hatching (Fig. 7-7b). Then individuals in CA showed significantly larger SL than individuals in ES after age 60 ($P \leq 0.01$, Fig. 7-7b). On the other hand, the growth pattern after fragmenting into two groups was different from the aforementioned pattern; growth rates of surf zone individuals decreased with their age, although long-term resident individuals increased (Fig. 7-7c). Growth rates of long-term resident individuals caught up with surf zone individuals at the age of 100-110 and even overtook after age of 110, although significance in difference was weak (P=0.08, Fig. 7-7c). SL of surf zone individuals were significantly larger than those of long-term resident individuals from 90 days old ($P \leq 0.01$, Fig. 7-7d), which is the major river ascending age for seabass juveniles. However, the difference disappeared at the age of 120 days ($P > 0.05$) reflecting the better growth in the freshwater environment.

Discussion

Combining the analysis of stable isotope ratio with body condition and otolith microstructure analyses is a useful method to investigate relationship between growth dynamics and migration pattern (Herzka, 2005). This study found that seabass juveniles migrate to the river at various intervals during three months in spring (Chapter 6). The categorization of juveniles according to residence period in the river would make it possible to evaluate the growth rates of juveniles after ascending into the river. This study successfully corroborated the migratory signals of stable carbon isotope ratio with the body condition and otolith microstructure analysis, and revealed the relationship between migratory patterns and growth trajectories.

Growth before fragmenting into two groups

The significantly higher K' in the surf zone individuals than that in the river ascending individuals (Fig. 7-2) suggests that juveniles in a relatively poor condition ascended the river, while others in a good condition remain in CA. Results of growth back-calculation also indicate that juveniles that experienced relatively lower growth ascended the river (Fig. 7-7). Growth is known as a major factor that affects migration routes in some fishes (Jonsson and Jonsson, 1993; Chapman et al., 2012). Juveniles with higher growth rates of Atlantic salmon *Salmo salar* and white perch remain resident in the natal habitats, while fish with lower growth rates migrate to the other areas (Bujold et al., 2004; Kraus and Secor, 2004a). The migration pattern of seabass juveniles is similar to these fishes.

Temperate seabass has a planktonic stage of ca. 50 days after hatching in the offshore area, and then settles and resides until ca. 90 days old in the coastal area (Islam et al., 2010). Back-calculated growth rates and SL started to split significantly around 50-60 days after spawning, corresponding to the beginning of their settlement phase (Fig. 7-7). This means that the variance of growth of juveniles increased in this stage. This variability can be caused by density dependent competition. Li and Brocksen (1977) reported that variance of growth of rainbow trout *Oncorhynchus mykiss* increased with their density. They considered density dependent intra specific competition would lead to this phenomenon. Olsson et al. (2006) found that higher density dependent competition led to a higher proportion of migration behavior of brown trout *Salmo trutta.* Density dependent effects on growth and mortality start to occur from the settlement stage in the case of flatfishes (van der Veer et al., 2000). The critical period for fish density dependent survival would occur in the settlement phase rather than the larval phase because of the distribution pattern and their habitat changes drastically in this transition phase (Juanes, 2007). It is reported for temperate seabass that juveniles showed density dependent growth rates during 50 – 100 days old in the Chikugo River estuary (Shoji and Tanaka, 2007a). Density dependent competition among seabass larvae after settlement might start to increase the variance in growth and be a determinant in the migration pattern in the juvenile stage. Yearly dynamics of abiotic and biotic environmental factors relating to density-dependent effects, e.g., temperature, larval density and prey availability in the field, may have an important role for regulating the dynamics of partial migration of temperate seabass.

Body condition and growth after fragmenting into two groups

The body condition and growth of juvenile seabass showed a similar pattern: those vital rates in ES caught up with CA after ca. one month stay in ES (Figs. 7-2 and 7-7). Ohta (2004) also reported that juveniles of temperate seabass showed higher growth rates in the Chikugo River estuary than in the surf zone after juvenile stage in the Ariake Bay. In most cases of partial migration, similar patterns of migration and growth were detected (Jonsson and Jonsson 1993; Kerr and Secor, 2009); migrant individuals grow faster than resident group after splitting into two groups. Kerr et al. (2009) considered that high productivity in the brackish area would lead to higher growth of larvae that migrated to the brackish area than those that remained in the freshwater. Salmonid fishes show a similar pattern; drifters grow bigger than residents during their life in the polar ocean, where the productivity is apparently higher (Jonsson and Jonsson, 1993). Therefore, the migration ecology of temperate seabass could have common characteristics with other species: individuals which experience poor growth migrate to other places and subsequently show better growths than the resident individuals. Kasai et al. (2010) reported that primary production is much higher in the lower reach of the Yura River (ES in this study) than in the adjacent coastal area (CA in this study). This would lead to a good prey environment and feeding condition for juvenile in ES as shown by the ambient mysids density and gut fullness index in Chapter 5. In the case of Japanese flounder *Paralichthys olivaceus*, juvenile gut fullness index was affected by prey environment (Tanaka et al., 2006). Juveniles grew faster in the area with enough prey than the area with poor prey environment (Fujii and Noguchi, 1996). Islam and Tanaka (2005) showed that gut fullness index and body condition of seabass juveniles reflects the prey condition in ambient water in the Chikugo River estuary. Higher gut fullness index in ES (Chapter 5) could also indicate the better prey condition in ES and lead to better growth in ES than in CA. Additionally, temperature could be another reason for good growth in ES. Temperature in ES was always ~1 degree higher than CA from April to July (Chapter 3). Higher temperature leads to higher growth rates of juveniles of temperate seabass within temperature range from 8 to 20 C° under laboratory and natural conditions (Hirata, 1967; Shoji and Tanaka, 2007b). The temperature observed in the Yura River estuary during April and May was lower than 20 °C (Chapter 3), indicating that juveniles in ES experienced better temperature condition for higher growth than juveniles in CA. Growth rates in CA showed a decreasing tendency after day 90 (Fig. 7-7c). This matches with the seasonal change of primary production in the Tango Sea. Chlorophyll-*a* concentration showed higher values in the coastal area (CA in this study) in April than May (Kasai et al., 2010). After April, the productivity of the coastal area in the Tango Sea decreases because the phytoplankton community in the river has utilized most of nutrients from upstream and then depleted in the coastal area (Kasai et al., 2010). This study showed the mysids densities were considerably low in the coastal area in May (Chapter 5). These factors would lead to a decrease in growth rates of surf zone individuals. This could be the reason that the growth of individuals in ES exceeded CA individuals.

Table 7-1 Classification of *Lateolabrax japonicus* by their $\delta^{13}C$ signals and sampling zones (the estuary: ES or the coastal area: CA)

Zones	Signals		
	MA (marine)	TS (transient)	UE (upper estuary)
CA	Surf zone individuals (no residence)		
ES	River ascending individuals (several days)	Short-term resident individuals (several weeks)	Long-term resident individuals (over a month)

Parenthesis notations indicate the residence time scale in ES expected from the half-life (ca. 20 days, Suzuki et al. 2005).

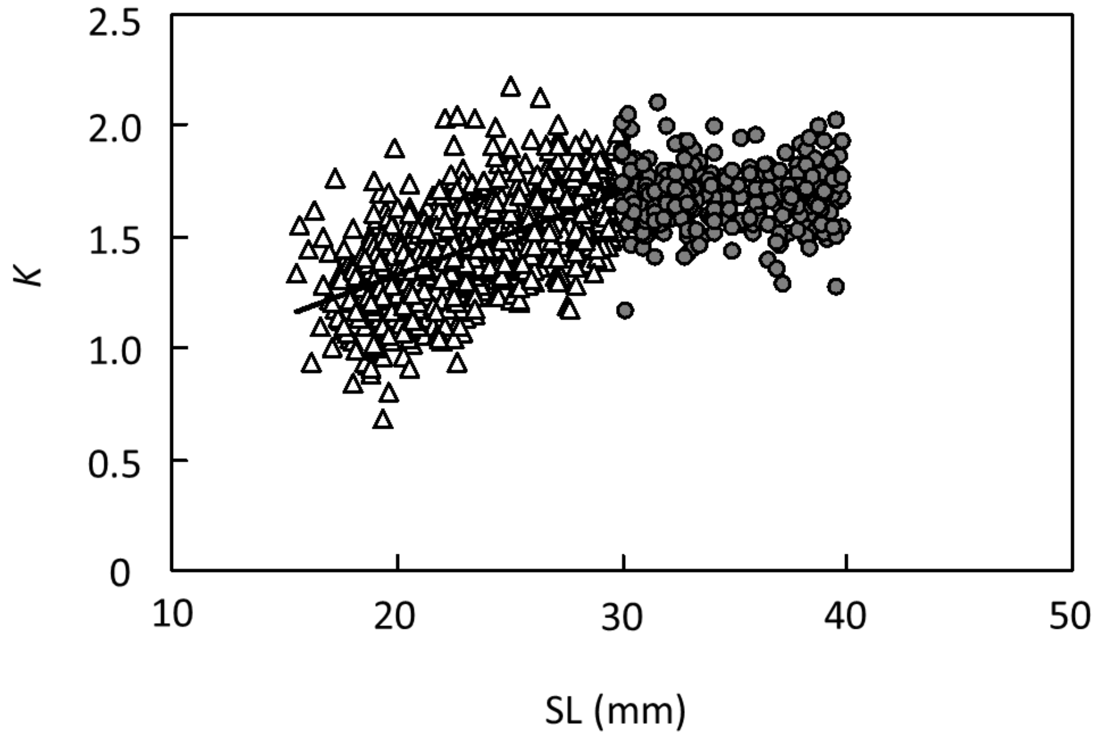

Fig. 7-1 Relationship between standard length (SL) and Fulton's *K* of *Lateolabrax japonicus* smaller (open triangles) and larger than 30 mm SL (closed circles). The line showed the linear regression formula between SL and *K* for ≤ 30 mm SL ($K = 0.04$ SL $+ 0.59$; $R^2 = 0.35$, $n = 1254$, $P \leq 0.05$).

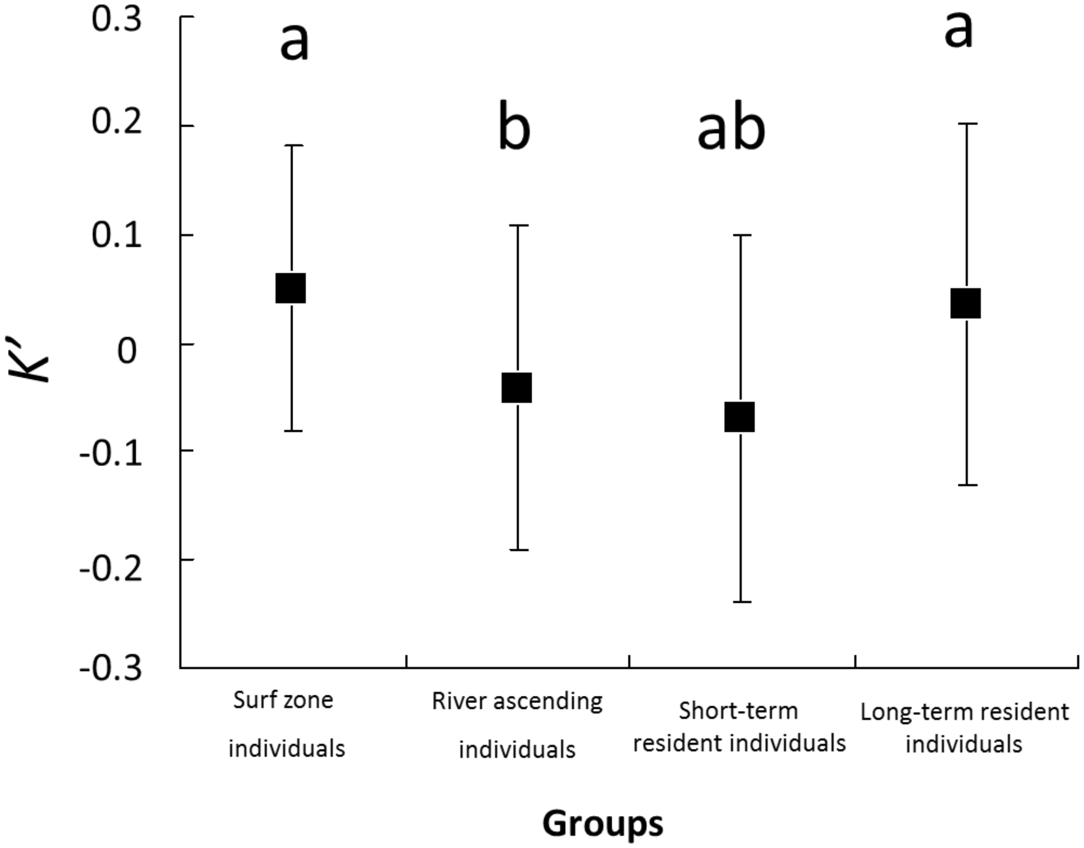

Fig. 7-2 Mean condition coefficient (*K'*) of *Lateolabrax japonicus* for surf zone individuals, river ascending individuals, short-term resident individuals and long-term resident individuals. Error bars indicate standard deviations. Different superscripts on the top of the bars indicate significant difference (ANOVA followed by Tukey's test, $P \leq 0{\cdot}01$).

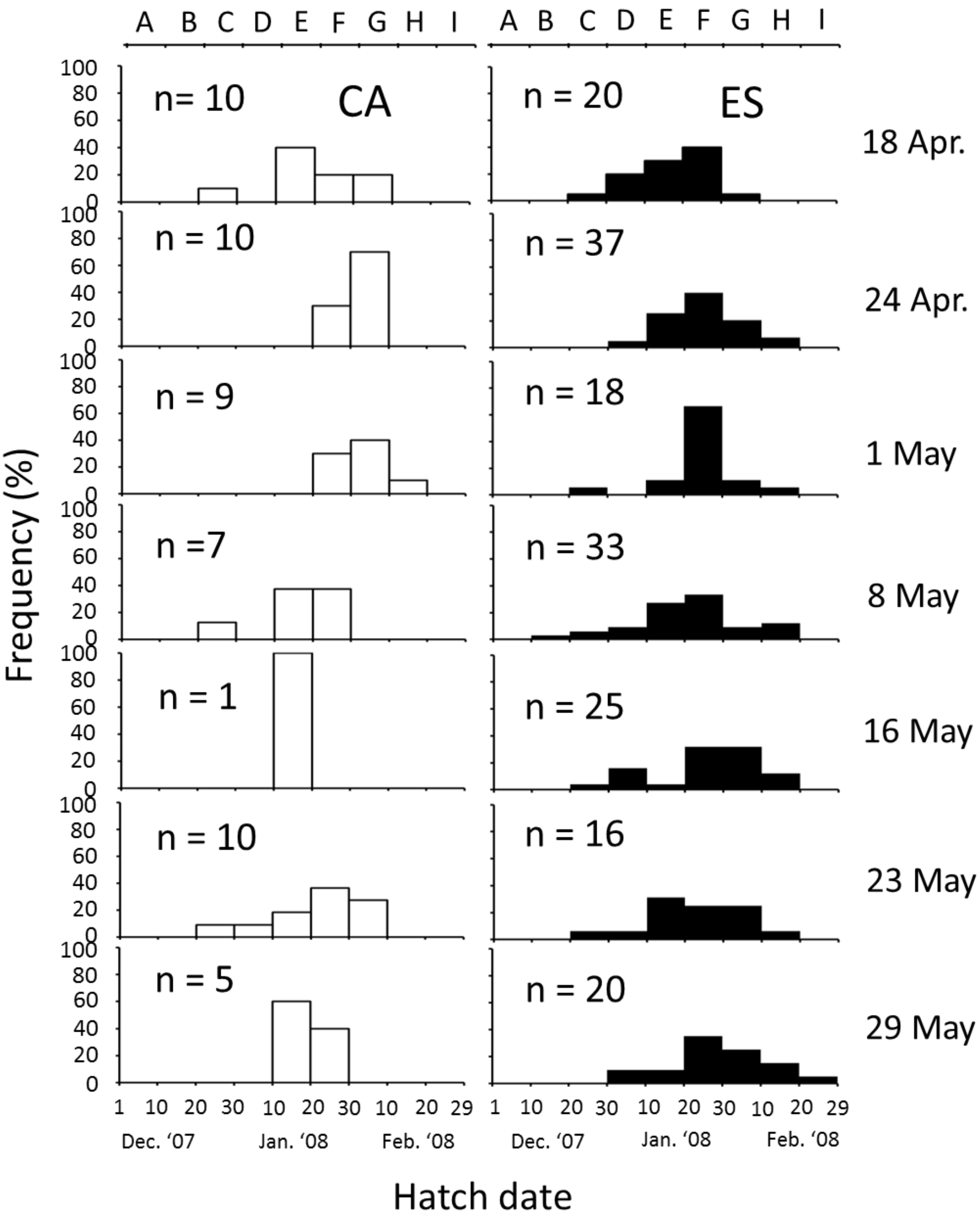

Fig. 7-3 Time series of juvenile hatch date composition in the coastal area (CA) and the estuary (ES) in April and May 2008. n indicates number of juveniles analyzed. Alphabet letters on the top of figure show the cohorts.

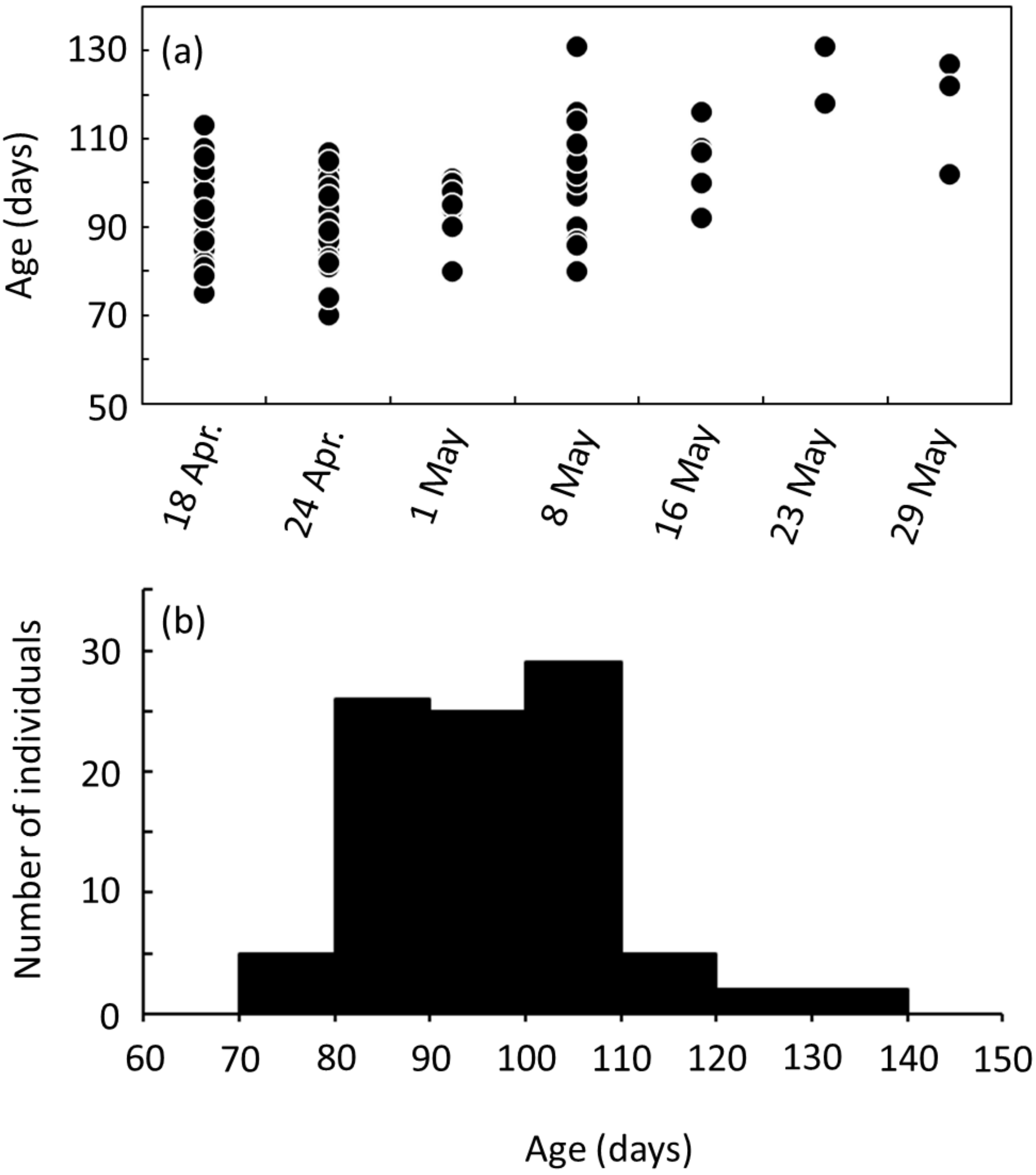

Fig. 7-4 (a) Time series of age compositions of river ascending individuals in 2008. (b) Age distribution of the river ascending individuals.

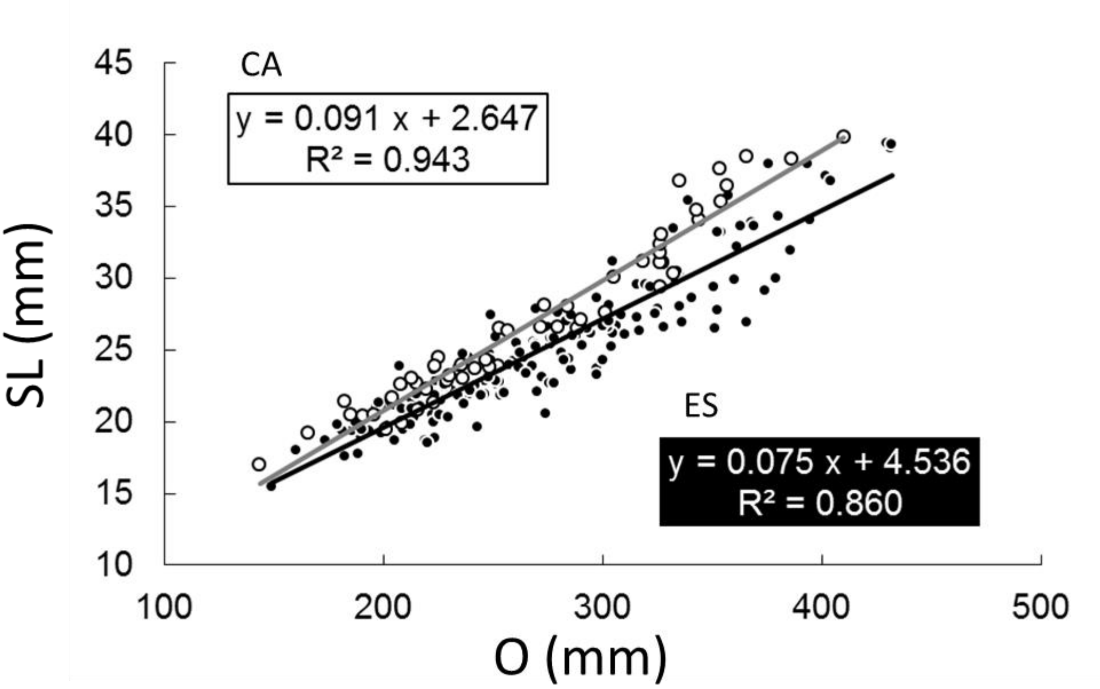

Fig. 7-5 Relationships between standard length (SL) of *Lateolabrax japonicus* juveniles and otolith radius (O) for individuals in coastal area (CA: white) and in the estuary (ES: black) in 2008.

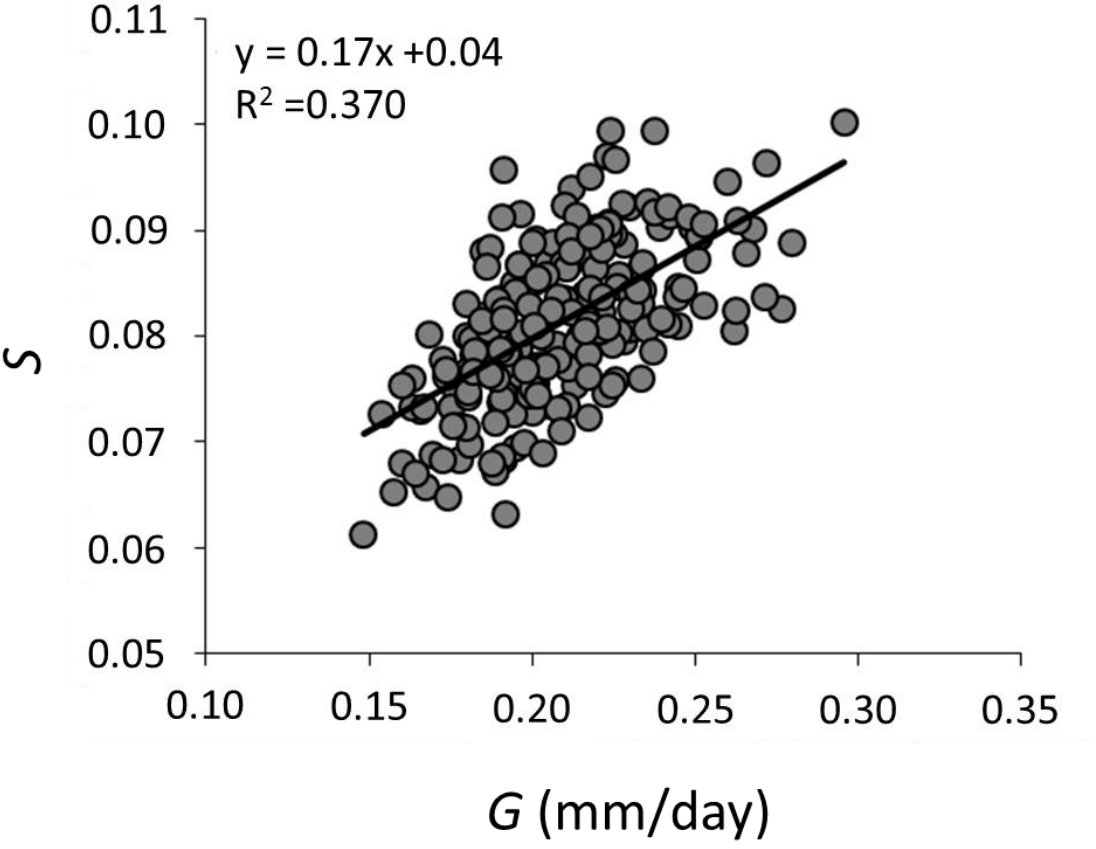

Fig. 7-6 Relationship between the slope of the SL-O relationship (*S*) and absolute body growth rate (*G*) calculated using individual juveniles of *Lateolabrax japonicus* collected in 2008.

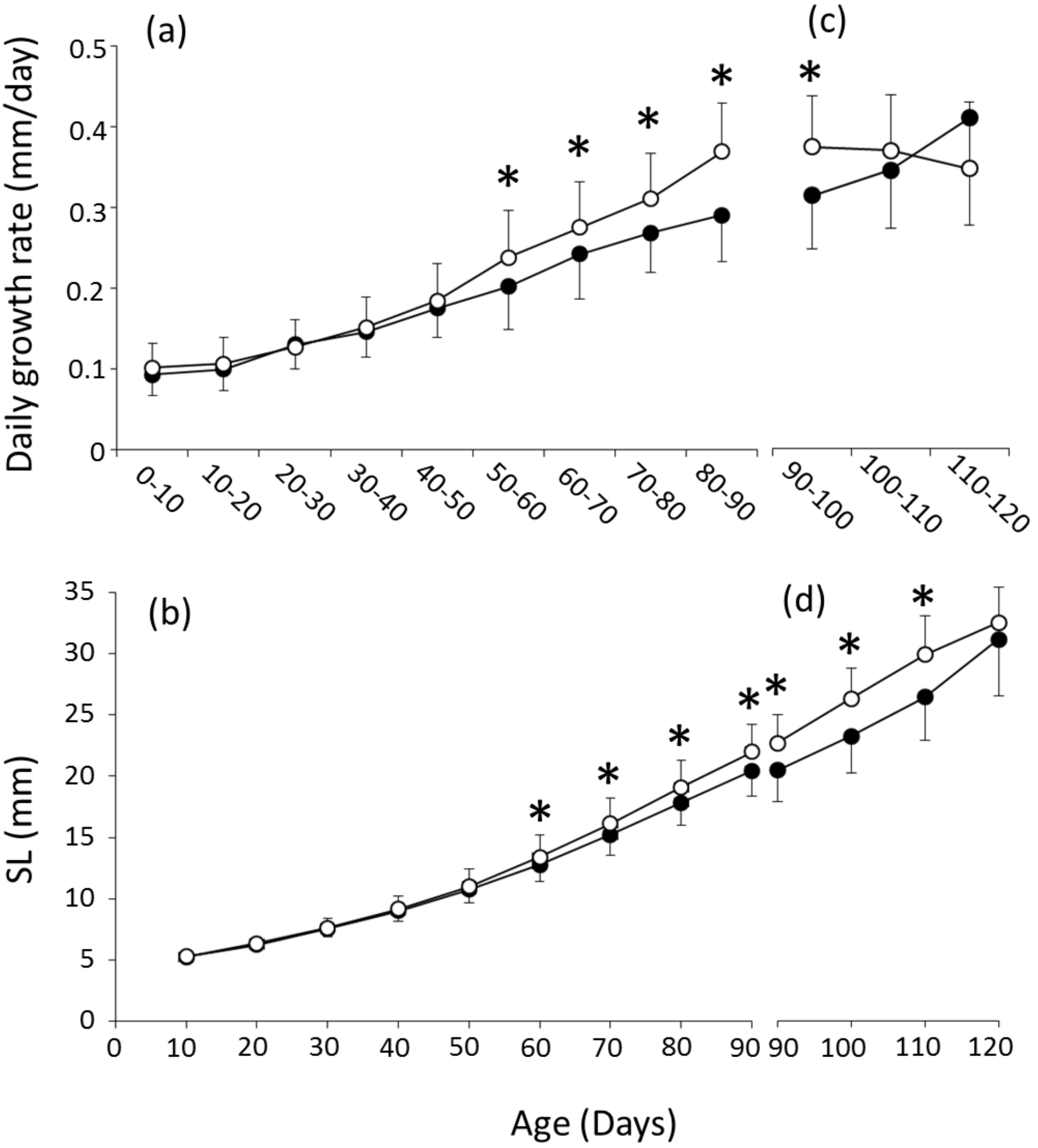

Fig. 7-7 (a) Back-calculated growth rates and (b) standard lengths (SL) of under 90 day old juveniles of *Lateolabrax japonicus* collected in CA (white circles; n=46) and ES (black circles; n=131). (c) Back-calculated growth rates and (d) SL over 90 day old for long-term resident individuals (black circles; n=43) and juveniles in CA (white circles; n=28). Error bars indicate standard deviations. Asterisks indicate significant difference between two groups (Student's t-tests, $P \leq 0.01$).

Chapter 8

Main factor of the mortality during the estuarine juvenile stage of temperate seabass

Introduction

Survival mechanisms of seabass juveniles during the estuarine residence stage are important to understand the role of the estuarine habitats. There are two prominent factors affecting juvenile survival during their stay in estuaries; environmental variations caused by river discharge and density-dependent mechanisms (Strydom et al., 2002; Ueda et al., 2004; Whitfield and Harrison, 2003; Costa et al., 2007; Martinho et al., 2012).

Juveniles in the estuarine nurseries are sometimes exposed to extreme flood events. Many studies have focused on the effects of river flows on community structure, distribution and mortality of estuarine fishes (Loneragan and Bunn, 1999; Kimmerer, 2002; Whitfield and Harrison, 2003; Eyre et al., 2006; Costa et al, 2007; Purtlebaugh and Allen, 2010). For example, Whitfield and Paterson (1995) observed dead fish from many taxa after a flood in the Sunday Estuary and hypothesized that clogging of the fish gill filaments by suspended sediments, osmoregulatory and other stress factors would cause the mass mortality. Unfavorable salinity condition and unstability of water column caused by flood events could be another impact on estuarine ecosystems, leading to high mortality of larvae and juveniles of black bream *Acanthopagrus butcheri* (Jenkins et al., 2010). Clupeidae *Gilchristella aestuaria* larvae and juveniles appear to be flushed out in the Great Fish system as a result of the excessive amount of river flow (Strydom et al., 2002). Some studies reported the decrease of prey abundance because of flood events (Ueda et al., 2004; Islam and Tanaka, 2007; Cardoso et al., 2008; Vinagre et al., 2011). However, most of these studies just compared the environmental factors and fish densities. Few study confirmed the mechanisms underlying the relationship between the river discharge and juvenile mortality by fine scale surveys over the periods including flood events.

Density-dependent mechanism is also considered to be important for the mortality in the juvenile stage in various coastal fishes, including many estuarine dependent fishes (Buckel et al., 1999; Iles and Beverton, 2000; Kimmerer et al., 2000; van der Veer et al., 2000; Hixon and Jones, 2005). Both competition and predation have long been recognized as the sources of direct density dependence (Hixon and Jones, 2005). Martino and Houde (2012) reported the importance of density-dependent regulation of year-class strength in age-0 juvenile striped bass *Morone saxatilis*. They found prey consumption was limited in the estuaries except for low-juvenile abundance years. The density-dependent feeding by predators (bluefish *Pomatomus saltatrix*) also responds according to increases in juvenile striped bass density (Buckel et al., 1999). However, few studies focused on the effects of environmental factors on the density-dependent mortality. For example, high river discharge could reduce the amount of prey items in the estuaries (Ueda et al., 2004; Islam and Tanaka, 2007), and lead to higher density-dependent effects on the mortality.

The objective of this study is to describe the effects of changes in river flow on the mortality of juvenile temperate seabass by comparing the observational results in five years.

Materials and methods

Samplings were conducted at stations of the estuarine sampling indicated in Chapter 3. Surveys were conducted from March to July during 2008-2012. Detailed methods of the estuarine sampling (towing of seine net and sledge net and temperature measurements) were described in Chapter 3 and Chapter 5. The distances of seine net and sledge net towing were recorded at each station to calculate the densities of juveniles and prey items (mysids). All juveniles were counted and measured standard length (SL) to the nearest 0.1 mm. Mean daily river discharge of the Yura River observed in Fukuchiyama (Fig. 2-1) was obtained from Ministry of Land, Infrastructure, Transport and Tourism.

Based on Chapter 6, riverine stations (R2-R5) were selected for analyzing the mortality of juveniles in the estuary. Densities in all stations in the estuary were averaged for each sampling date. The dates when the mean density reached to highest value in the year were defined as the immigration day in this chapter. Juvenile temperate seabass migrate seaward after July in the Yura River estuary (Chapter 6). Given this migration schedule, daily mortality rates were estimated using juvenile densities during the periods between immigration days and the end of June to avoid the effects of emigration from the Yura River estuary.

Daily mortalities (Z_t) were estimated for each sampling interval applying the exponential model (Shoji and Tanaka, 2007b) as:

$$D_{t+1} = D_t e^{-Z_t},$$

where D_t mean fish densities among estuarine stations (ind. m^{-2}) at the sampling date t (day). D_t was estimated by using only fish captured within ± 5 mm SL of the mode size (Purtlebaugh and Allen, 2010) or using all individuals. The results of these two ways of analysis were compared to check that the error of analysis were not significant.

Temperature and river discharge data were averaged for every two continuous sampling days to compare with every Z_t in all estuarine sampling stations. Mysids are the most important prey items during estuarine residence period (Chapter 5). Mysids densities were estimated by following the method in Chapter 5. The densities of mysids at all estuarine stations (R2-R5) were averaged for every month. The competition index (C_t) was calculated as follows,

$$C_t = \frac{M}{D_t},$$

where M is the mean density of mysids for each month. M in the same month with sampling date t was used for calculating C_t.

Pearson's correlation coefficient was used for relationship between the river discharge and M. Spearman's rank correlation coefficient was used to evaluate other relationships because of non-normal distributions of data.

Results

Immigration days were 18 April 2008, 15 April 2009, 28 April 2010, 18 May in 2011 and 23 April 2012 (see Chapter 3). Immigration day was delayed in 2011 because of lower temperature and delayed hatch days (Chapter 4). The Yura River discharge during sampling periods varied across the observational years (Fig. 8-1). It was low and no apparent flood events occurred in 2008 and 2009. On the other hand, there were a few flood events during the sampling periods in the other three years. Especially, river discharge was extremely high in 2011 (1725 m^3s^{-1} on 30 May).

Mean densities of juveniles decreased after immigration (Fig. 8-1). In general, densities of individuals of all size range showed small difference from those of individuals within ± 5 mm from the mode sizes (Fig. 8-1). Z_t ranged from -0.08 to 0.50 in using mode size ± 5 mm and -0.07 to 0.47 in using all size individuals (Fig. 8-2). Hereafter, negative values of Z_t were excluded from the analysis. Z_t was highest during the first interval of the sampling days every year (Fig. 8-2). Highest Z_t was observed at the first interval in 2011 with the value of 0.47 and 0.50 in the case of using all individuals and mode size ± 5 mm, respectively (Fig. 8-2). No significant relationship was detected between mean river flow during each sampling interval and Z_t ($P>0.05$, Fig. 8-3). Z_t showed significant positive relationship with D_t (All individuals: $r = 0.57$, $P \leq 0.05$; Mode ± 5 mm: $r = 0.56$, $P \leq 0.05$, Fig. 8-4), and significant negative relationship with C_t (All individuals: $r = -0.62$, $P \leq 0.05$; Mode ± 5 mm: $r = -0.80$, $P \leq 0.05$, Fig. 8-5). Two methods of estimating Z_t showed no apparent difference in all aforementioned analyses. Mean mysid densities decreased with the increase of the river discharge before one month of the sampling day (Pearson's correlation, $r=-0.70$, $P \leq 0.01$; Fig. 8-6).

Discussion

Many studies showed the positive correlation between river flow and mortality of fish based on the comparison between averaged environmental factors, e.g., river discharge or salinity, and fish densities (Whitfield and Paterson, 1995; Whitfield and Harrison, 2003; Eyre et al., 2006). The sudden environmental changes in flood events have been considered as the major cause of higher mortality in years of high river discharge. For example, the flood events drastically change salinity, turbidity, temperature and dissolved oxygen (Whitfield and Paterson, 1995; Whitfield and Harrison, 2003; Eyre et al., 2006; Kasai et al., 2010). Higher river flow can also flash out the larvae and juveniles from estuarine nurseries (Cardoso et al., 2008; Strydom et al., 2002; Ueda et al., 2004; Shoji and Tanaka, 2006b). These effects have been considered to lead to high mortality of larvae and juveniles in estuaries. On the other hand, this study found no direct effects of flood events on the juvenile mortality by the fine scale field sampling during the periods including large flood events (Fig. 8-3). This result indicates that sudden environmental changes induced by flood events were not the main cause of the juvenile mortality in the case of temperate seabass. This species would be resistant to the various environmental fluctuations. Juveniles of this species can distribute in various temperature, salinity and turbidity (Kinoshita, 2002), suggesting the tolerance to the fluctuations of environmental factors caused by flood events. In addition, they might also be resistant to the strong seaward current caused by flood events. The mechanism of juvenile residence during flood events has not been clarified. Ueda et al. (2004) reported that estuarine copepods maintain their position on the bottom of submerged channels outside the river mouth during a river flood to avoid to be flashed out. Similar mechanism is also considered in the case of juvenile temperate seabass. It was reported that juveniles distribute in the bottom layer of the Chikugo River estuary during ebb tide to avoid the strong seaward tidal currents (Ohta, 2004).

Juvenile temperate seabass is valunerable to density-dependent mortality (Fig. 8-4). Density-dependent mechanism is common for various coastal fishes in the juvenile stage, including many estuarine dependent fishes (Iles and Beverton, 2000; Hixon and Jones, 2005). Both competition and predation have long been recognized as the sources of direct density dependence (Buckel et al., 1999; Hixon and Jones, 2005; Martino and Houde, 2012). Intensive competition of the juvenile temperate seabass for prey items led to the higher mortality, suggesting the importance of intraspecific competition (Fig. 8-5).

Juvenile temperate seabass consumes preys corresponding to 12.8 % of their body weight per day (Hatanaka and Sekino, 1962b). Given the mean body weight of juveniles in estuaries (ca. 0.4 g: Chapter 3), an individual is estimated to feed on ca. 50 mg of preys per day. Mean wet weight of one individual mysid *Neomysis awatschensis* is ca. 2 mg (Fuji, unpublished data). As a result, a juvenile temperate seabass feeds on ca. 25 individual mysids per day. Considering that juvenile seabass is only species feeding on mysids in the Yura River estuary (Aoki et al., 2013), this would mean C_t should be higher than 25 to maintain the juvenile population in the estuary. In this study, Z_t drastically increased below 25 of C_t, while is stable beyond 25 of C_t (Fig. 8-5). This supports the importance of competition for prey items for the juvenile mortality. The mass mortality of larvae and juveniles of marine fishes is considered to be mainly caused by predation (Tsukamoto et al., 1989; Takasuka et al., 2003; Hixon and Jones, 2005 Kinoshita et al., 2013). On the other hand, estuaries are generally considered to act as the refuge and shelter from predators because of its high turbidity and low salinity (Yamashita et al., 2000; North and Houde, 2001; Shoji and Tanaka, 2006b). Not the top-down control observed in the marine environments, but the bottom-up control, i.e., the juvenile competition for prey items, would be important for mortality of the juvenile temperate seabass in the estuaries.

Few studies showed the possibility of environmental effects on the density-dependent mortality. This study showed the effects of the river discharge on the prey abundance in the estuary (Fig. 8-6). The river discharge would change the density-dependent mortality relationship by changing prey abundance. Although mysids distributed more in the Yura River than the adjacent coastal area (Chapter 5), better feeding environment in the river would be broken by increase in river discharge. Komatsu and Hoshino (2010) reported higher mortality of juvenile temperate seabass in the Naka River than Hinuma brackish lake. They considered the unstable environment in the river may lead to higher mortality than the lake. The temperate seabass juveniles utilizes various habitats as nurseries, e.g., tidal flats, sand beach, eelgrass beds and estuaries (Arayama et al., 2002; Kinoshita, 2002; Hibino et al., 2006; Islam et al., 2011). Many studies suggested the importance of estuarine nursery area for juvenile temperate seabass (Islam et al., 2011). However, a part of juveniles reside in the coastal areas regardless of many merits of estuaries. This study suggested that the unstability of the nursery value of estuaries could be the reason why all of juveniles do not migrate into estuaries. The strategy of juveniles to use only estuaries as nursery grounds may be risky. Kerr et al. (2010) showed by the theoretical study that partial migration of white perch stabilizes and maximizes their population. The multi-way migration of the juveniles would benefit fish production, as in the case for temperate seabass juveniles shown in this chapter.

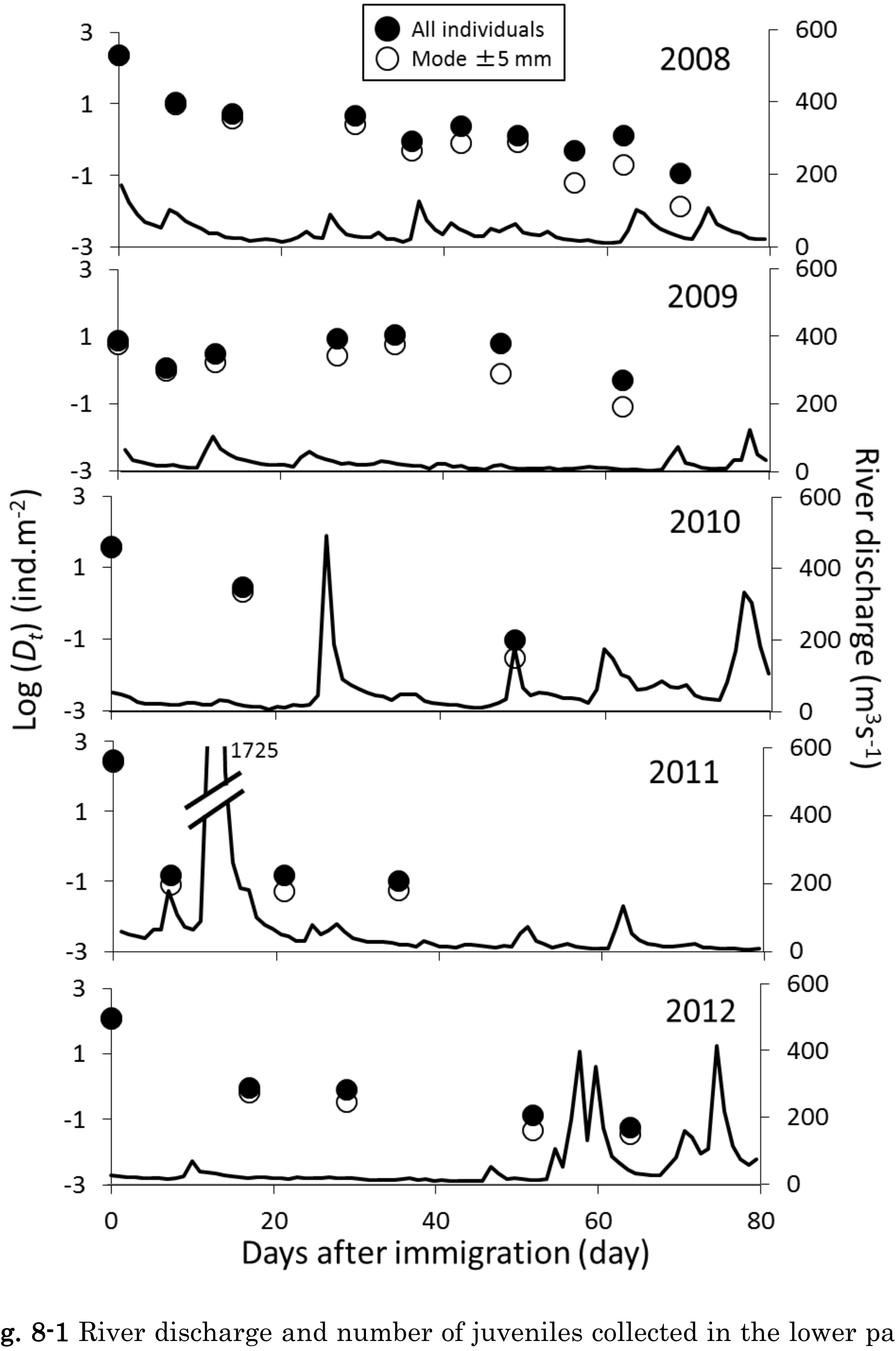

Fig. 8-1 River discharge and number of juveniles collected in the lower part of the Yura River. Lines indicate the river discharge and circles the numbers of juveniles.

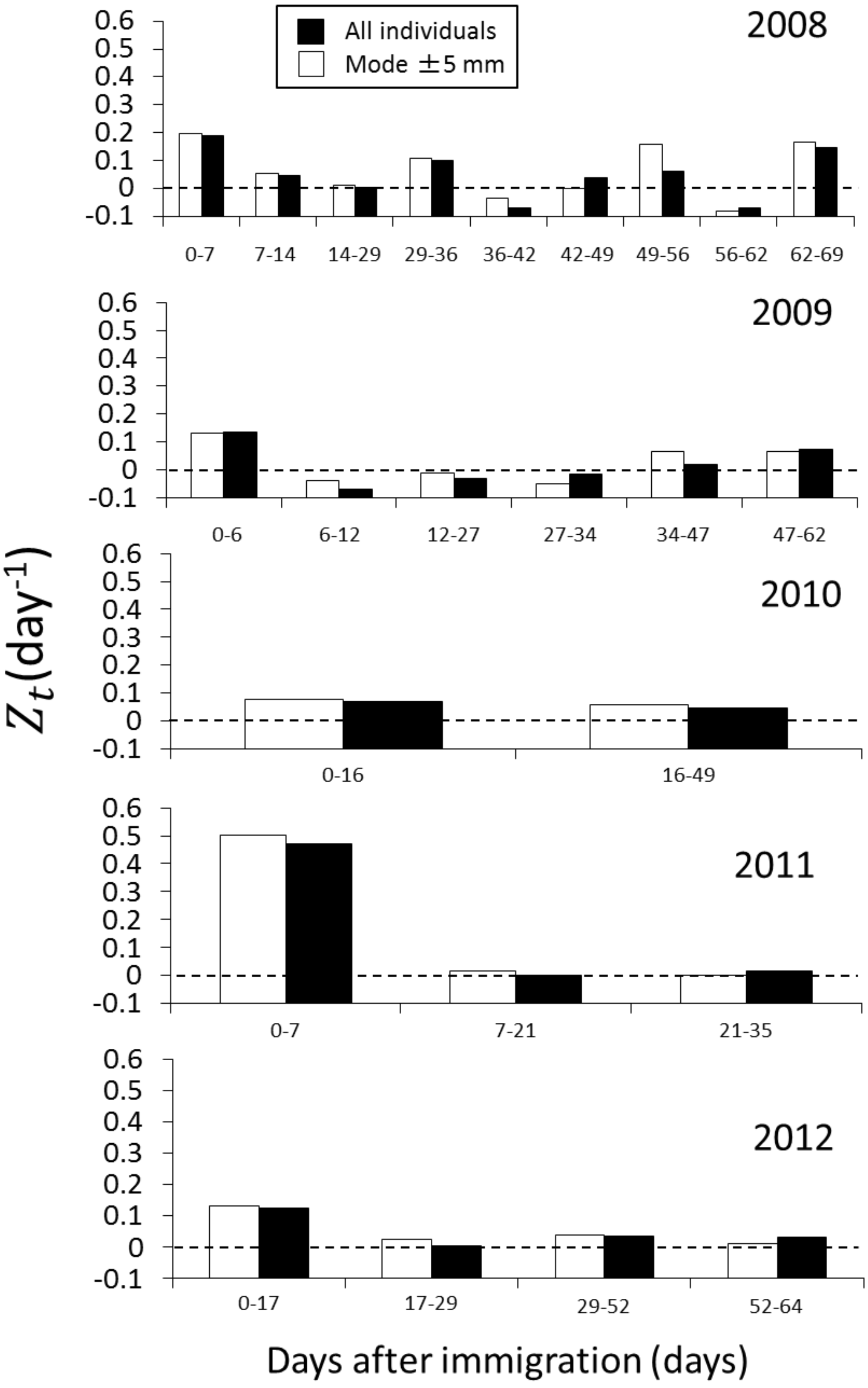

Fig. 8-2 Daily instantaneous mortalities of seabass juveniles in the Yura River.

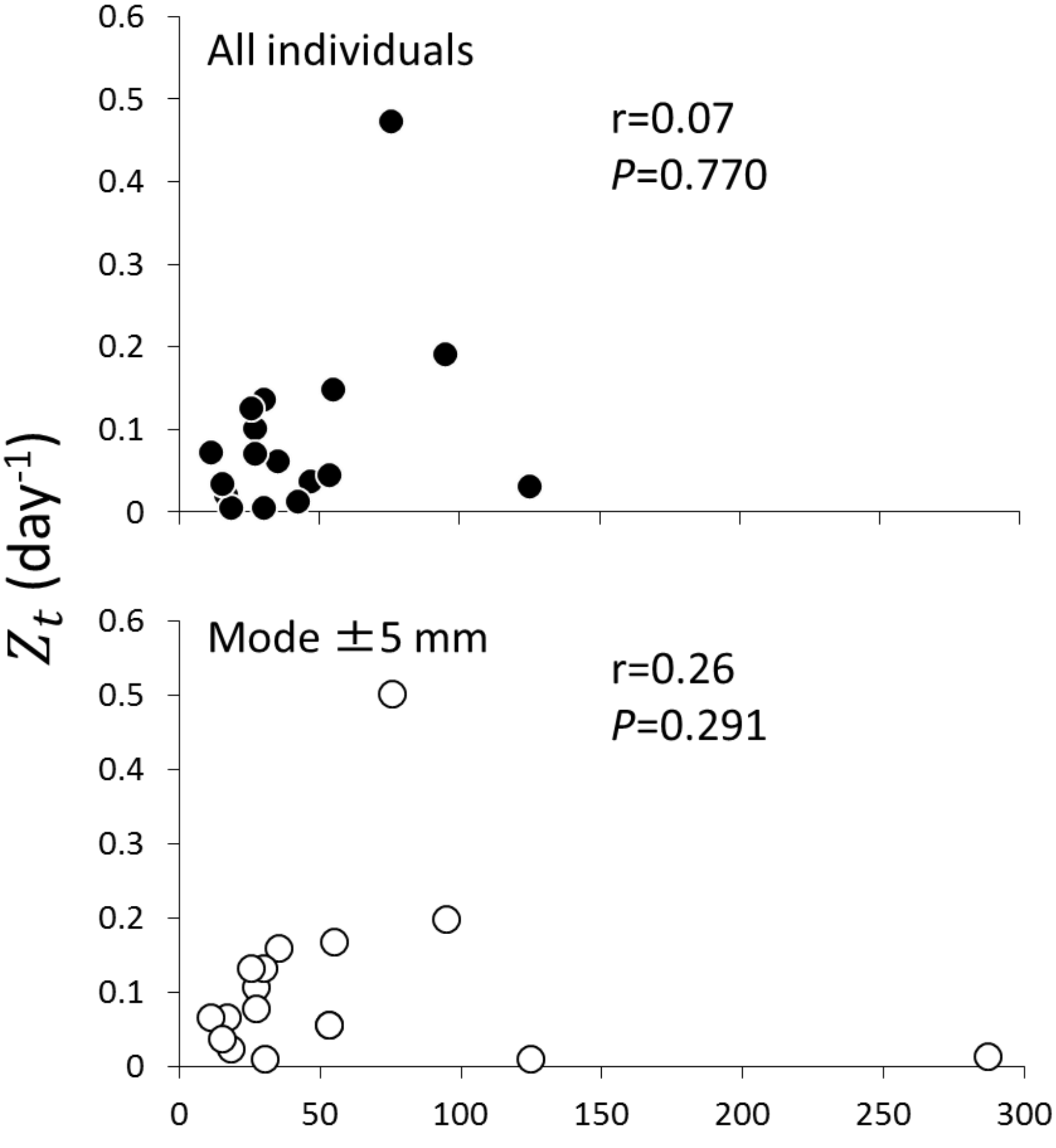

Fig. 8-3 Relationships between mean river discharge and daily mortality.

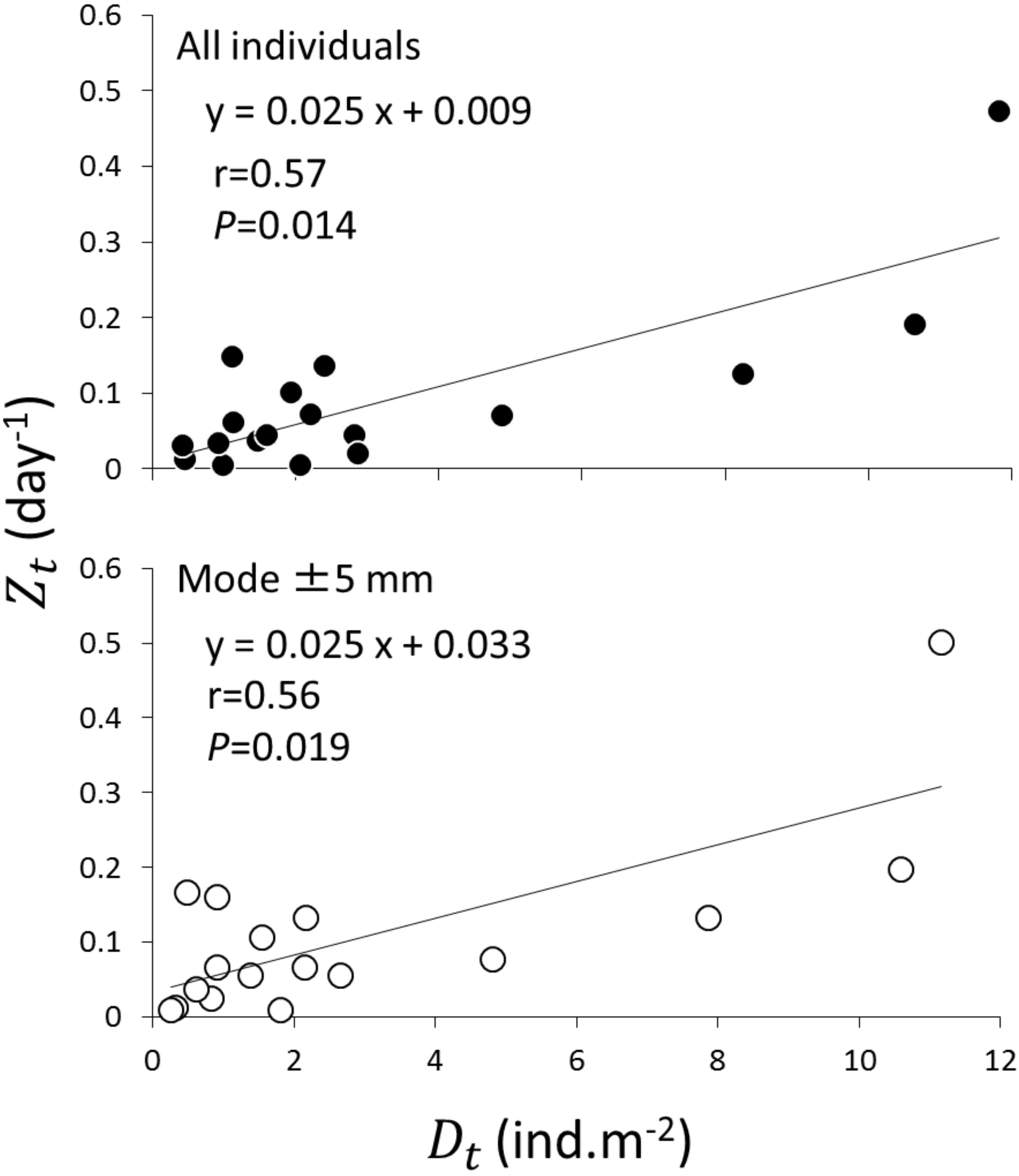

Fig. 8-4 Relationships between densities of seabass juveniles and mortalities in each sampling interval.

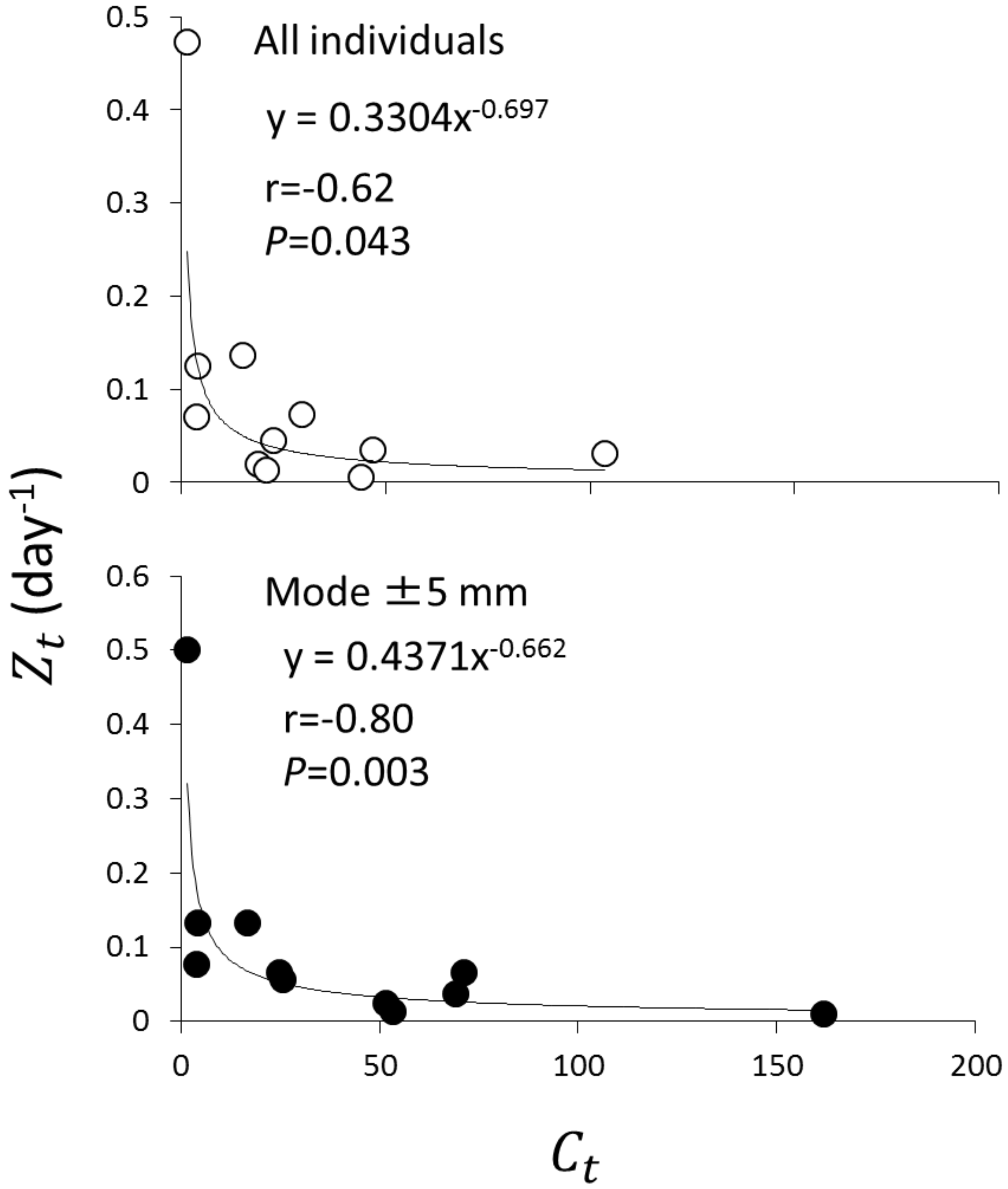

Fig. 8-5 Relationships between competition index (C_t) and daily mortality (Z_t) of seabass juveniles.

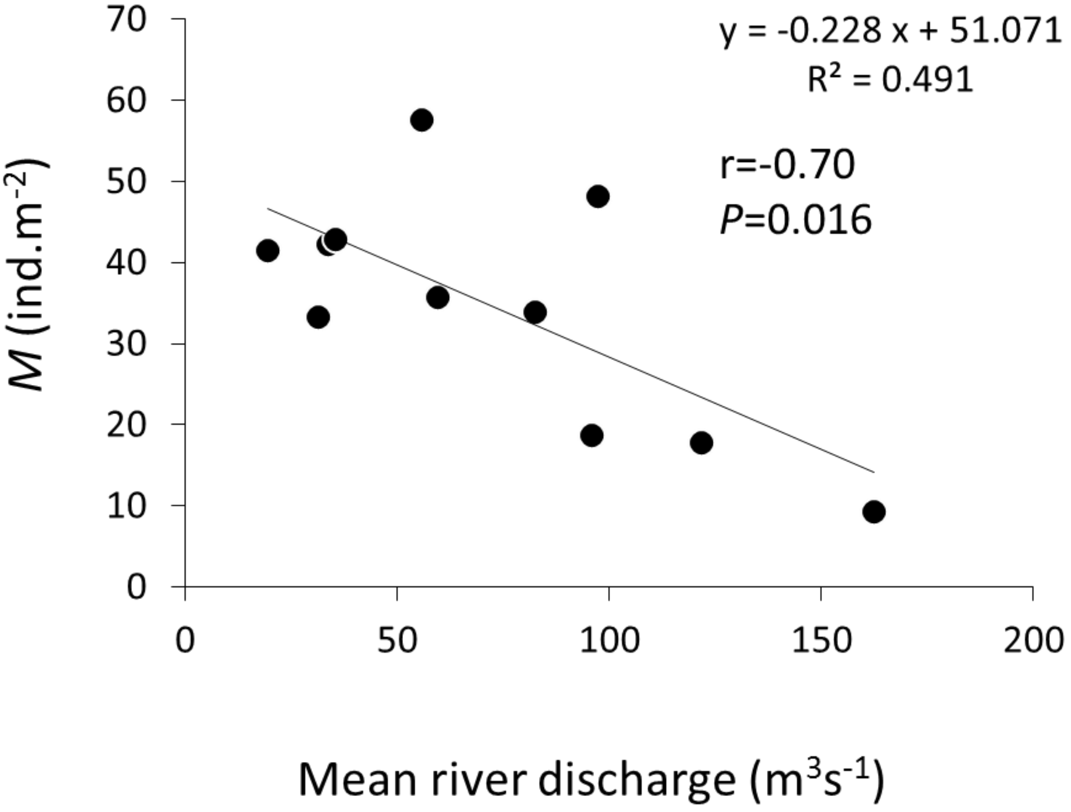

Fig. 8-6 Relationships between mean river discharge and mean mysid density (M) in the Yura River estuary.

Chapter 9

Relative contribution of the estuarine nursery areas to temperate seabass adult population in the Tango Sea revealed by otolith Sr:Ca ratio

Introduction

Many coastal fishes have several different nursery habitats. Density of individuals and vital rates (e.g. feeding condition, growth and survival) can vary substantially among habitats, but it is not always clear how different habitats compare with respect to the contributions to the dynamics of population abundance. The relative contribution of each nursery area to the adult population is essential to evaluate the nursery values (Beck et al., 2001). Especially, it is important to compare the nursery values on a unit-area basis because the conservation of habitats that contribute disproportionately to the production of adults is essential for stock management (Beck et al., 2001). This need is even more pressing if these habitats are relatively uncommon.

Much like tree-rings, the layered structure of otoliths can be used to retrospectively study the size and age of individual fish, and trace elements within the otolith layers are sometimes reflective of time spent in different habitats (Gillanders et al., 2003). Recently the otolith microchemistory analysis has been getting attention as a tool in providing information on environmental conditions juveniles experienced (Secor and Rooker, 2000; Gillanders et al., 2003). Many elements alone and/or combination of those elements have been used as fingerprints of the nursery origins of many fishes (Kraus and Secor, 2004a; Fodrie and Levin, 2008; Morais et al., 2011). Especially, the strontium:calcium ratio (Sr:Ca) in otoliths has been reported to be influenced by salinity and thus used as the natural tag for tracing diadromous migrations (Tsukamoto et al., 1998; Yamashita et al., 2000; Kraus and Secor, 2004a and b).

Secor et al. (1998) and Ohta (2004) studied possibility of otolith Sr:Ca as the natural tag for temperate seabass by culturing juveniles in various salinity conditions. Sr:Ca decreased significantly only in salinity lower than 5 (Ohta, 2004). Then he applied the experimental results to the adult seabass in the Ariake Bay to estimate the contribution of estuarine nursery areas to the adult population. However, the estuary with salinity higher than 5 occupied large parts in the Chikugo River estuary, so that the contribution of estuaries might be underestimated (Ohta, 2004). On the other hand, the Yura River estuary is classified into microtidal estuary and salinity in most part of shallow area where juveniles distributed is lower than 5 (Kasai et al., 2010; Chapter 3). This means that the environmental condition in the Yura River estuary allow us to evaluate the contribution of estuarine nursery habitats to the adult population of the temperate seabass using otolith Sr:Ca. The objective of this study is therefore to evaluate the contribution of the estuarine nursery to the spawning stock of temperate seabass in the Tango Sea.

Materials and methods

Juveniles

Juveniles were collected in the coastal area (station S1), estuarine area (station R3) and freshwater area (stations R4' and R6, Figure 9-1) on 6 June 2008, 19 May, 7 August 2009 and 28 August 2013 to determine the criterion of Sr:Ca to classify individuals by their nursery origins with different salinity conditions. Juveniles were collected by the seine net or gill net. Temperature and salinity were observed with an environmental monitoring system (YSI 556 MPS, YSI Inc., U.S.A.). The information of the juvenile analyzed and environmental condition is listed in Table 9-1.

The extracted otoliths (sagitta) were embedded in epoxy resin (Epofix, Struers) and ground to expose the core using a grinding machine equipped with a diamond cup-wheel (Discoplan-TS, Struers). They were further polished with OP-S liquid (Struers), cleaned using distilled water prior to examination. For electron microprobe analysis, otoliths were Pt-Pd coated by a high vacuum evaporator. Sr and Ca concentrations of each otolith were measured in a line along the longest axis of each otolith from the core to the anterior edge (Fig. 9-2) using a wavelength-dispersive X-ray electron microprobe analyzer (JXA-8230, JEOL) installed at the Atmosphere and Ocean Research Institute, The University of Tokyo. $CaTiO_3$ and $SrTiO_3$ were used as standards. The accelerating voltage and beam current were 15 kV and 12nA, respectively. The electron beam was focused on a point 10 μm in diameter, with measurements spaced at 10 μm intervals. The Sr:Ca ratio data were smoothed with the moving average method for five points. Juveniles immigrate to the Yura River estuary mainly at ca. 20 mm SL in April (Chapter 6). Given this migratory ecology, Sr:Ca ratio beyond 0.4 mm from the core, coinciding with larger than 20 mm SL (Ohta, 2004), was averaged for every juvenile sample. Standard deviations were calculated for each sampling area (coastal area, estuary, freshwater area). Mean value minus standard deviation of Sr:Ca ratio of the coastal area was used as the criteria to estimate the migration pattern of adult individuals.

Adults

Adults were collected by the set nets around the Tango Sea coastal areas (Fig. 9-1). Adult seabass was collected on 3 or 4 occasions in each of 2 consecutive years (28 January, 1, 3, 4 February 2011; and 11, 18 January, 14 February 2012). A similar period of sampling was chosen in each year to ensure that seabass was sampled in the spawning season (from January to February; Chapter 2 and Chapter 7). All adults were measured standard length (SL) and sexed. The scales and otoliths were removed for age determination and microchemistory analyses, respectively. Gonads were weighed and body weight was recorded. Examination of gonads confirmed that individuals in the collections were matured adults. The annuluses of scales were counted for each individual to estimate the age (Hatanaka and

Sekino, 1962c; Kimura, 1995). For the otolith microprobe assay, individuals were randomly subsampled from our collections (2011: n = 53; 2012: n = 54). Specimens of adult otoliths were prepared following the aforementioned methods. The analysis was focused on the otolith area within 3 mm from the core which coincides with the young-of-year period (Ohta, 2004). The Sr:Ca ratio data were smoothed with the moving average method for five points.

Individuals with Sr:Ca ratio values lower than the criteria value more than 10 points continuously (coincide with ca. 2 weeks; Ohta 2004) were considered to enter the low salinity area of the estuary. Juveniles immigrated into the Yura River estuary mainly with size ranged from 18 to 30 mm SL (Chapter 6). On the other hand, juveniles larger than 30 mm SL also migrated to the estuary incidentally (Chapter 6). These two migration patterns were considered to have different ecological meanings. It is considered that juveniles immigrate into estuaries at the size of smaller than 30 mm to use estuaries as the nursery area (Islam et al., 2011). On the other hand, juveniles migrated with larger size are considered to migrate opportunistically (Chapter 6). Then individuals which showed decreasing Sr:Ca ratio within and beyond 1 mm from the otolith core (coincide with 30 mm SL; Ohta, 2004) were classified into the "river migrant group" and "late river migrant group", respectively. Individuals showing steadily higher Sr:Ca ratios than the criteria were categorized into "coastal resident group".

Results

Juveniles

Salinity was 29.9 and 0.7 at S1 and R3 respectively on 6 June 2008, 0.4 at R3 on 19 May, and 0.0 at freshwater station on 7 August 2009 and 28 August, respectively (Table 9-1). The size of analyzed juveniles ranged from 20.8 to 99.6 mm SL (Table 9-1). The Sr:Ca ratio chronologies of juveniles were different among areas (Figs. 9-3, 9-4 and 9-5). Most of juveniles collected in the coastal area showed steady Sr:Ca ratios with high values of ca. 5.0 × 10^{-3} or over (Fig. 9-3). On the other hand, Sr:Ca of juveniles in the estuarine area decreased from ca. 0.4 mm from the core of otolith, coinciding with 20 mm SL of juveniles (Ohta, 2004; Fig. 9-4). The minimum of Sr:Ca ratios ranged from 1.9 × 10^{-3} to 3.9 × 10^{-3}. Juveniles collected in the freshwater area showed the lowest Sr:Ca ratios ranged from 0.6 × 10^{-3} to 2.5 × 10^{-3} (Fig. 9-5). The mean value of Sr:Ca ratios showed significant differences among the areas (ANOVA followed by Tukey's test, $P \leq 0.05$, Fig. 9-6). Mean Sr:Ca ratio values were 4.9 × 10^{-3}, 4.0 × 10^{-3} and 2.4 × 10^{-3} in the coastal area, estuarine area and freshwater areas, respectively. Mean minus standard deviation of Sr:Ca ratio of coastal area was 4.4 × 10^{-3}. In this study, this value was used as the criterion in the following analyses, to estimate the juvenile stayed in the freshwater area. 13 of 14 juveniles caught in the estuarine and freshwater area were categorized as river migrant group or late river migrant group and 7 of 8 juveniles collected in lower estuary were categorized as coastal resident group.

Adults

Size of adults collected during 2 years distributed between 264 and 715 mm SL (Fig. 9-7, Table 9-2). Age composition in 2 years ranged from 2 to 12 years (Fig. 9-7, Table 9-2).

Otolith Sr:Ca ratio profiles showed various pattern. Individuals were classified into three groups according to the criterion (Figs. 9-8, 9-9 and 9-10). 53, 39 and 15 of 107 individuals were classified into the coastal resident group, river migrant group and later river migrant group, respectively (Figs. 9-8, 9-9 and 9-10). River migrant group contributed 42 % and 31 % of spawning adult population in 2011 and 2012, respectively. In total, 36 % of spawning adult in the Tango Sea utilized the estuary as a nursery area during their juvenile stage. Fifty one % of individuals entered the river during the first year of their life (the composition of individuals of the river migrant group and the later river migrant group).

Smaller and young adults tended to comprise largely of coastal resident group (Figs. 9-11 and 9-12). The composition of the river migrant group increased in larger and older adults (Figs. 9-11 and 9-12). Contributions of river migrant group were higher in older cohort than younger cohorts both in 2011 and 2012 (Figs. 9-11 and 9-12). Contributions of the river migrant group varied between 27 to 100 % among age classes of more than five individuals (Fig. 9-12).

Discussion

The juvenile otolith Sr:Ca ratios showed the significant difference among the habitats with different salinity (Figs. 9-3, 9-4, 9-5 and 9-6). Classification of juveniles according to the criterion almost coincided with the sampling areas they collected. This supports the validity of this method to classify adults into three migration groups. Most of adults showed typical 3 patterns of Sr:Ca ratio chronologies. However, a few juveniles and adults showed complex Sr:Ca ratio patterns (Figs. 9-3, 9-4, 9-5, 9-8, 9-9 and 9-10). Some individuals were considered to migrate back and forth between higher and lower salinity area during their juvenile stage (e.g., individual code NA-5 in Fig. 9-9). However, no juveniles migrating back and forth between the coastal area and the Yura River estuary within a few weeks were observed in Chapter 6. The Yura River estuary is characterized by salt-wedge intrusion (Kasai et al., 2010). Therefore, even though salinity was low in the shallow edge of the river, where juveniles were collected, deeper area near the river center could be occupied by salt water (Kasai et al., 2010). This means juvenile could experience various salinity conditions even through their continuous residence in the estuary.

This study found ca. 36 % of the seabass spawning adults utilized estuaries as nursery area. This value was higher than the value reported in the Ariake Bay (ca. 20 %; Ohta, 2004). One of the possible reasons of the apparent difference comes from the difference in the salinity distribution between these two estuaries. Sr:Ca ratios of temperate seabass decreases significantly only under salinity condition lower than 5 (Ohta, 2004). The Chikugo River estuary is classified into macrotidal estuary and occupied by broad brackish area (Suzuki, 2010). Juveniles distributed widely in the estuary and a part of them resided in brackish area with salinity higher than 5 (Matsumiya et al., 1982; Suzuki et al., 2008a). On the other hand, the Yura River estuary is categorized into microtidal estuary and salinity in the shallow area of most of estuarine area is lower than 5 (Kasai et al., 2010; Chapter 3). Juveniles distributed in the shallow area of the estuary and most of them are considered to be exposed to lower salinity or freshwater environment (Chapter 3).

The contributions of each nursery area would be mainly determined by two factors; the productivity and the vastness of nurseries. The nursery value is defined as the production of adults from each juvenile habitat on a per area basis (Beck et al., 2001; Kraus and Secor, 2005). The vastness of nursery areas is estimated to calculate the nursery values for temperate seabass in the Tango Sea. The stock structure of the temperate seabass in the Sea of Japan is unknown. Ishido et al. (1982) reported that adult seabass sometimes moves more than 300 km. Therefore, the whole western part of the Sea of Japan was included to estimate the area of two types of nurseries (Fig. 9-13). Juvenile temperate seabass utilizes various types of shallow coastal areas, e.g., sandy beach (Chapter 3), tidal flats (Hibino et al., 2002), seagrass and eelgrass beds (Hatanaka and Sekino, 1962a; Fujita et al., 1988) as nurseries (Chapter 3). Vertical precipitous rocky shores and protected shores would not be nurseries for temperate seabass (Kusakabe et al., 1994). According to this information, coastal habitat size is estimated by using shoreline distance of natural coasts as an index of habitat size (Fig. 9-13). The shoreline distance of the natural sandy coasts of western part of the Sea of Japan was derived from Nature Conservation Bureau, Environment Agency and Marine Parks Center of Japan (1998). The total shoreline of these potential coastal habitats was found to be 1163 km. On the other hand, the estuarine nursery area would be defined by the distance of saltwedge intrusion (Chapter 5). Small and shallow rivers were neglected in this study, because no saltwedge would intrude into the rivers. Given this, the first class rivers are considered to be the main estuarine nurseries for juvenile temperate seabass (Fig. 9-13). The information about the distances of the saltwedge intrusion in each first-class river within this area was obtained from Ministry of Land, Infrastructure, Transport and Tourism. Given the information, the estuarine area is considered to be 181 km (Fig. 9-13). Then the contributions of each nursery area per unit coastal line (nursery value) were calculated as 0.06 % km^{-1} and 0.20 % km^{-1} in coastal and estuarine habitats, respectively. This estimation indicates that juvenile production per unit habitat area was considerably higher in the estuary than in the marine habitats. This high productivity of estuaries would be supported by its higher prey density and fewer predators (Chapter 5, Yamashita et al., 2000). Some studies on the flatfishes also reported high contribution of estuaries regardless of its narrow area than the others (Yamashita et al., 2000; Brown, 2006). This high nursery value also means that the impact of exploitation of estuaries would be considerably severe for temperate seabass.

Contributions of estuarine nurseries in each year class would be affected by two factors: annual variation of juvenile recruitments into estuaries and adult mortalities after recruitments. Azeta (1986) reported that red seabream *Pagrus major* juveniles of dominant year class utilize wider and various habitats than cohorts of lower recruitment level. Kraus and Secor (2004a and 2005) also reported that abundant annual cohorts showed different pattern of the nursery usage from minor annual cohorts. Difference in the distribution pattern of juvenile temperate seabass between dominant cohort and the other cohort is unknown. Long term monitoring for distribution pattern of juveniles is necessary to confirm this possibility. On the other hand, the adult mortality of the river migrant group might be lower than coastal resident group. The migration patterns in the adult stage would affect the adult mortality caused by fishing activities or some other reasons, e.g., ill or parasites. It is well known that a part of adult temperate seabass also migrate to rivers and others reside in the coastal areas during summer season (Shoji et al., 2002). If juveniles migrated into estuaries come back again to estuaries during the adult stage, their nursery habitat usage pattern could be linked to their adult mortalities. Yamazaki (2000) and Komatsu and Yamazaki (2006) released temperate seabass juveniles marked by the alizarin complexone in the blackish Hinuma Lake and re-catch after one or two years in the same lake. This means that many individuals of river migratory group again entered the lower salinity areas in the adult stage. The migration patterns in the early life history control adult migration pattern in white perch and Japanese eel (Kraus and Secor, 2004a; Yokouchi et al., 2012). Generally speaking, most of fishing activities on temperate seabass are conducted in the coastal area and seabass would be able to escape from the fishing activities when they migrate into rivers (Shoji et al., 2002). Otsuka et al. (2007) found that the intensity of parasitic copepods on temperate seabass decreases during summer in the Ariake Bay. They considered that freshwater migration of adults would kill the parasites. These reports imply that the river migrant group might have longer life span than the coastal resident group. In general, larger and older individuals would have many eggs per individual (Kurita, 2010). Larger adults often have larger eggs, leading to larger sizes and high survival of larvae (Kurita, 2010). These characteristics would lead to important unique role of larger and older individuals in the population dynamics (Kurita, 2010). Study on the relationship between the juvenile migratory strategy and adult migration pattern of temperate seabass is necessary to confirm this hypothesis.

Table 9-1 Environmental condition and size of juveniles in each sampling area

	Date	Station	Temperature	Salinity	n	SL range (mm)	Mean SL ± SD (mm)
Coastal area	6 June 2008	S1	19.2	29.9	8	36.6–50.6	42.2±5.7
Estuary	6 June 2008	R3	19.5	0.7	3	28.3–40.8	33.2±6.7
	19 May 2009	R3	19.8	0.4	5	20.8–45.0	31.9±8.2
Freshwater	10 July 2008	R4’	24.8	0.0	1	79.0	
	28 August 2013	R4’	25.8	0.0	1	67.4	
	7 August 2009	R6	23.8	0.0	4	74.8–99.6	90.0±11.9

SL: standard length, SD: standard deviation

Table 9-2 Information of adult samples

Code	Sampling Date	Sampling site	SL (mm)	BW (g)	Age (year)	Birth year	Sex	Migration pattern
AR-1	1 Feb. 2011	Araizaki	558	1961	7	2004	♀	R
AR-2	1 Feb. 2011	Araizaki	648	3264	7	2004	♀	R
AR-3	1 Feb. 2011	Araizaki	527	1899	9	2002	♂	L
AR-4	1 Feb. 2011	Araizaki	622	2929	8	2003	♀	L
IN-1	28 Jan. 2011	Ine	648	3450	8	2003	♀	C
IN-2	18 Jan. 2012	Ine	425	891	4	2008	♂	R
IN-3	18 Jan. 2012	Ine	433	920	4	2008	♀	C
IN-4	18 Jan. 2012	Ine	397	707	3	2009	♀	C
IN-5	18 Jan. 2012	Ine	415	842	3	2009	♀	C
IN-6	18 Jan. 2012	Ine	388	605	3	2009	♂	C
IN-7	18 Jan. 2012	Ine	375	650	3	2009	♂	R
IN-8	18 Jan. 2012	Ine	422	790	5	2007	♀	C
IN-9	18 Jan. 2012	Ine	415	800	4	2008	♂	C
NA-1	28 Jan. 2011	Naryu	490	1210	5	2006	♀	C
NA-2	28 Jan. 2011	Naryu	394	690	3	2008	♀	R
NA-3	28 Jan. 2011	Naryu	367	625	2	2009	♀	R
NA-4	28 Jan. 2011	Naryu	406	813	4	2007	♀	C
NA-5	28 Jan. 2011	Naryu	616	3150	7	2004	♀	R
NA-6	28 Jan. 2011	Naryu	510	1520	7	2004	♀	R
NA-7	28 Jan. 2011	Naryu	476	1450	5	2006	♀	C
NA-8	28 Jan. 2011	Naryu	458	1330	4	2007	♀	C
NA-9	28 Jan. 2011	Naryu	452	930	5	2006	♀	C
NA-10	28 Jan. 2011	Naryu	475	1270	4	2007	♀	L
NA-11	28 Jan. 2011	Naryu	429	890	4	2007	♀	R
NA-12	28 Jan. 2011	Naryu	404	760	3	2008	♀	C
NA-13	28 Jan. 2011	Naryu	377	670	3	2008	♀	C
NA-14	28 Jan. 2011	Naryu	438	950	4	2007	♀	C
NA-15	28 Jan. 2011	Naryu	562	1855	5	2006	♀	R
NA-16	4 Feb. 2011	Naryu	434	1082	5	2006	♀	L
NA-17	4 Feb. 2011	Naryu	405	1005	6	2005	♀	R
NA-18	4 Feb. 2011	Naryu	433	1010	4	2007	♂	R
NA-19	4 Feb. 2011	Naryu	439	1230	3	2008	♀	C
NA-20	4 Feb. 2011	Naryu	398	750	3	2008	♂	C
NA-21	4 Feb. 2011	Naryu	473	1355	6	2005	♀	R
NA-22	4 Feb. 2011	Naryu	528	1580	8	2003	♂	R
NA-23	4 Feb. 2011	Naryu	590	2385	11	2000	♀	R
NA-24	4 Feb. 2011	Naryu	494	1592	5	2006	♀	C
NA-25	18 Jun. 2012	Naryu	506	1755	6	2006	♀	C
NA-26	18 Jun. 2012	Naryu	467	1193	5	2007	♀	R
NA-27	18 Jun. 2012	Naryu	425	1131	4	2008	♀	C
NA-28	14 Feb. 2012	Naryu	521	1419	5	2007	♀	C
NA-29	14 Feb. 2012	Naryu	525	1461	5	2007	♀	C
NA-30	14 Feb. 2012	Naryu	511	1532	4	2008	♀	C
NO-1	14 Feb. 2012	Nohara	478	935	3	2009	♂	L
NO-2	14 Feb. 2012	Nohara	432	925	4	2008	♀	C
NO-3	14 Feb. 2012	Nohara	420	420	4	2008	♀	R
NO-4	14 Feb. 2012	Nohara	501	501	4	2008	♀	R
NO-5	14 Feb. 2012	Nohara	530	530	6	2006	♀	C
SA-1	1 Feb. 2011	Sabaka	264	355	2	2009	?	C
SA-2	1 Feb. 2011	Sabaka	322	460	3	2008	♂	C
SA-3	1 Feb. 2011	Sabaka	373	750	3	2008	♀	C
SA-4	1 Feb. 2011	Sabaka	423	1162	4	2007	♀	C

Migration pattern C: coastal migrant group, R: river migrant group, L: late river migrant group SL:standard length BW: body weight

Table 9-2 Continued

Code	Sampling Date	Sampling site	*SL* (mm)	*BW* (g)	Age (year)	Birth year	Sex	Migration pattern
SE-1	4 Feb. 2011	Sezaki	480	1422	5	2006	♀	C
SE-2	4 Feb. 2011	Sezaki	466	1150	4	2007	♀	L
SE-3	4 Feb. 2011	Sezaki	470	1380	4	2007	♀	L
SE-4	4 Feb. 2011	Sezaki	496	1440	6	2005	♀	L
SE-5	18 Jan. 2012	Sezaki	472	1328	3	2009	♀	C
SE-6	18 Jan. 2012	Sezaki	462	1348	6	2006	♀	C
SE-7	18 Jan. 2012	Sezaki	494	1492	6	2006	♀	R
SE-8	18 Jan. 2012	Sezaki	417	1090	4	2008	♀	C
SE-9	18 Jan. 2012	Sezaki	430	1040	4	2008	♀	L
SE-10	18 Jan. 2012	Sezaki	473	1142	6	2006	♀	R
SE-11	18 Jan. 2012	Sezaki	482	1170	4	2008	♀	R
SE-12	18 Jan. 2012	Sezaki	383	762	2	2010	♀	L
SE-13	18 Jan. 2012	Sezaki	350	545	4	2008	♂	L
SE-14	18 Jan. 2012	Sezaki	379	763	2	2010	♀	C
TA-1	3 Feb. 2011	Tai	488	1410	5	2006	♀	R
TA-2	3 Feb. 2011	Tai	500	1565	7	2004	♀	R
TA-3	3 Feb. 2011	Tai	344	717	3	2008	♀	R
TA-4	3 Feb. 2011	Tai	339	602	3	2008	♂	C
TA-5	3 Feb. 2011	Tai	386	712	3	2008	♂	C
TA-6	3 Feb. 2011	Tai	398	900	4	2007	♀	C
TA-7	3 Feb. 2011	Tai	452	1010	5	2006	♂	L
TA-8	3 Feb. 2011	Tai	440	1230	4	2007	♀	C
TA-9	3 Feb. 2011	Tai	376	873	2	2009	♀	R
TA-10	3 Feb. 2011	Tai	584	2448	7	2004	♀	R
TA-11	3 Feb. 2011	Tai	495	1623	6	2005	♀	C
TA-12	3 Feb. 2011	Tai	473	1427	5	2006	♀	R
TA-13	3 Feb. 2011	Tai	523	1700	4	2007	♀	R
TA-14	3 Feb. 2011	Tai	494	1710	5	2006	♂	C
TA-15	3 Feb. 2011	Tai	542	2060	5	2006	♀	R
TA-16	3 Feb. 2011	Tai	428	1110	3	2008	♀	R
TA-17	11 Jan. 2012	Tai	577	2870	4	2008	♀	C
TA-18	11 Jan. 2012	Tai	683	3940	5	2007	♀	L
TA-19	11 Jan. 2012	Tai	584	2340	4	2008	♀	C
TA-20	11 Jan. 2012	Tai	667	4530	12	2000	♀	R
TA-21	11 Jan. 2012	Tai	520	1595	4	2008	♀	C
TA-22	11 Jan. 2012	Tai	530	1925	5	2007	♀	L
TA-23	11 Jan. 2012	Tai	715	4490	7	2005	♀	R
TA-24	11 Jan. 2012	Tai	537	1980	6	2006	♀	C
TA-25	11 Jan. 2012	Tai	395	795	3	2009	♀	C
TA-26	11 Jan. 2012	Tai	526	1950	4	2008	♀	C
TA-27	11 Jan. 2012	Tai	465	1260	4	2008	♀	R
TA-28	11 Jan. 2012	Tai	415	1040	3	2009	♀	C
TA-29	11 Jan. 2012	Tai	380	775	3	2009	♀	R
TA-30	11 Jan. 2012	Tai	465	1365	4	2008	♀	C
TA-31	11 Jan. 2012	Tai	385	778	3	2009	♀	C
TA-32	11 Jan. 2012	Tai	437	960	3	2009	♀	R
TA-33	11 Jan. 2012	Tai	456	1130	4	2008	♀	R
TA-34	11 Jan. 2012	Tai	457	1125	4	2008	♀	C
TA-35	11 Jan. 2012	Tai	433	1170	5	2007	♀	R
TA-36	11 Jan. 2012	Tai	385	745	3	2009	♀	R
TA-37	11 Jan. 2012	Tai	414	980	4	2008	♂	C
TA-38	11 Jan. 2012	Tai	533	2068	6	2006	♀	R
YO-1	11 Jan. 2012	Yoro	423	960	4	2008	♀	L
YO-2	11 Jan. 2012	Yoro	423	960	3	2009	♂	C
YO-3	11 Jan. 2012	Yoro	408	935	4	2008	♀	C

Migration pattern C: coastal migrant group, R: river migrant group, L: late river migrant group SL:standard length BW: body weight

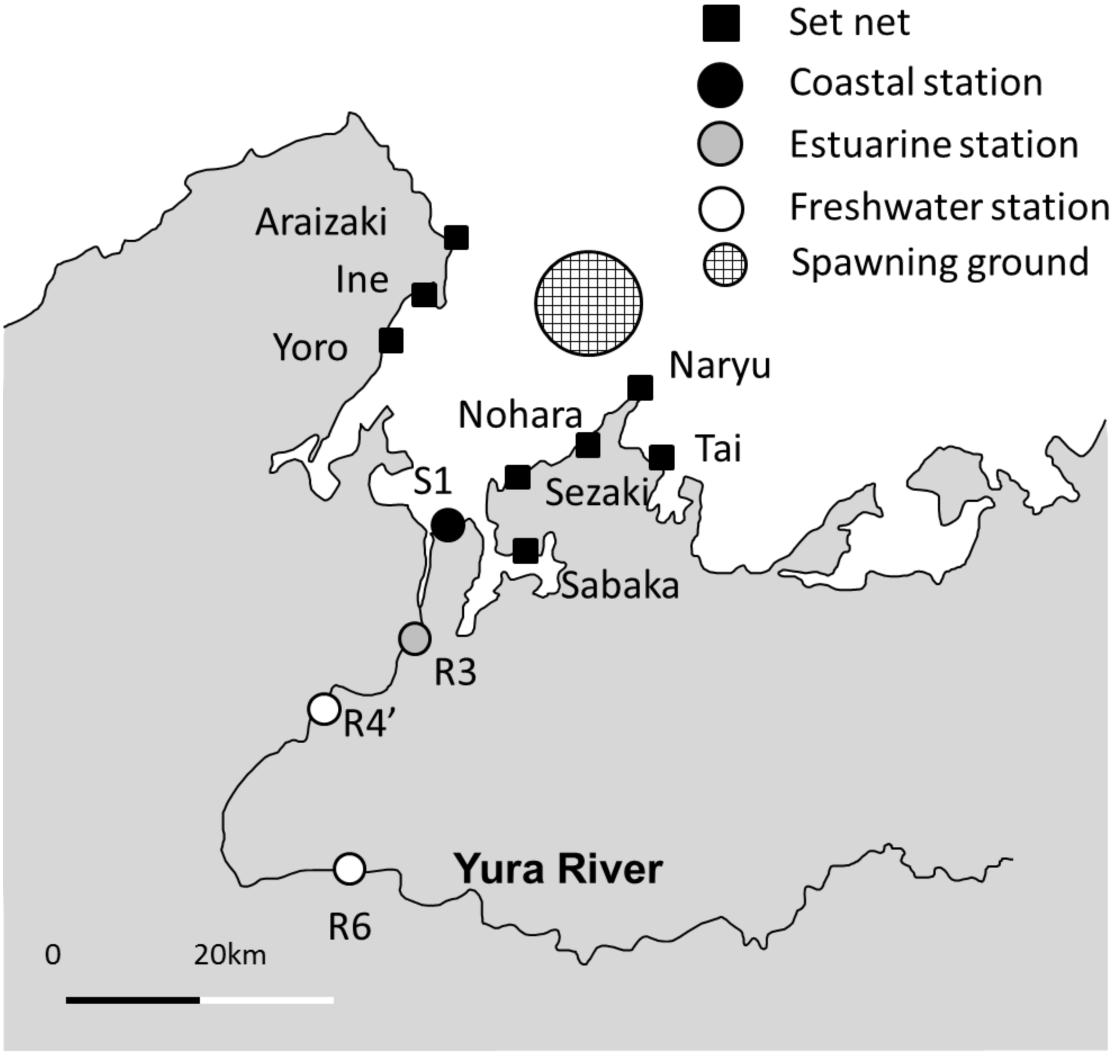

Fig. 9-1 Location of sampling stations.

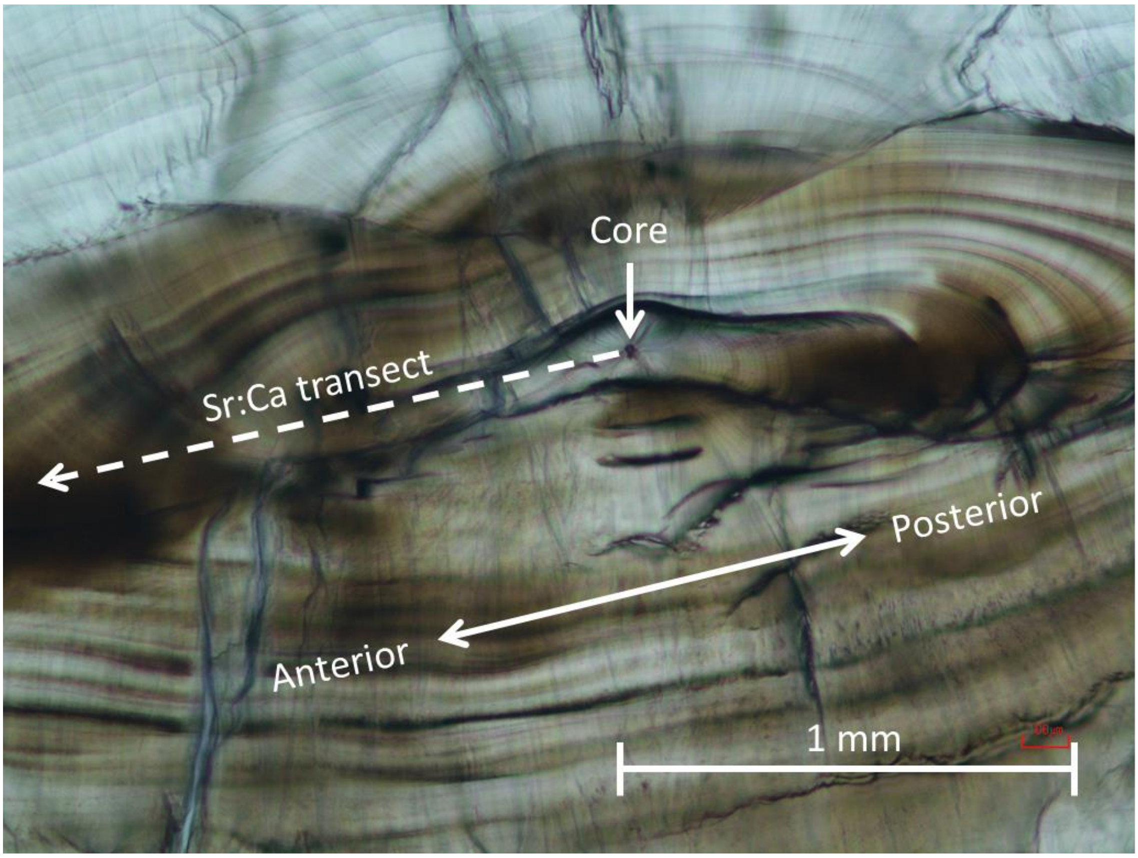

Fig. 9-2 Representative image of a transverse section for a temperate seabass otolith. Sr:Ca measurements were conducted ca. 3 mm from the core along the anterior direction.

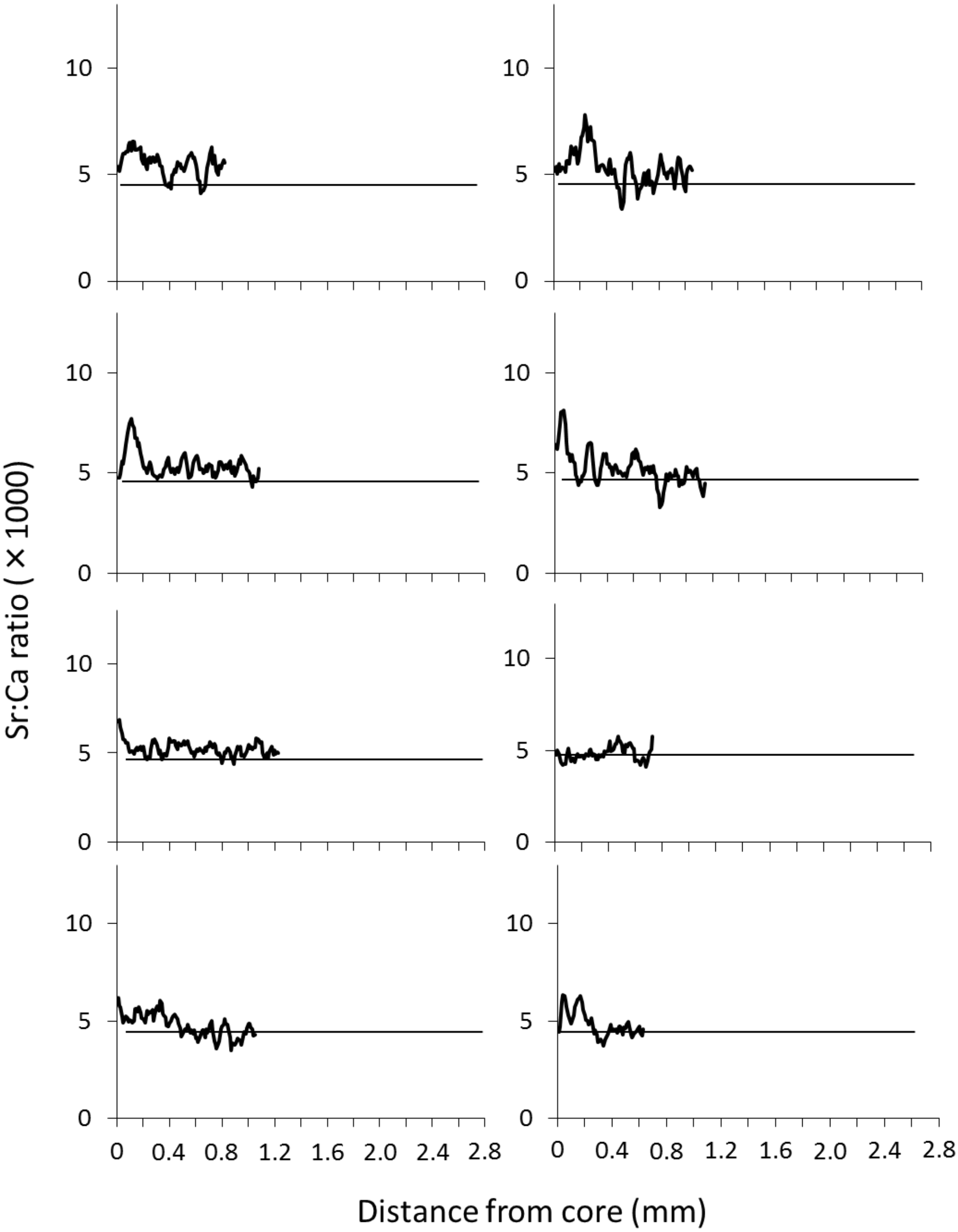

Fig. 9-3 Sr:Ca ratios of juveniles collected in the coastal station (S1). Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

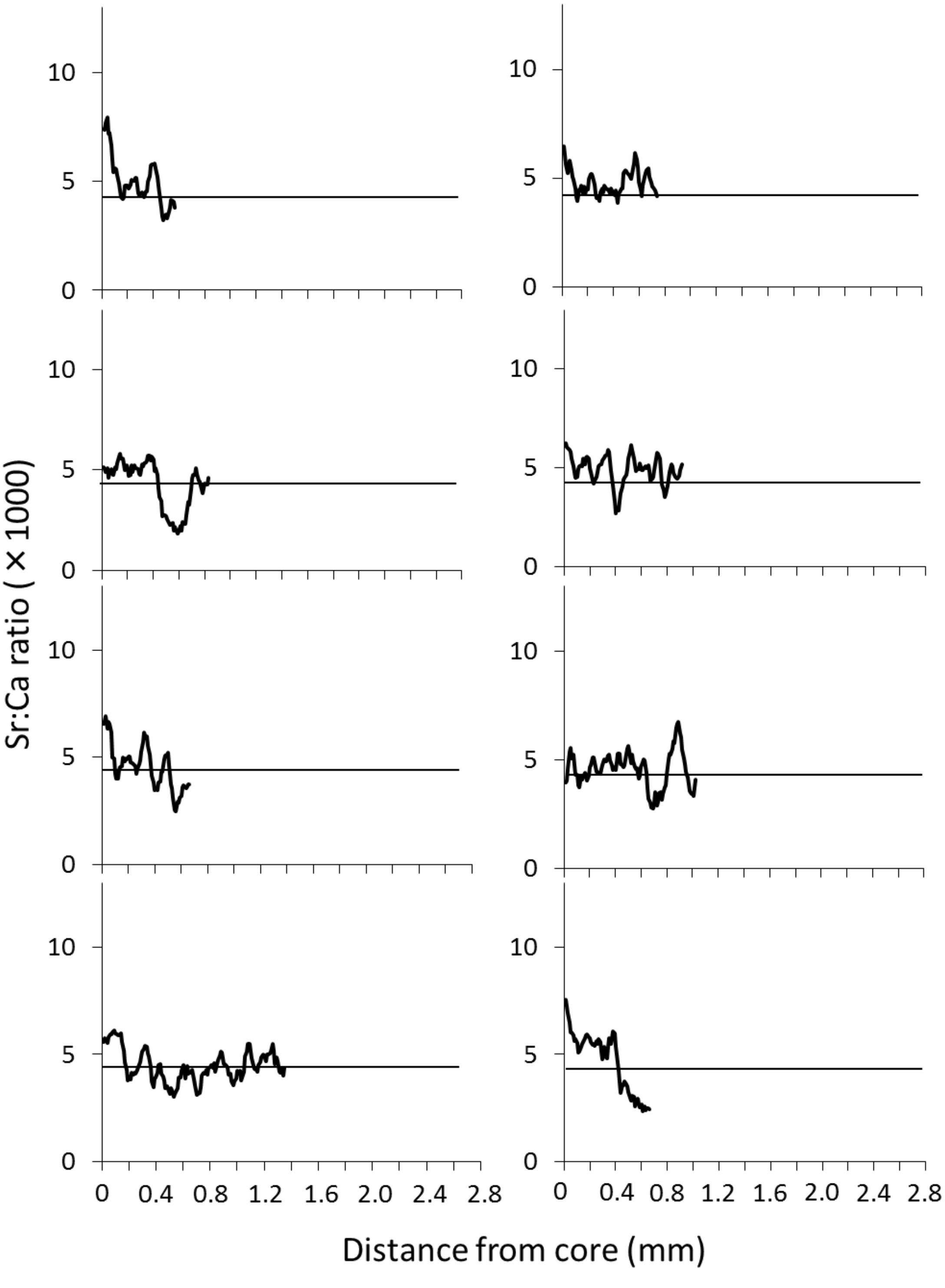

Fig. 9-4 Sr:Ca ratios of juveniles collected at the estuarine station (R3). Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

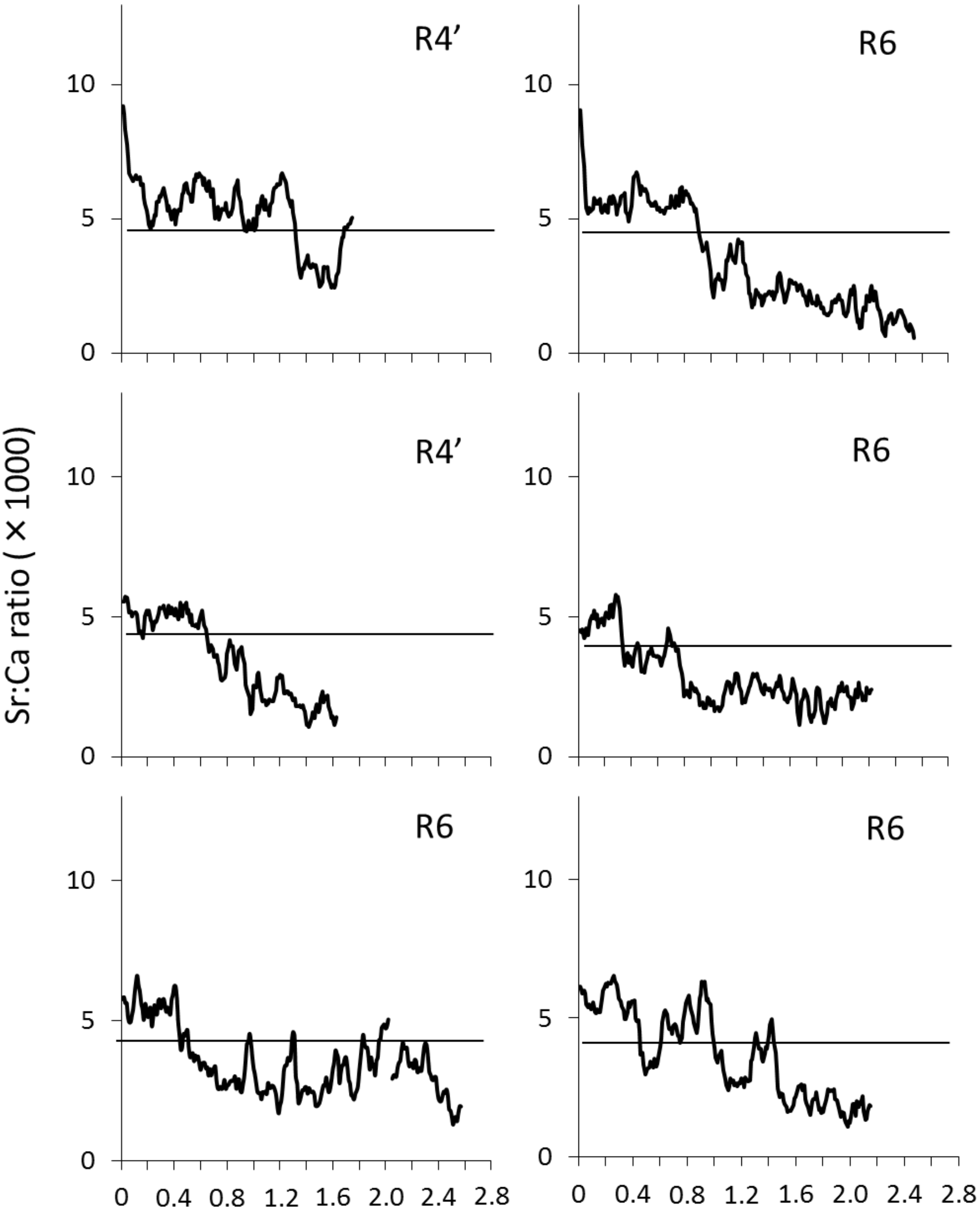

Fig. 9-5 Sr:Ca ratios of juveniles collected in the freshwater stations (R4’ and R6). Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

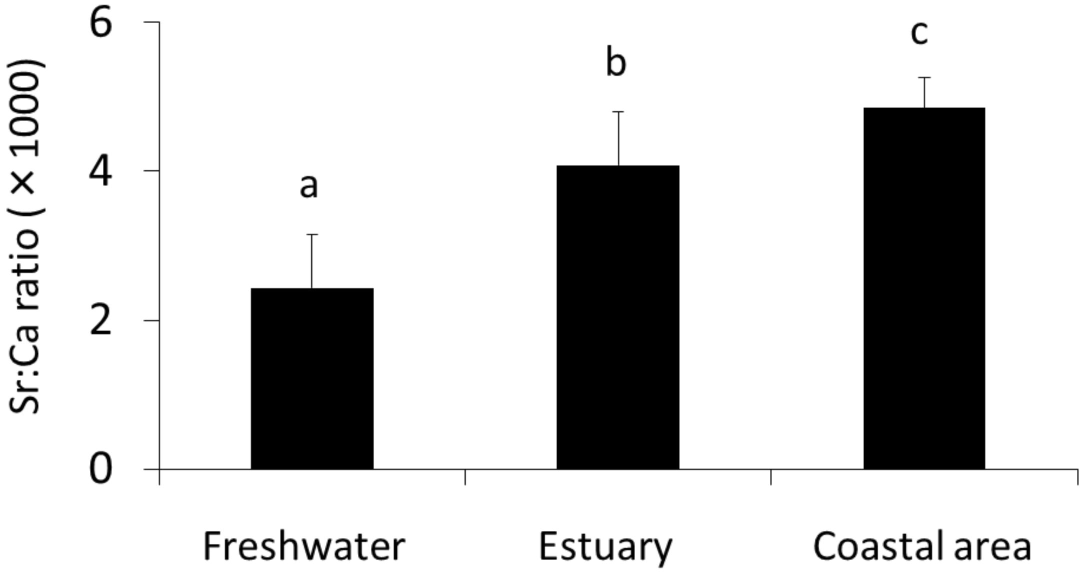

Fig. 9-6 Mean Sr:Ca ratios at the edge of the otolith of juveniles collected in each area. Vertical bars mean the standard deviations. Different superscripts on the top of the bars indicate significant difference (ANOVA followed by Tukey's test, $P \leq 0.01$).

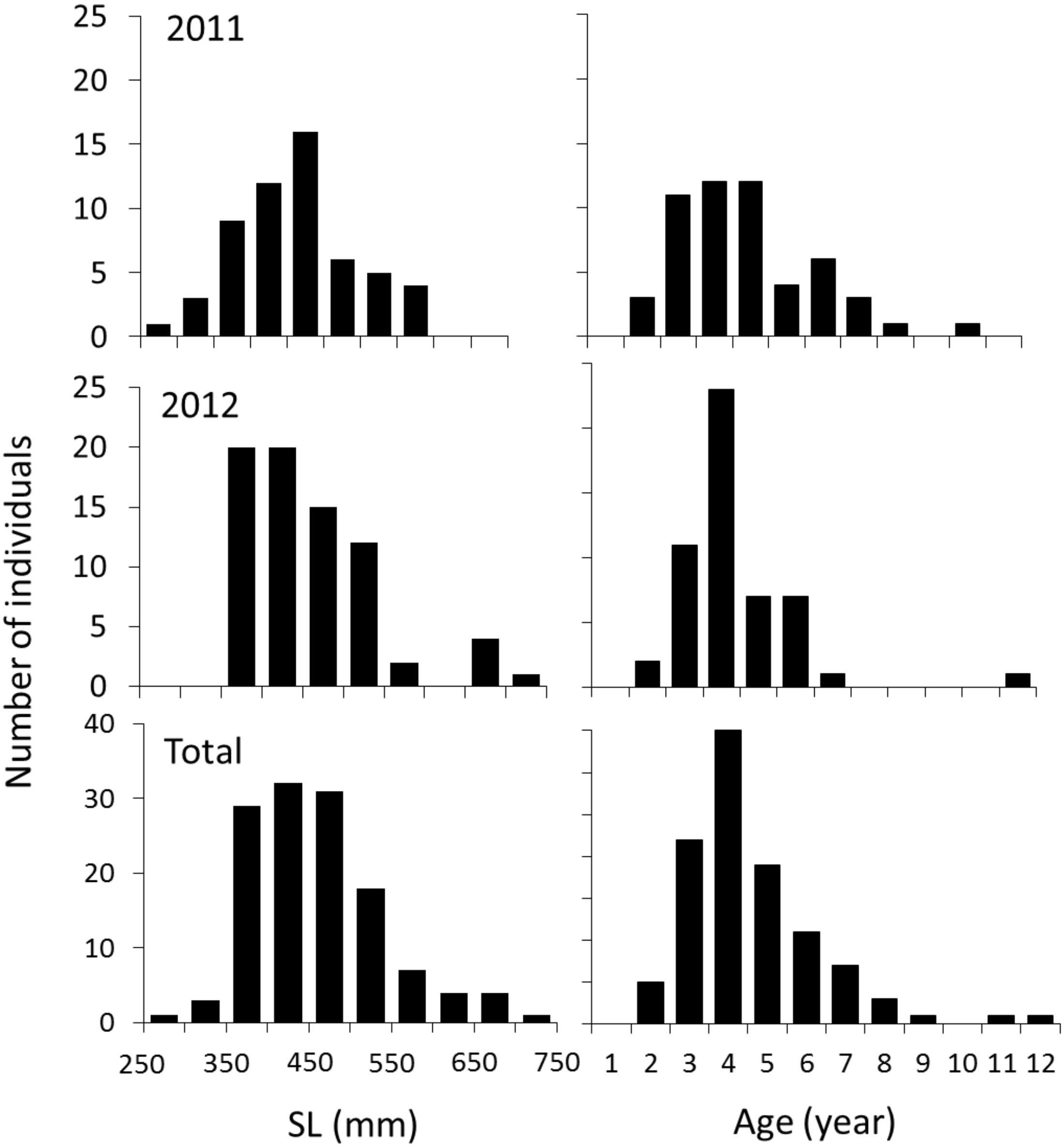

Fig. 9-7 Standard length (SL) and age distributions of adults collected by set nets in the Tango Sea.

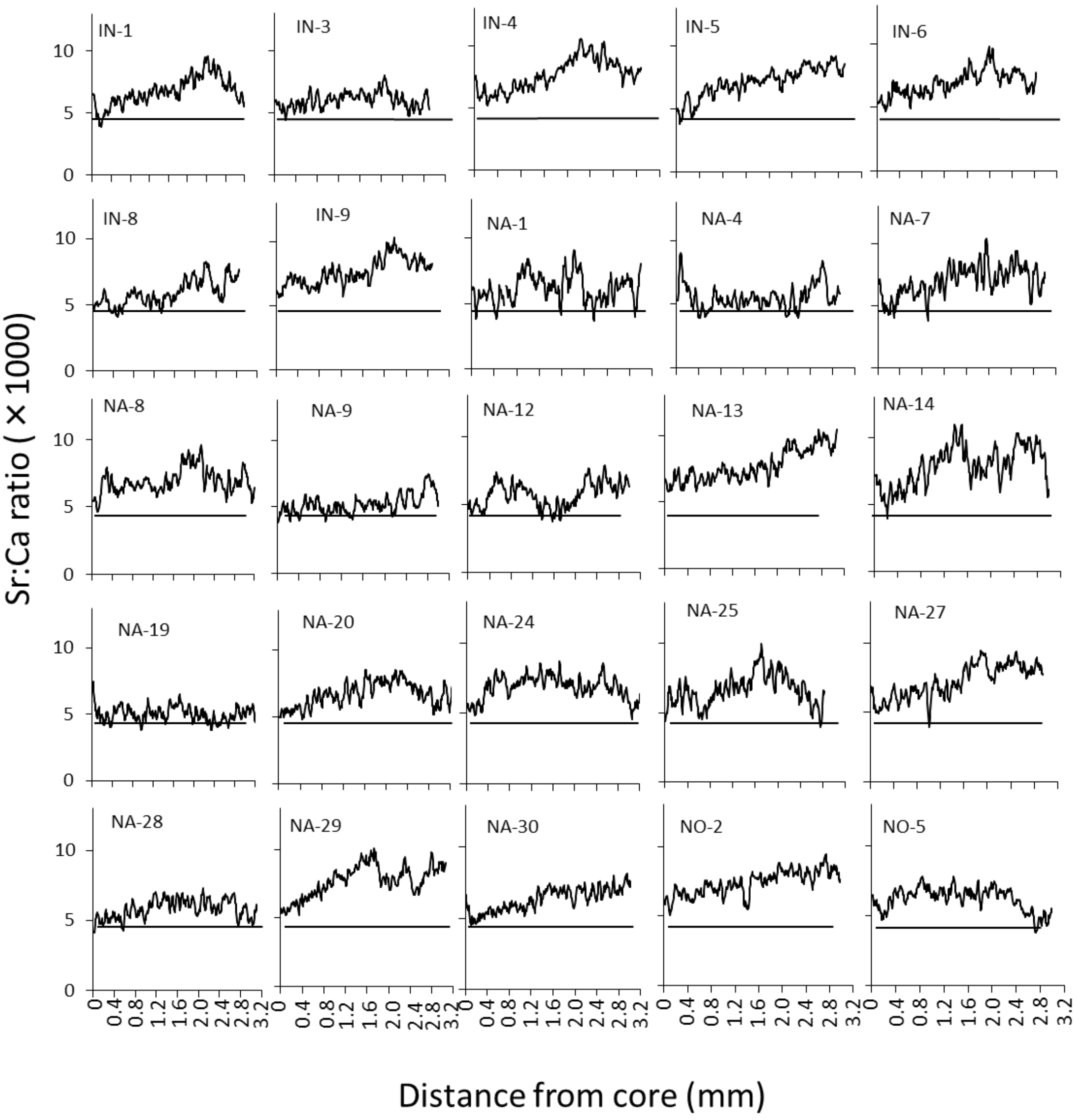

Fig. 9-8 Sr:Ca ratios of adults classified into the coastal resident group. Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

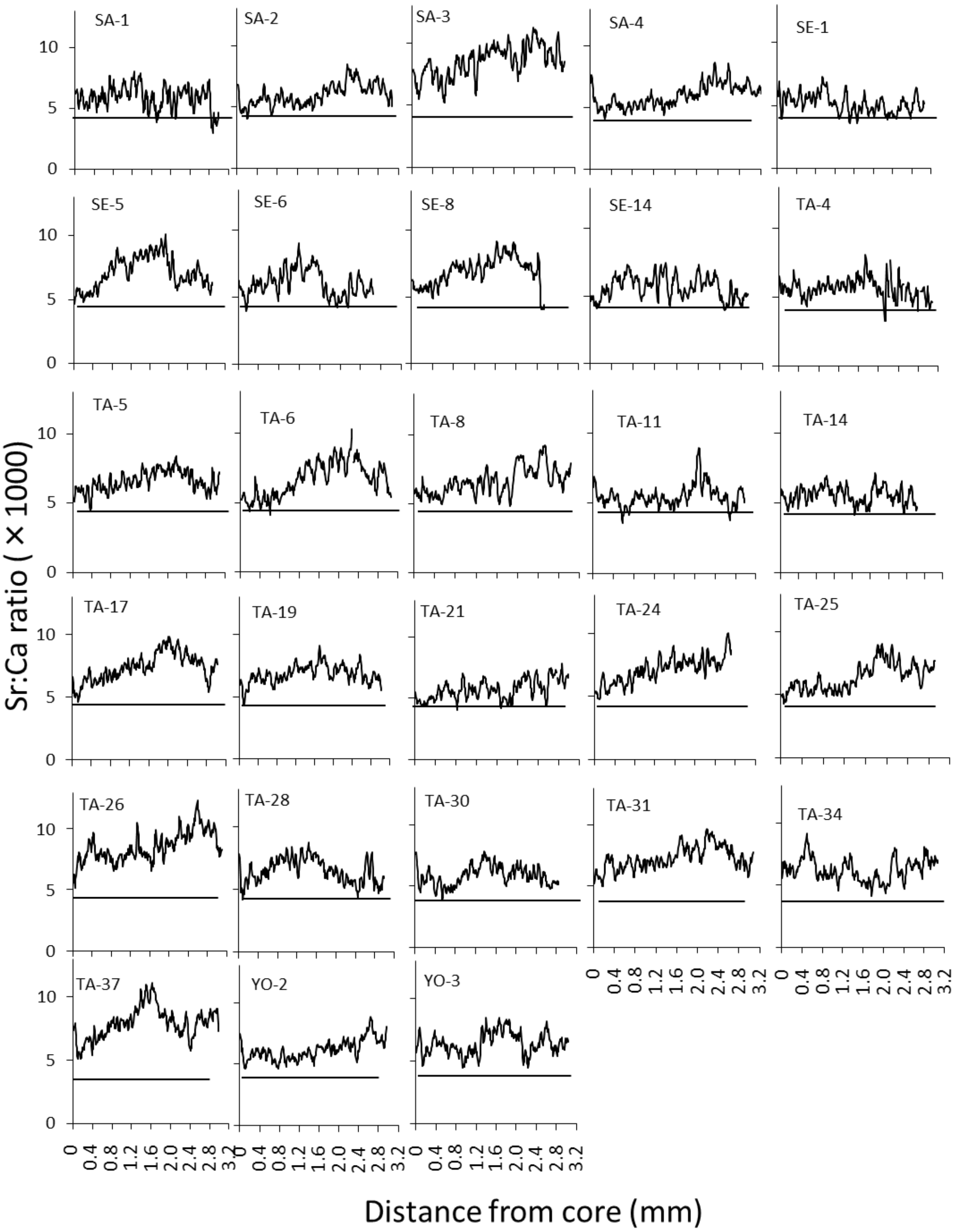

Fig. 9-8 Continued.

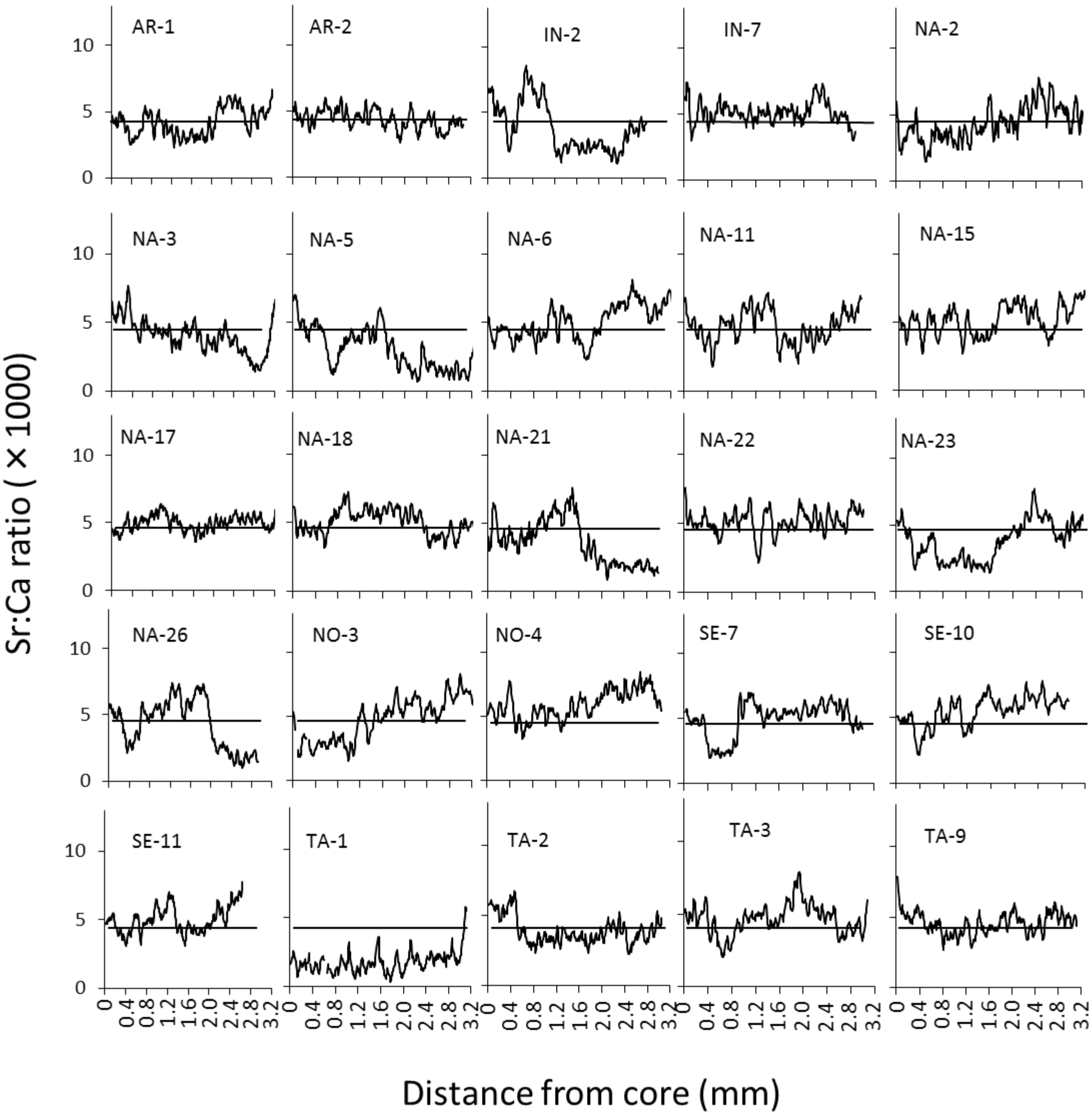

Fig. 9-9 Sr:Ca ratios of adults classified into the river migrant group. Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

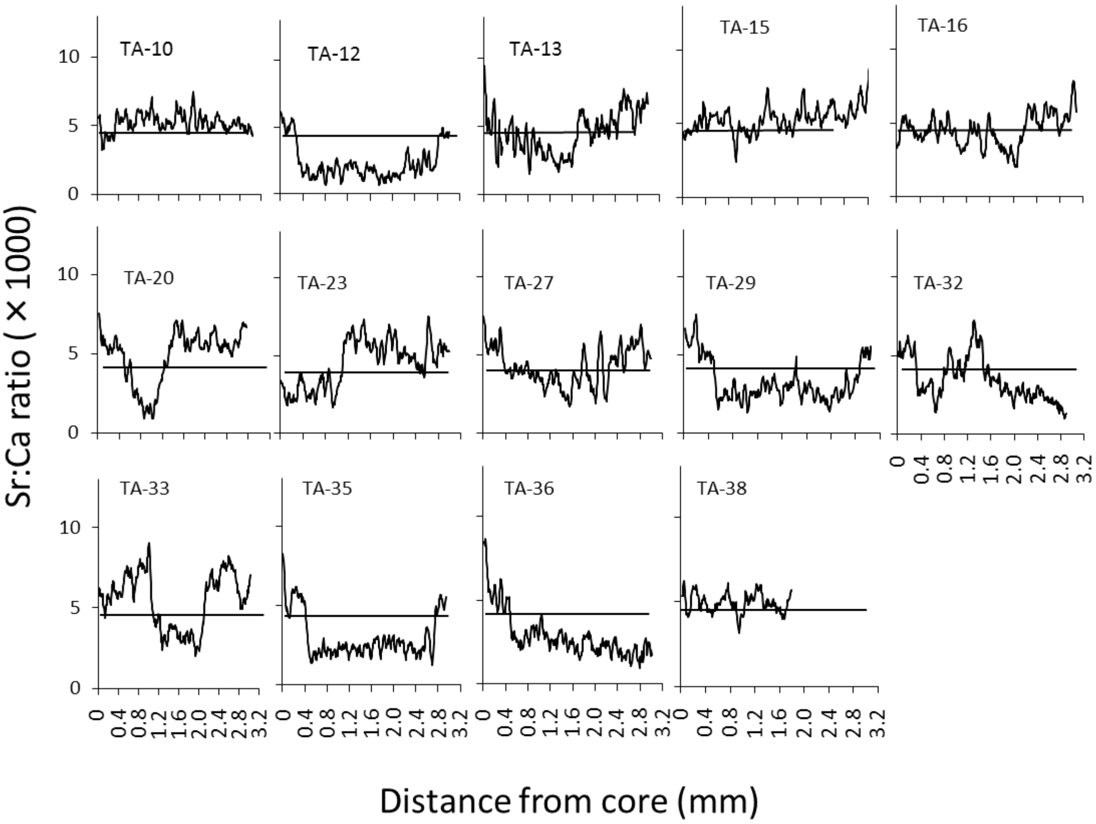

Fig. 9-9 Continued.

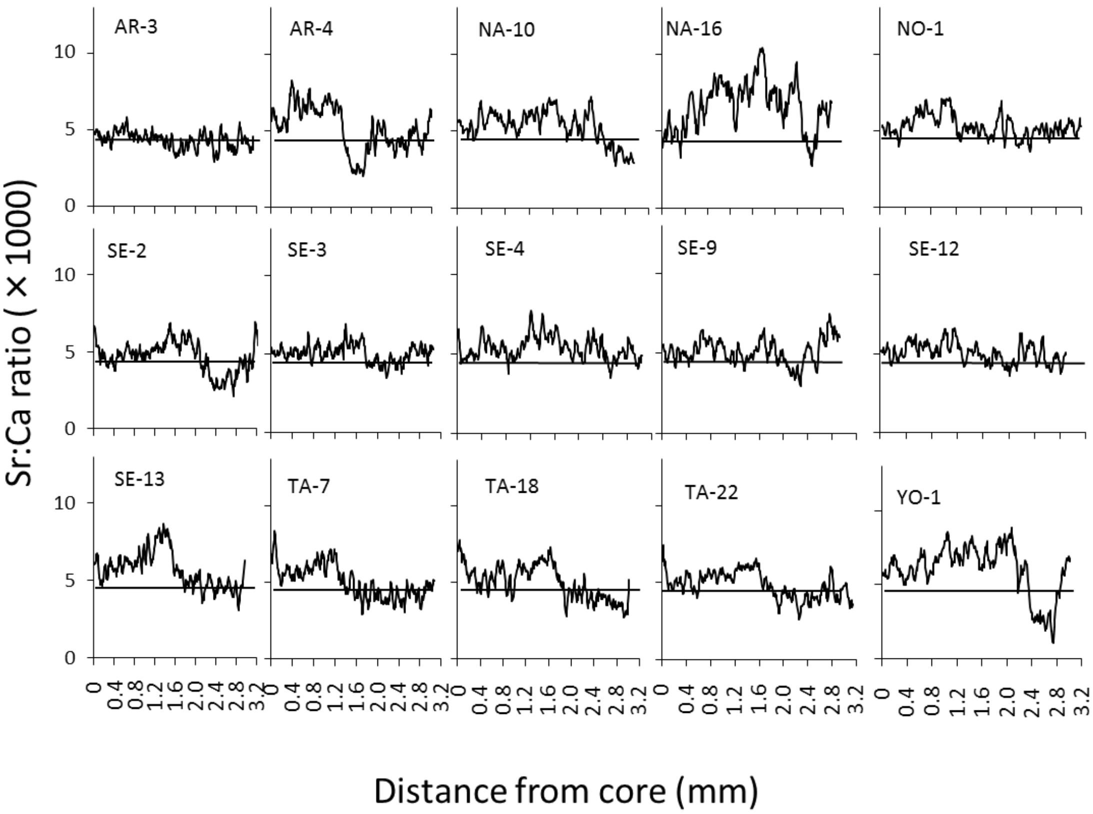

Fig. 9-10 Sr:Ca ratios of adults classified into the late river migrant group. Horizontal lines show the criterion at 4.4×10^{-3} (see Results).

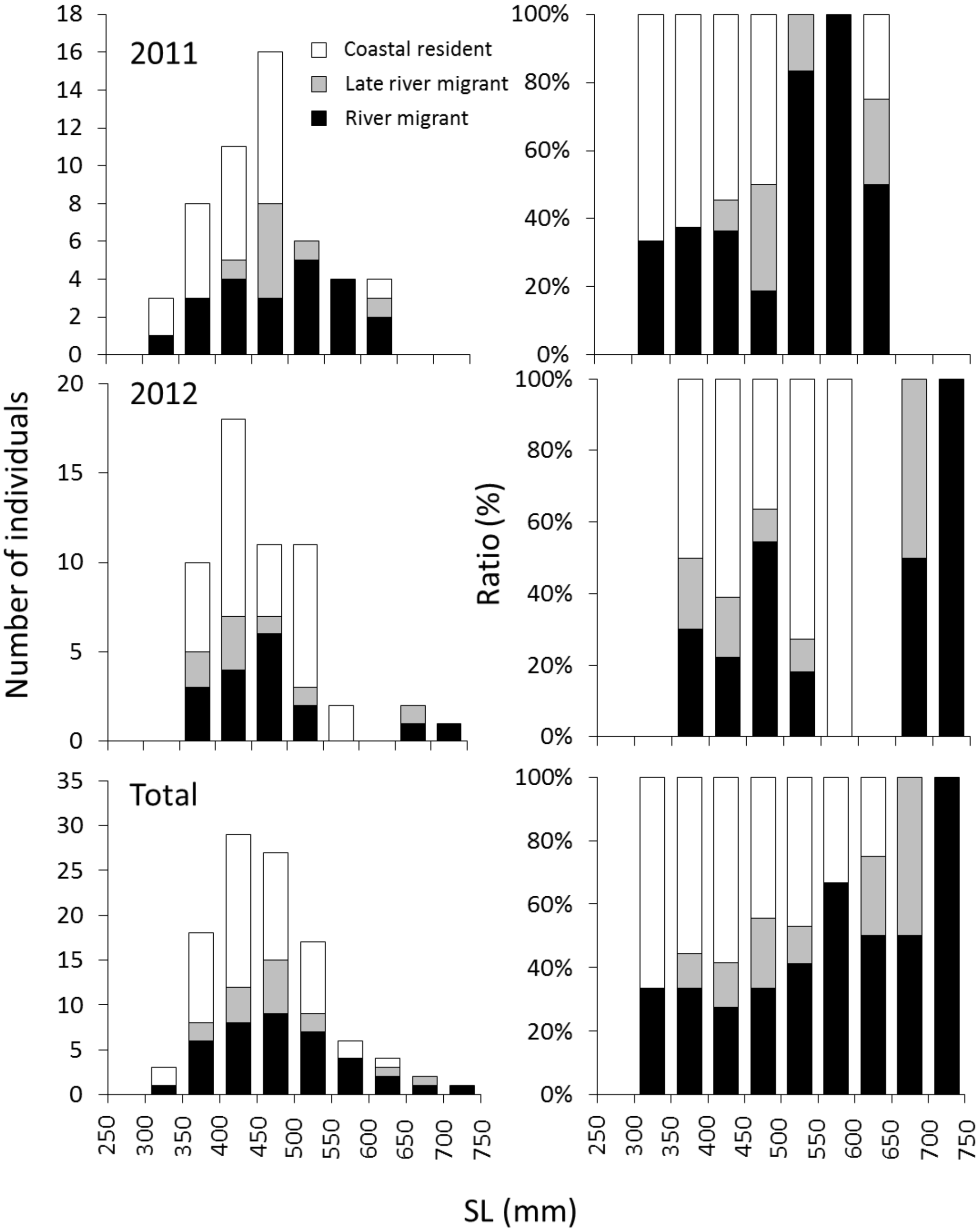

Fig. 9-11 Standard length (SL) compositions of each migration pattern in 2011, 2012 and total.

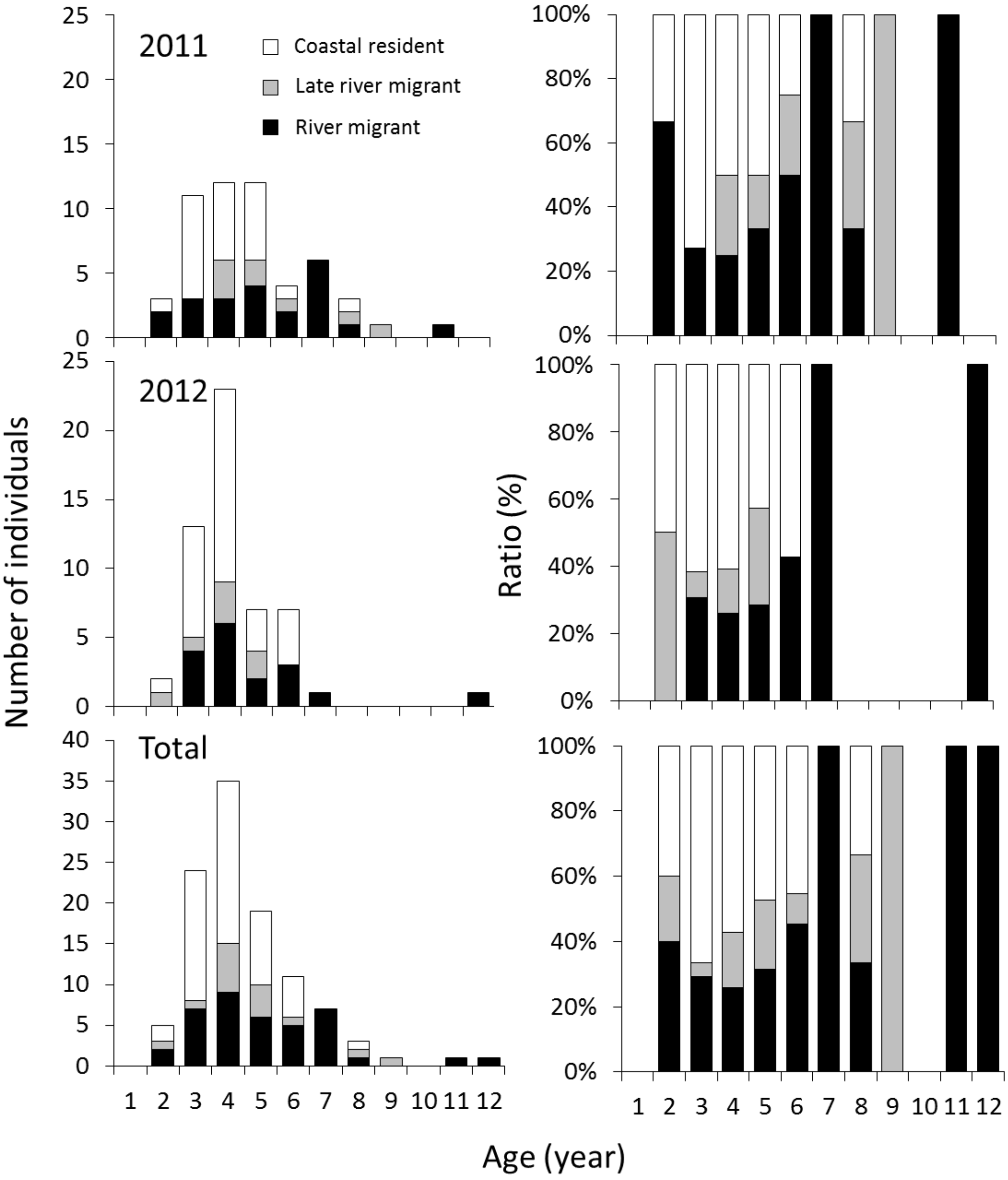

Fig. 9-12 Age composition for each migration pattern in 2011, 2012 and total.

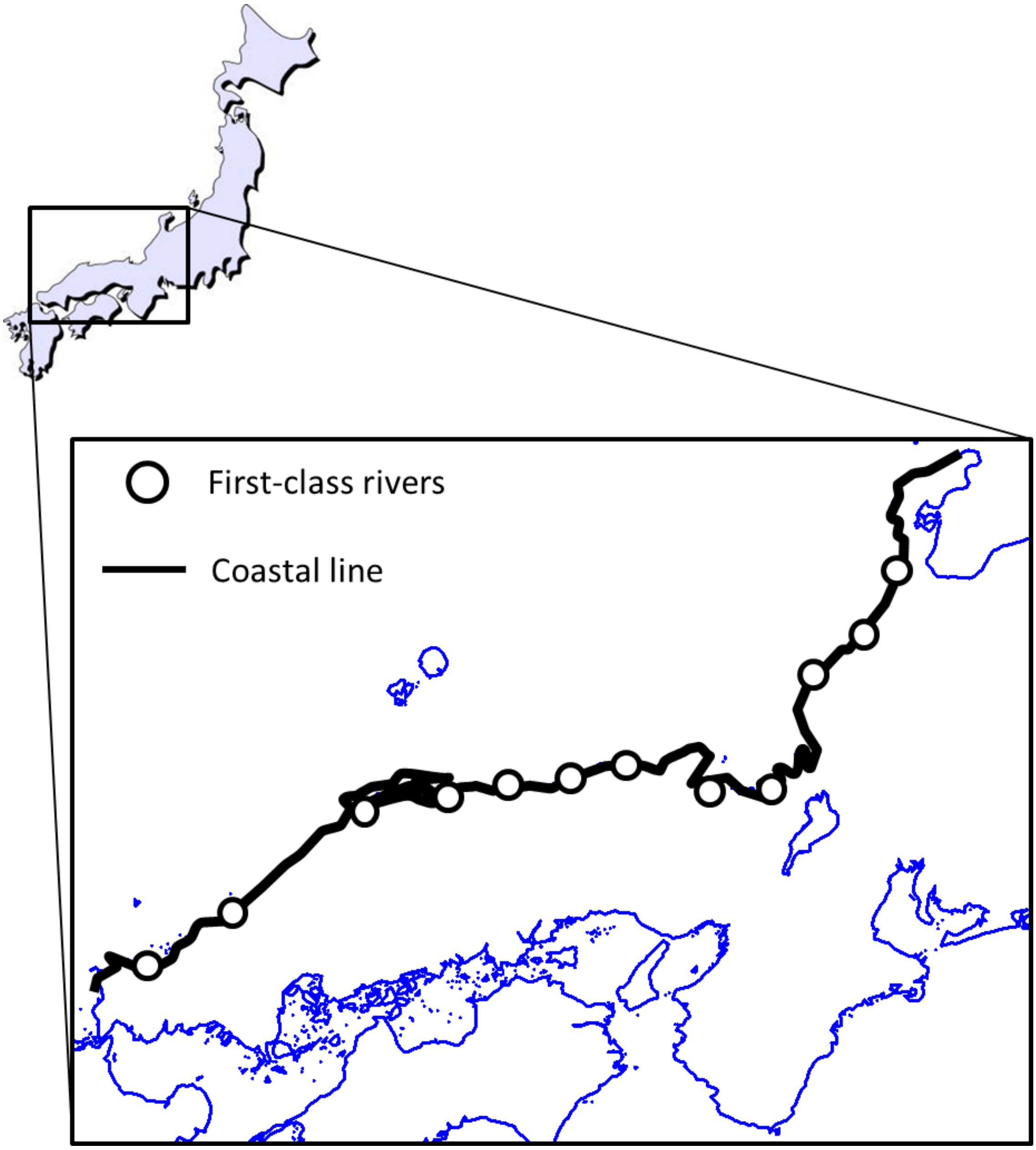

Fig. 9-13 Coastal line of western part of the Sea of Japan and the positions of first-class rivers.

Chapter 10

General discussion

The roles of river-estuarine systems for the early life history of temperate seabass

The survival mechanism during early life history and schematic image of life history of temperate seabass revealed in this study are indicated in Figure 10-1. This study indicated mainly two important roles of river-estuarine system for the early life history of temperate seabass (Fig. 10-1). First, river water inputs improve the recruitment of larvae from offshore into coastal areas. The river plume would affect the transport and prey condition for the planktonic larvae in the offshore area of the Tango Sea (Chapter 2). Second, in the juvenile stage, estuaries serve an important role as nurseries. Estuaries would supply juveniles the good prey condition (Chapter 5) and juveniles achieve high growth (Chapter 7) during their three-month stay in the estuary (Chapter 6), leading high contribution of the river ascending group to adult spawning population (Chapter 9). However, at the same time, density-dependent mortality was important for juveniles in the estuary caused by the intraspecific competition for prey items (Chapter 8). It is worth noticing that main factors affecting the mortality in the early life history of coastal fishes were different between larval stage and juvenile stage (Bailay and Houde, 1989; Shoji and Tanaka, 2008; Martinho et al., 2012). Density-independent mechanism is important in the larval stage, while density-dependent mechanism is the major factor in the juvenile stage (Fig. 10-1).

Potential impacts of human activity on the temperate seabass

Many studies emphasized the importance of estuaries as nurseries (Elliot et al., 2007). The river discharge from estuaries also affects the larval recruitment to the coastal areas and estuaries (Chapter 2). We have to take notice this point as one of the important functions of estuaries, because the modification of estuaries by human can affect the freshwater supply from estuaries to the adjacent coastal areas (Nichols et al., 1986). This would mean that the modification of estuaries affects not only juveniles but also planktonic larvae leading to considerable effects on the fish recruitments.

There are many modifications of estuarine environment by human activities, which potentially have considerable effects on biotic community of estuaries, e.g., reclamation of wetlands, introduction of exotic species, reduction of freshwater inflow, and continued disposal of toxic wastes (Nichols et al., 1986). Results in this study especially suggest the demerits to instruct the dams and estuarine weirs cutting off the connectivity between rivers and seas. Dam constructions lead to reduction of river inflow to the sea (Kennish, 2002). Estuarine weirs are constructed near the river mouths to block the salt-wedge intrusion and gain freshwater resource for the agricultures and the industries. These constructions would lead to 1) diminish of recruitments of the seabass larvae because of reduction of the river discharge in winter (Chapter 2), and 2) juveniles could not overcome the estuarine weirs because of the prevention of salt-wedge intrusion (Chapter 4). Fish-way is sometimes attached to estuarine weirs, however, most of them are too steep for small juveniles like seabass, with poor swimming ability. The prevention of ascending of juveniles means the degradation of estuarine nursery habitats leading to population decrease because narrower nursery would lead to higher density dependent mortality (Chapter 8). Therefore, constructing estuarine weirs would have negative impacts on population of the temperate seabass.

The importance of the partial migration strategy on the population dynamics of temperate seabass

The strategy of temperate seabass juveniles is characterized by its partial migration pattern: they use both coastal areas and estuaries as nurseries (Chapter 3 and Chapter 6). This strategy has also been observed in salmonid fishes, smelts, white perch and some coastal fishes (Potter et al., 1990; Kaeriyama, 1996; Asami, 2004; Kraus and Secor, 2004a; Able, 2005; Aoki et al., 2013). The advantage of this strategy has been studied well in salmonid fishes, smelts and white perch. These fishes and temperate seabass showed similar pattern in the relationship between the growth and migration. A part of individuals of fishes with poor growth and poor body condition migrates to the other area and, while others reside in the natal area (Kaeriyama, 1996; Asami, 2004; Kraus and Secor, 2004a and Chapter 7 in this thesis). Kaeriyama (1991) compared the ratio of migratory individuals (smolt individuals) in the population of sockeye salmon *Oncorhynchus nerka* in the Lake Shikotsu for 10 years and found positive relationship between population size and the percentage of migratory individuals. Asami (2004) found the available prey abundance for juvenile Japanese smelt *Hypomesus nipponensis* is important factor to decide the migratory rate of smelt population in the Lake Abashiri. These studies indicate that the migration of these fishes occurs when the carrying capacity of natal habitats is too small to support whole populations. In addition, Kaeriyama (1985) compared the dependency on the ocean among salmonid fishes and found positive relationship between ocean dependencies and population sizes in the salmonid fishes. From these results, both Kaeriyama (1996) and Asami (2004) considered that the partial migration strategy would enhance total carrying capacity for juveniles relative to the single nursery area. In the case of temperate seabass, juveniles use various coastal environments (Kinoshita, 2002). However, their distribution is generally restricted in the shallower areas (Ohmi, 2002), meaning the limited carrying capacity of coastal areas. Therefore, using extra areas of higher productivity than coastal areas, i.e., estuaries would considerably increase carrying capacity of seabass like the case of salmonid and smelt fishes. On the other hand, why all juveniles do not utilize river-estuarine habitats regardless the high potential as nurseries? In the case of salmonid and smelt fishes, lower predation pressure in the lakes and rivers than the ocean would be another important merit of residence strategy (Asami, 2004). However, seabass spawns in the sea and the resident group would experience high predation pressure (Yamashita et al., 2000; Shoji and Tanaka, 2006b). Thus the predation risk is not the reason of resident strategy of the temperate seabass in the coastal areas. One possible reason is the smallness of the area of estuaries. The estuarine nursery area is considerably smaller than the other coastal areas (Chapter 9). The area of nurseries restricts the population size of coastal fishes, because density-dependent mortality is important after juvenile stage (Chapter 8; van der Veer et al., 2000). Estuaries would be too small to support all of seabass population. Unstability of estuarine environment is another possible reason (Chapter 8). Flood events in the Yura River (Kasai et al., 2010; Chapter 8) caused the worse ambient prey condition for jvueniles leading to the worse survival (Chapter 8). This means that intensive dependence of juveniles on estuarine habitats sometimes leads to destructive recruitment of juveniles to the adult population. The partial migration would contribute to the stability of the population (Secor, 1999). This idea is supported by a theoretical study (Kerr et al., 2010).

The role of estuaries for population dynamics of temperate seabass and the other coastal fishes in Japan

The early life histories of coastal fishes are categorized into six patterns according to their dependence on the estuaries as shown schematically in Figure 10-2. Typical species of each category and their early life histories are listed in Table 10-1. Spawning ground and nurseries are located around estuaries in group A, e.g., herring *Clupea pallasii*. Groups B and C are characterized by their intensive dependence on not only coastal areas but also estuaries as their nurseries. Spawning ground is around bay mouth for group B including the temperate seabass, and offshore area for group C including the Japanese eel. Fishes using the coastal surf zone and around the river mouth as nurseries, including black seabream is classified into group D. Group E shows similar pattern of the early life history to group D but its nurseries are deeper than group D, e.g., red seabream and Japanese flounder. Group F is most independent from the estuaries, because its nursery area is deeper than other groups, such as the ribbon fish *Trichiurus lepturus*. The dependency on estuaries during the early life histories increases from group F to group A.

Group A is most-dependent on estuaries during their early life history. This group needs the brackish water condition for their egg development, larval and juvenile nursery grounds (Hoshikawa et al., 2002; Sasaki et al., 2002). Therefore, they have been recognized as the coastal fish depending on the rivers. On the other hand, the importance of estuaries for the other group fishes has not been recognized well in Japan (Ministry of Agriculture, Forestry and Fisheries, 2011). River plume could have important role for onshore larval migration of fishes in group B, C and D which use near-shore area as nurseries (Chapter 2). Especially, it might be important in the waters with small tidal range such as the Sea of Japan, because tidal currents are too small to use tidal selective transportation. Effects of river discharge on the larval recruitments are different among species according to their spawning season and larval vertical distributions as already discussed in Chapter 2.

Density dependent mechanism in the juvenile stage surpresses the recruitment variability induced during the planktonic larval stage (Iles and Beverton, 2001). This is the reason why the population biomass and variability of recruitment of demersal fishes is often restricted by the size of the area of their nurseries (van der Veer et al., 2000). The quality and quantity of nurseries would affect the biomass and fluctuations of the stock of the coastal fishes (Gibson, 1994; Beverton, 1995; Iles and Beverton, 2001). To identify the difference in the stock fluctuation and the biomass among several coastal fishes with different dependency on estuaries, coefficient of variation (CV) and mean value of catch of several fishes including temperate seabass are compared. Here, catches of fishes are used as the index of biomass of fishes. Temperate seabass, black seabream, Japanese flounder, red seabream and ribbon fish are selected according to their categories of the early life history (Table 10-1; Fig. 10-2). Detailed characteristics of each species are listed in Table 10-2. These species commonly use offshore area around bay mouths with the depths of 30-130 m as their spawning area (Tashiro, 1991; Goto et al., 1989; Munekiyo, 1991; Kuwatani, 1962). Their larval periods are commonly ca. one month, implying similar scale of survival variability during larval periods. In this case, the recruitment variability and following stock fluctuation would be restricted by the carrying capacities of nurseries (van der Veer et al., 2000). The fluctuation of stock will be surpressed when the carrying capacity of their nurseries is small relative to the juvenile amount. The depth ranges of nursery habitats for each species are listed in Table 10-2. The nursery areas of black seabream and temperate seabass are most-restricted, because they mainly use only shallower coastal areas. The black seabream is also known to distribute in estuaries but they rarely ascend to lower salinity area and residence period in the estuaries is shorter than temperate seabass (Aoki et al., 2013). The temperate seabass uses not only shallower coastal area but also estuaries as nurseries. Juvenile red seabream and Japanese flounder are known to mainly distribute the area with the depth shallower than 20 m. They rarely migrate into low salinity areas. Ribbon fish is known to distribute the bottom layer of 20-50 m depth during their juvenile stage. The catch data of these fishes are compared. Catch data of 30 years from 1976 to 2005 are derived from website of Ministry of Agriculture, Forestry and Fisheries (http://www.maff.go.jp/e/index.html). The ten areas around Japanese coasts are selected (Table 10-3). The landing data of five fishes are summed up for each water area and CV and mean landing of 30 years are calculated for each area.

Both black seabream and temperate seabass utilize shallower areas as nurseries. However, the CV and mean catch were different. The CV and mean catch of black seabream were lower than species using deeper broader area such as red seabream, Japanese flounder and ribbon fish (Fig. 10-3). On the other hand, temperate seabass showed similar values to red seabream and Japanese flounder. Iles and Beverton (2001) compared the recruitment variations among 63 fish stocks and found that species showing high densities during their juvenile stages indicate small variations in recruitments because of the density-dependent mechanisms. Small variation and biomass of black seabream would be caused by the smallness of its shallower nurseries of small carrying capacity. Shallower areas are considered to have several advantages relative to deeper area; higher temperature, lower predation pressure, and good prey environments (Gibson, 1994). However, the smallness of shallower nursery area would often lead to small stock biomass such as black seabream. On the other hand, the large carrying capacity of estuaries as nursery areas (Chapters 5 and 9) would lead to larger total capacity of nurseries of temperate seabass than those of black seabream, resulting in the higher biomass and larger variation in the catch of temperate seabass than black seabream.

Kusakabe et al. (1994) collected the larvae and juveniles distributed around the vertical protected coastal area in the Osaka Bay and found almost no black seabream and temperate seabass juveniles regardless of their occurrence in the sand beach near the sampling station. That is, shore protections and land filling would reduce the nursery areas especially for juveniles using shallower surf zones such as fishes categorized into group A to D (Fig. 10-2; Table 10-1). Especially, fishes of group D such as black seabream would be vulnerable to coastal degradations because they can use limited area of estuaries and the carrying capacity of their nursery area is small.

Future works

Some studies pointed out the relationship between the landing of temperate seabass and climate changes. Kuwatani (1962) compared the catch fluctuation of temperate seabass among several areas in Japanese coasts and found the synchronized pattern. Katayama et al. (2009) reported that this pattern can be related to the decadal change in winter climate indicated by Aleutian Low Pressure Index. Winter weather can relate to the winter river discharge affecting the recruitment of temperate seabass in the Tango Sea (Chapter 2). Temperature in the early spring could also affect the mortality of juveniles (Shoji and Tanaka, 2007b). Further analysis using model simulation would be necessary.

The nursery value of estuaries would differ among bays. Estuaries in the eutrophic waters could have lower nursery value than estuaries in oligotrophic areas because of the following possible reasons. First, this study found that larvae with better growth reside in the coastal areas after juvenile stage (Chapter 7). Eutrophic area would support the good prey condition leading to high larval growth potentially leading to residence in the sea after juvenile stage. Second, high productivity of the eutrophic area would lead to high survival rate in the coastal areas as well as estuaries. Therefore the relative importance of estuaries would be lower than the oligotrophic areas. Gross et al. (1988) hypothesized that the balance of prey availability between ocean and the river affect the direction of diadromous migration and lower prey abundance in the ocean would accelerate the catadromous migration of fishes. Tsukamoto et al. (2009) reported the higher contribution of migratory eels to the local population in the southern area than northern area of Japan. If similar pattern happens for temperate seabass, it means that the value of each estuary would differ among various conditions in each area.

Many studies reported the distribution of juvenile temperate seabass in the coastal areas (e.g., Kinoshita, 2002). However, detailed information of the juvenile ecology in the coastal area is still missing. The temperate seabass juveniles are distribute in various environments, e.g., eelgrass beds, seagrass beds and sand beach (Chapter 3). However, the difference in the quality among these nurseries is unknown. Especially, eelgrass beds are considered to be important as nurseries, because they supply the refuge from predators for juveniles (Kinoshita, 2002; Shoji et al., 2007). It is thus important to compare the resident periods, feeding habits, growth and survival among various environments in the coastal areas.

Table 10-1 Group classification based on the styles of early life history of coastal fishes.

Group	Examples	References
A	Herring *Clupea pallasii*	Hoshikawa et al. (2002); Sasaki et al. (2002)
B	Temperate seabass *Lateolabrax japonicus*	This thesis
	Mullet *Mugil cephalus*,	Takasaki et al. (2008)
	Starry flounder *Platichthys stellatus*	Tomiyama and Omori (2008)
C	Japanese eel *Anguilla japonica*	Kaifu et al. (2013)
D	Black seabream *Acanthopagrus schlegelii*	Fujita (2004)
	Stone flounder *Platichthys bicoloratus*,	Tomiyama and Omori (2008)
	Croaker *Nibea albiflora*,	Takita (1974)
	Puffer *Takifugu rubripes*	Takita and Intong (1991)
	Rock fish *Sebastes cheni*	Nagasawa (2001); Kuwabara and Suzuki (1983b)
E	Japanese flounder *Paralichthys olivaceus*	Takeno (2010)
	Red seabream *Pagrus major*	Tanaka (1986)
	Tongue fish *Cynoglossus joyneri*	Minami (1983)
F	Ribbon fish *Trichiurus lepturus*	Munekiyo (1991)

Table 10-2 Characteristics of each species

Species	Depth of spawning ground (m)	Number of eggs per adult	Larval period (days)	Nursery areas
Black seabream	30	$1–2 \times 10^5$	30	< 2 m coastal area and around river mouths
Temperate seabass	50–80	$1–2 \times 10^5$	40	< 2 m coastal area and estuaries
Japanese floudner	20–60	$1–2 \times 10^5$	35	< 20 m coastal area and around river mouths
Red seabream	30–100	$1–2 \times 10^5$	30	< 30 m coastal area
Ribbon fish	110–130	$0.8–1 \times 10^5$	30–60	20–50 m coastal area

Table 10-3 Classification of Japanese coastal area

Area name	Data source of prefectures	Ratios of coastal protection (%)
Ariake Bay	Kumamoto	48.0
Western part of sea of Japan	Shimane, Tottori, Kyoto, Fukui	32.1
Northern part of sea of Japan	Ishikawa, Toyama, Niigata, Yamagata, Akita	45.2
Western part of Seto Inland Sea	Oita, Hiroshima, Ehime	53.4
Eastern part of Seto Inland Sea	Okayama, Kagawa, Osaka	61.8
Western part of Pacific coast	Miyazaki, Kochi, Tokushima, Wakayama	30.2
Ise Bay	Mie, Aichi	51.0
Middle part of Pacific coast	Shizuoka	31.5
Tokyo Bay	Kanagawa, Chiba	61.3
North-eastern coast of Japan	Miyagi, Iwate, Ibaragi, Fukushima	35.1

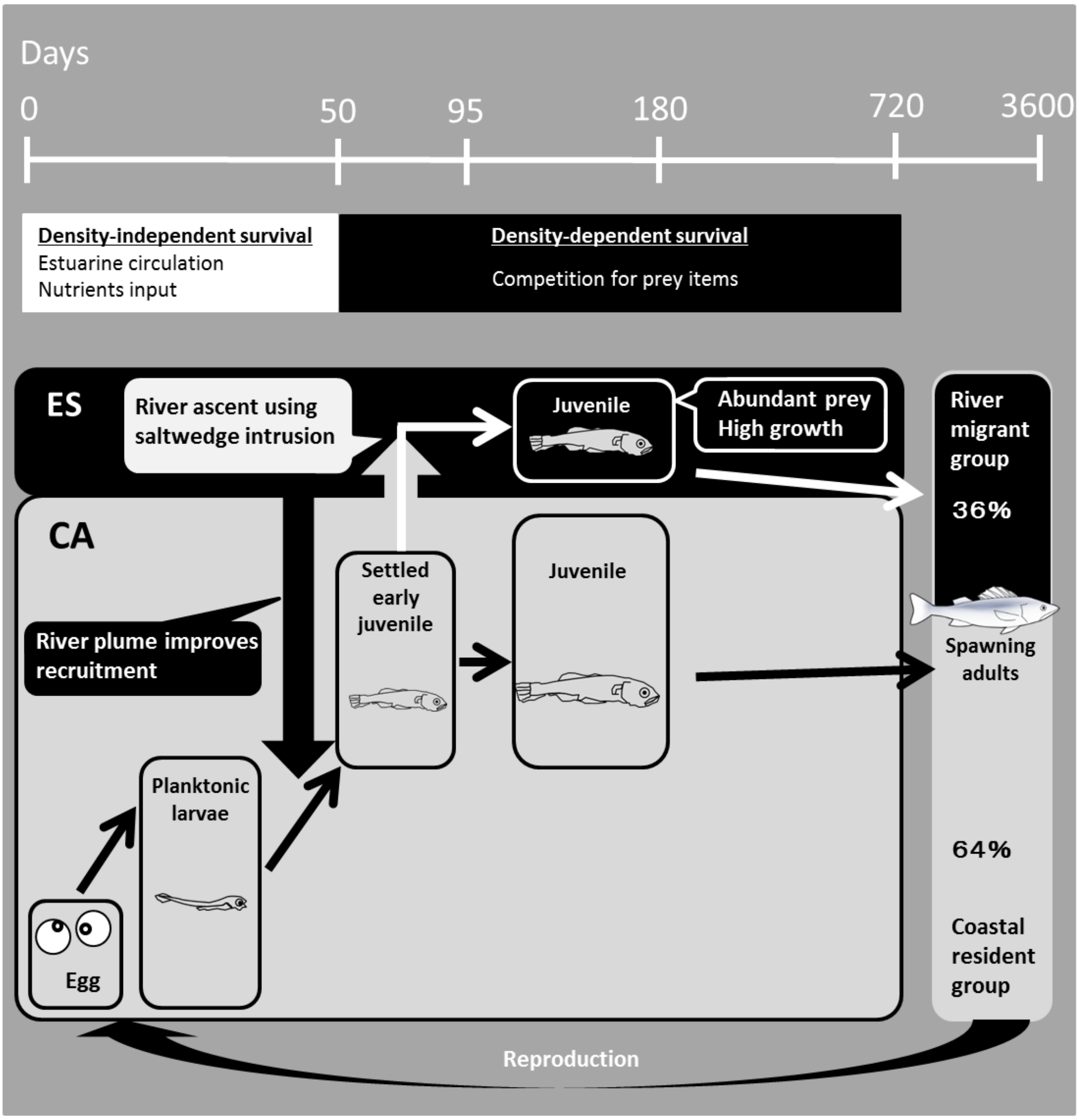

Fig. 10-1 Schematic image of the early life history of temperate seabass and importance of river-estuarine system. ES and CA indicate estuary and coastal area, repectively.

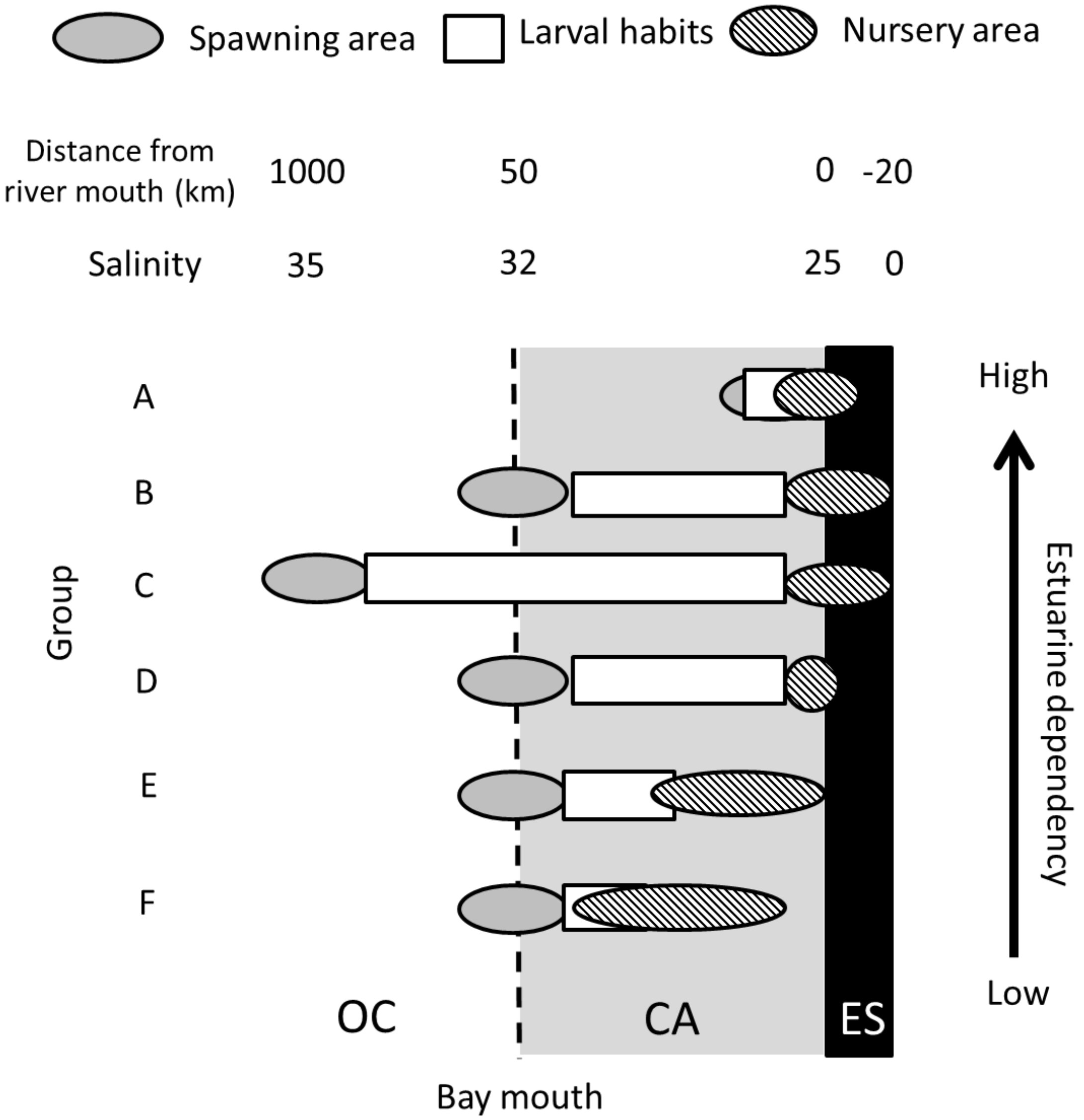

Fig. 10-2 Schematic image of early life histories of each classification. ES: estuary, CA: coastal area, OC: ocean.

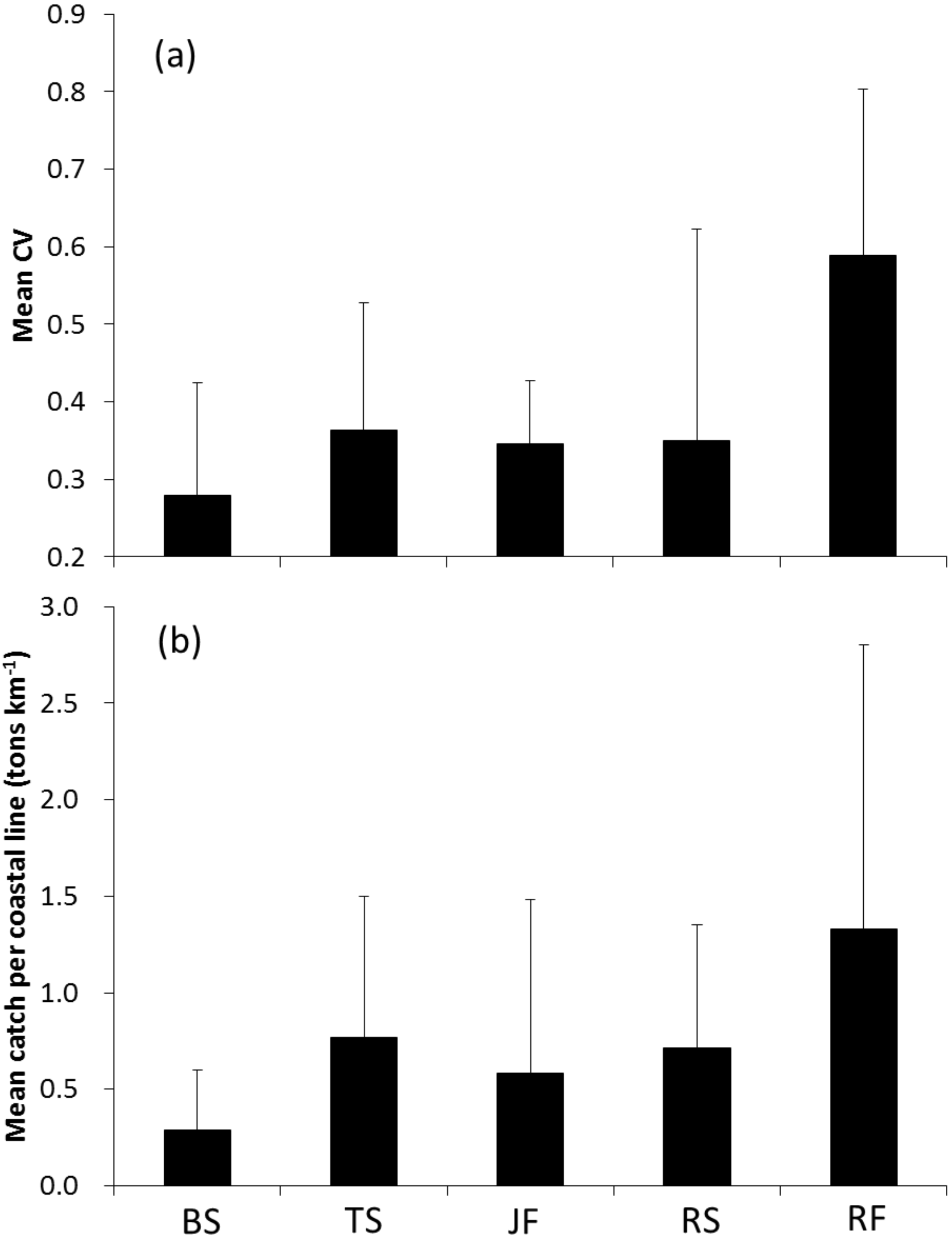

Fig. 10-3 (a) Mean coefficients of variance (CV) and (b) mean catch per coastal line of five coastal fishes. BS: black seabream, TS: temperate seabass, JF: Japanese flounder, RS: red seabream and RF: ribbon fish.

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