Fisheries Science (2018) 84:163–172
https://doi.org/10.1007/s12562-017-1167-0

SPECIAL FEATURE: ORIGINAL ARTICLE

Coastal Ecosystem Complex (CEC)

Upstream migration mechanisms of juvenile temperate sea bass *Lateolabrax japonicus* in the stratified Yura River estuary

Taiki Fuji[1,4] · **Akihide Kasai**[2,5] · **Yoh Yamashita**[2,3]

Received: 27 April 2017 / Accepted: 24 October 2017 / Published online: 14 February 2018
© Japanese Society of Fisheries Science 2018

Abstract

Hydrographic conditions and distributions of juvenile temperate sea bass *Lateolabrax japonicus* were observed in early spring from 2009 to 2012 in the Yura River estuary, which is highly stratified due to its small tides and consequent seawater intrusion into the bottom layer of the river as a salt wedge. In all four studied years, the upstream expansion of their distribution coincided with the timing of the salt wedge intrusion from the lower to upper estuary, indicating that juvenile fish used salt wedge intrusions to ascend the estuary in early spring. However, juveniles sometimes remained in the nearshore area even when the salt wedge intrusion had already occurred, indicating that other triggers are also likely to be necessary. We therefore evaluated the effects of temperature on upstream migration behaviors. The relationship between the mean temperature they experienced from hatch until starting the ascent and mean age of each cohort at the upstream migration fitted with the law of effective cumulative temperature. Most cohorts ascended the river at an effective cumulative temperature of approximately 500 °C–days. This suggests that higher temperatures would lead to a shorter period prior to the upstream migration.

Keywords Salt wedge intrusion · River ascending · Catadromous migration · Juvenile

Introduction

Temperate sea bass *Lateolabrax japonicus* is an important euryhaline species for Japanese coastal fisheries (Shoji et al. 2002). Its utilization of the "coastal ecosystem complex (CEC)" is characterized as follows; (1) ontogenetic shift of habitats and (2) parallel utilization of various habitats (Watanabe et al. 2018). This fish, along with some other coastal fishes, is known to change its habitats ontogenetically during its early life history. Temperate sea bass usually spawn offshore (around and outside of the bay mouth) during the 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 in nearshore areas (Fujita et al. 1988; Ohmi 2002; Arayama et al. 2002) and utilize these as nursery areas (Hatanaka and Sekino 1962; Matsumiya et al. 1982; Hibino et al. 2002; Kinoshita 2002; Yamazaki 2002; Fuji et al. 2010; Iwamoto et al. 2010; Nakane et al. 2010; Tamura et al. 2013; Fuji et al. 2016a). From the juvenile stage, they utilize various coastal environments in parallel as nurseries after early spring, e.g., sea grass beds (Hatanaka and Sekino 1962; Kinoshita 2002), sandy beaches (Fuji et al.

This article is sponsored by the Coastal Ecosystem Complex Project of the Ocean Resource Use Promotion Technology Development Program, the Ministry of Education, Culture, Sports, Science and Technology, Japan.

✉ Taiki Fuji
tfuji114@affrc.go.jp

1 Kyoto University, Graduate School of Agriculture, Oiwake, Kitashirakawa, Sakyo, Kyoto 606-8502, Japan

2 Kyoto University, Field Science Education and Research Center, Oiwake, Kitashirakawa, Sakyo, Kyoto 606-8502, Japan

3 Kyoto University, Field Science Education and Research Center, Nagahama, Maizuru 625-0086, Japan

4 Present Address: Tohoku National Fisheries Research Institute, Japan Fisheries Research and Education Agency, 25-259 Shimomekurakubo, Same, Hachinohe, Aomori 031-0841, Japan

5 Present Address: Faculty of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

2010; Nakane et al. 2010), tidal flats (Hibino et al. 2002; Tamura et al. 2013), and estuaries (Matsumiya et al. 1982; Yamazaki 2002; Fuji et al. 2010; Iwamoto et al. 2010). In particular, estuaries have been considered to be important nurseries for temperate sea bass because of their good prey environment (Fuji et al. 2016a) leading to high growth of juveniles (Fuji et al. 2011, 2014) and high contribution to the adult population, regardless of their small area relative to other coastal types (Fuji et al. 2016b). Success of migration into estuaries is one of the most important factors for juveniles to achieve good survival (North and Houde 2001). Estuaries, in which hydrodynamics are strongly affected by river flow and tidal conditions, are characterized by the complexity of the hydrology (Kasai et al. 2010). It is important to understand the mechanism of recruitment of juveniles into estuarine nursery areas to determine effective conservation and stock management strategies.

Environmental conditions control migration ecologies of juveniles, e.g., timing and distance of juvenile migration, through both physical and biological ways. First, hydrological conditions affect the movements of juveniles directly. Especially, juveniles need to overcome the river flow regardless of their poor swimming ability. Larvae of some species of fish including temperate sea bass use tidal currents to overcome this difficulty. They distribute in the surface or middle layers to migrate onshore and upstream with the onshore flood tidal currents. They move to the bottom layer and reside there during the ebb tide to avoid offshore currents. This mechanism is called “tidal selective transport” (Yamashita et al. 1996; Gibson 1997; Islam et al. 2007). However, in microtidal estuaries, fishes cannot use this mechanism, so they need another way to migrate. Salt wedge intrusion is another possible environmental factor which juveniles might use when they ascend microtidal estuaries, because water flows upstream in the salt wedge (Dyer 1973). This would be effective for juveniles to avoid flowing out by the river current and achieve efficient migration to upper estuaries. However, few researchers have focused on the relationship between juvenile river ascending and salt wedge intrusions.

Second, many studies have reported that there are various endogenous factors which start 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 juveniles undergo the physiological, morphological and behavioral changes necessary to migrate, 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 smolts of salmonid fishes, seasonal increases in day length and temperature are hypothesized to synchronize physiological and behavioral changes necessary for successful migration to the sea (McCormick et al. 1998). Therefore, many studies have 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 (Zydlewski et al. 2005; Nakamura and Kasuya 2004). 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 for considering 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).

The hypothesis in this study is that juvenile temperate sea bass use salt wedge intrusion for ascending microtidal estuaries. In addition, the relationship between effective cumulative temperature and timing of river ascent was also estimated to confirm that temperature is also an important factor for deciding the timing of river ascent.

Materials and methods

Sampling field

Observations and samplings were conducted along the lower reaches of the Yura River and adjacent coastal area during the spring of 2009–2012 (Fig. 1). The Yura River flows into the Sea of Japan, where the tides are generally small. As the typical tidal range in the estuary is < 0.5 m (Kasai et al. 2010), we were able to neglect the effect of tide on fish distributions and environmental conditions in this study. The river discharge of the Yura River shows typical seasonal variations, namely, large in the winter and spring due to melting snow and small in the summer and autumn (Kasai et al. 2010). In the winter, the whole estuary is filled with freshwater, and the water is homogeneous. Seawater starts to intrude into the lower layer of the estuary from early spring onwards, and by the summer, the lower layer is occupied by sea water up to approximately 15 km upstream from the river mouth, leading to strong stratification.

Field sampling

Six stations were set up along the lower reaches of the river from the coastal surf zone to 15 km upstream (St. 1–St. 6, Fig. 1). The distances from the river mouth were 0.5, 3.0, 7.5, 11.0 and 15.0 km at St. 2, St. 3, St. 4, St. 5 and St. 6, respectively. Another station (St. 1) was set on the sand

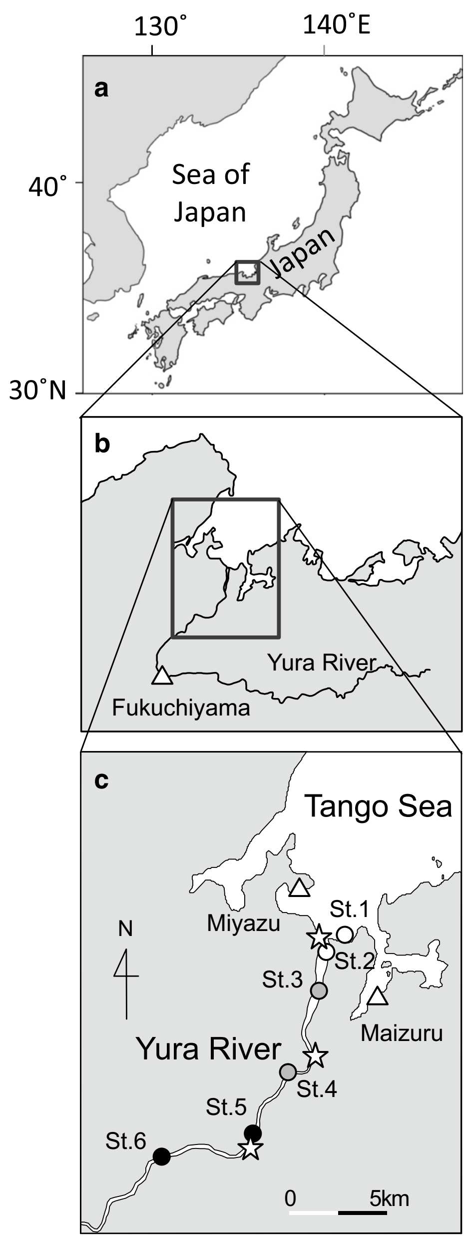

Fig. 1 Sampling stations along the Yura River estuary. Sampling stations were divided into three groups; coastal area indicated by *open circles* (St. 1 and 2), lower estuary indicated by *gray circles* (St. 3 and 4) and upper estuary indicated by *filled circles* (St. 5 and 6). Points that salinity loggers were set are indicated by *stars*. River level was monitored at the Fukuchiyama station indicated by a *white triangle*

beach adjoining the river mouth (1.0 km from the river mouth, Fig. 1).

In order to collect temperate sea bass 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 in March, April and May from 2009 to 2012. Three-minute tows were performed twice at each station. Sampling depth was 0.3–1.2 m at every station. The juveniles were frozen in dry ice immediately after the collection. Care of the fish and all procedures were done following the Guidelines for the Use of Fishes Research of the Ichthyological Society of Japan (2003).

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

Stations were divided into three groups; coastal area (St. 1 and St. 2), lower estuary (St. 3 and St. 4) and upper estuary (St. 5 and St. 6) for simplification. Standard length (SL: mm) was measured for every individual.

Laboratory analysis

Individuals for otolith analysis were haphazardly 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, 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 sagittal otoliths for sea bass juveniles of ca. 20–30 mm SL (Fujita 2004; Suzuki et al. 2008; Islam et al. 2009). Daily rings of otoliths were counted using a video monitor and an otolith reading system (ARP/W, Ratoc System Engineering). The age of a temperate sea bass juvenile 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. 2008).

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. 1b) were obtained from the Ministry of Land, Infrastructure, Transport and Tourism (http://www1.river.go.jp/cgi-bin/SiteInfo.exe?ID=306091286605030). As representative of the temperature in the Tango Sea, daily temperature data in the Tango Sea at a depth of 12 m in Miyazu (Fig. 1c) 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. 1c) were obtained from the Japan Meteorological Agency (http://www.data.jma.go.jp/kaiyou/db/tide/suisan/suisan.php).

Data analysis

The distance of salt wedge 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 salt wedge intrusion was defined here as the distance from the river mouth to the tip of the salt wedge, where salinity was five in the bottom water (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, salt wedge distance and juvenile ascending distance, were compared.

Standard length–daily age linear relationships were determined for every year. The ages of all individuals in each year were estimated by using these relationships and SL data. Individuals with SL that was out of the age range of samples for otolith analysis were eliminated from this estimation. In total, 6.3% (169 individuals) were eliminated from age estimations, as their ages were uncertain. Hatch dates were estimated from estimated age and collection date for each individual. Individuals were categorized into 10-day cohorts. Cohorts including more than five individuals were selected for further analysis.

River ascending indexes on *i*th sampling day (A_i) were defined for each cohort as follows;

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

where N_i is the total number of individuals collected in the lower and upper estuary on the *i*th sampling day. A_i was set as zero when N_i was smaller than N_{i-1}. $\%A_i$ was then calculated as follows;

$$\%A_i = \frac{A_i}{\sum A_i}, \tag{2}$$

where $\sum A_i$ means sum of A_i values for all sampling days of the year. Then $\sum \%A_i$ was obtained using the equation

$$\sum \%A_i = \sum_{j=1}^{i} \%A_j. \tag{3}$$

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

$$k = D(T - t), \tag{4}$$

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 a base temperature. Base temperature is defined as the lower limit below which the biological process will cease (Trudgill et al. 2005). In this study, juvenile ascent is considered to be 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 defined in two ways; first, days that individuals started to be collected in the lower or upper estuary (first ascending day) and main ascending days on which most of individuals ascend, which is defined as the day that $\%A_i$ exceeded 50. Both days were determined for each cohort. Parameters k and t were estimated by a linearizing transformation for the variable D resulting in the equation

$$\frac{1}{D} = -\frac{t}{k} + \frac{T}{k}. \tag{5}$$

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. Cumulative $\%A_i$ ($\sum \%A_i$) and effective cumulative temperatures were compared to detect the relationship between river ascending behavior and temperature.

Results

Dynamics of the salt wedge intrusion and juvenile river ascending

The fluctuation patterns of river discharge in spring were different among the 4 years (Fig. 2). River discharge in 2009 was low throughout the 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. The river discharge was low until April and then two heavy floods (over 1000 m^3/s) occurred in middle and late May 2011. In 2012, river flow was high until mid-April, but low after late April.

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

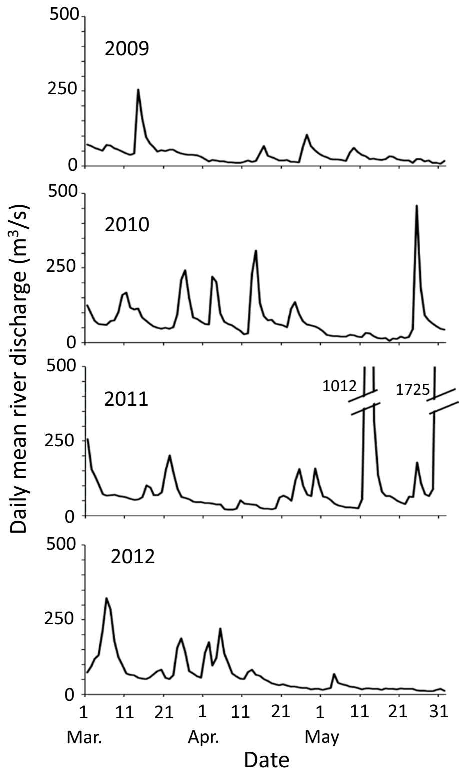

Fig. 2 Daily Yura River discharge from March to May in the 4 years

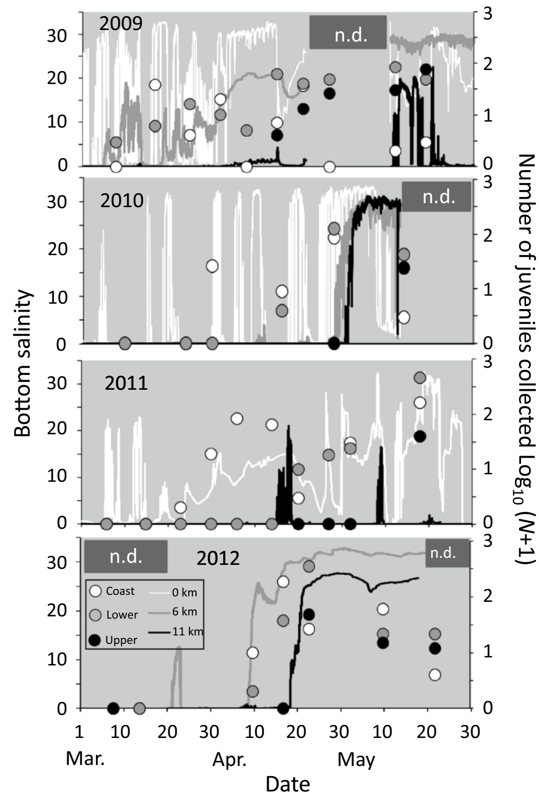

Fig. 3 Bottom salinity measured by salinity loggers (*lines, left vertical axis*) and total number of juvenile temperate sea bass *Lateolabrax japonicus* collected in each area (*dots, right vertical axis*). *Grey bars* with "n.d." mean the periods when there is no salinity data because of maintenance of the salinity loggers

Timings of juvenile movement from the coastal area to the lower estuary and the lower estuary to the upper estuary corresponded with salt wedge movements (Fig. 3). For example, in 2009, juvenile distributions were restricted to the coastal area and the lower estuary during March and the beginning of April, when the salt wedge intruded to 6 km upstream. Juveniles then reached the upper estuary from mid-April, corresponding to the rise of bottom salinity at 11 km upstream (Fig. 3). These correspondences were observed in all years. Comparison between estimated salt wedge intrusion distance and juvenile ascending distance showed juveniles rarely ascended further than the salt wedge intrusion (Fig. 4). Juveniles went beyond the salt wedge only on 15 April 2009 and 18 May 2011.

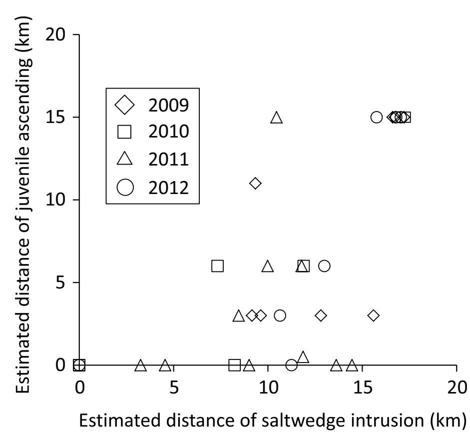

Fig. 4 Relationship between estimated distance of salt wedge intrusion and estimated distance of juvenile ascending

Temperature and timings of river ascending of juveniles

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

In total, ages of 204 individuals with a size range from 13.7 mm to 28.3 mm SL were determined and then age-SL relationships in each year were estimated (Table 1). Using these relationships, SL data were converted to daily age data. The hatch dates were distributed mainly from mid-January to mid-February (Fig. 6). The peak was at the end of January in 2009, 2010 and 2012, while it was mid-February in 2011. Samples were categorized into some cohorts (Fig. 6).

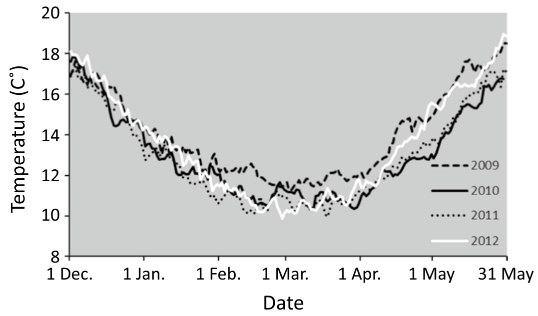

Fig. 5 Daily temperature observed at 12 m depth in Miyazu (see Fig. 1)

Table 1 Regressions for standard length (SL, mm) and age (days) for juveniles collected in the Yura River estuary from 2009 to 2012. All *P* values 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

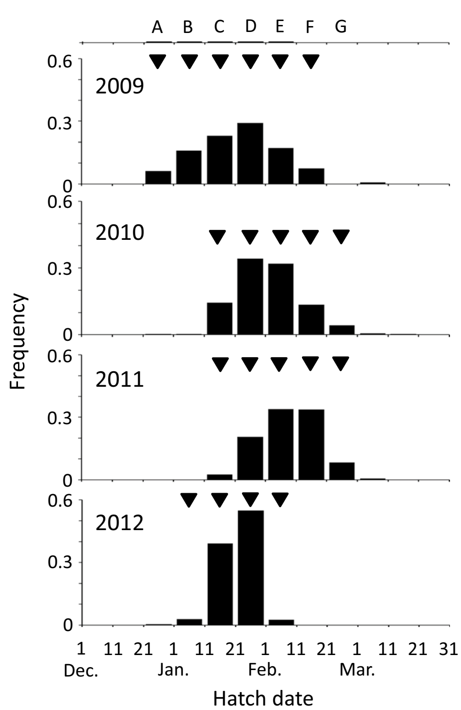

Fig. 6 Hatch date distributions of juvenile temperate sea bass. *Alphabet characters* indicate the cohorts. *Triangles* indicate cohorts used for further analysis

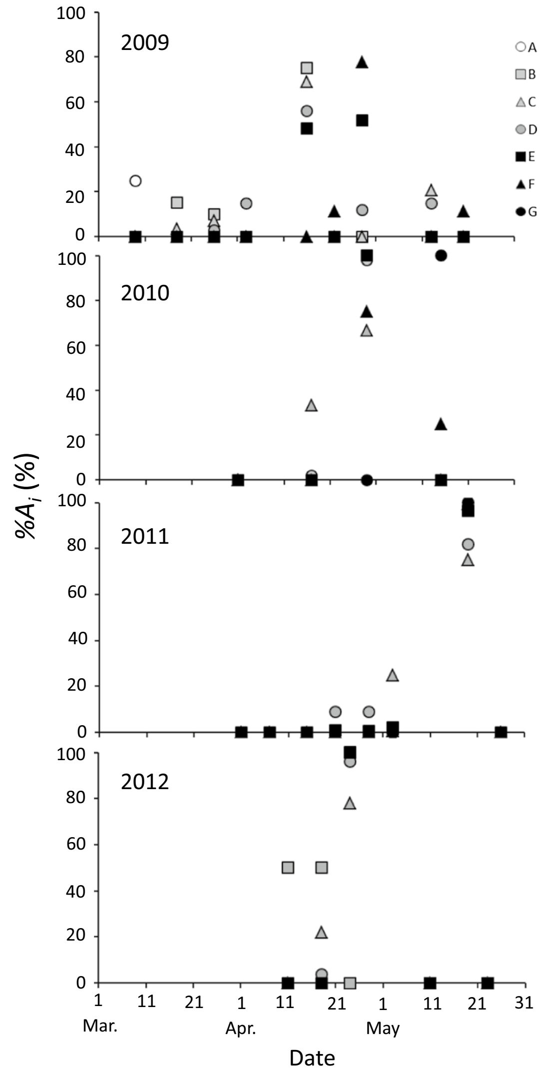

Fig. 7 River ascending index ($\%A_i$) of juvenile temperate sea bass for each cohort. *Alphabet characters* of legends agree with name of cohorts indicated in Fig. 6

$\%A_i$ change with time comprised mainly of two phases (Fig. 7); low intensity ascent (when $\%A_i$ were mostly lower than 30%) followed by mass ascent ($\%A_i > 50\%$). Different cohorts showed different timings of surge; earlier cohorts ascended earlier. The first day of ascending among cohorts ranged from 9 March (cohort A in 2009) to 18 May (cohort G in 2011). The day of main river ascending was very variable, ranging from 10 April (2012) to 18 May (2011). Mean temperature they experienced until the first ascending day (T) ranged from 11.0 to 12.7 °C (Fig. 8a), showing a significant correlation with $1/D$ (Pearson's correlation coefficient: $R^2 = 0.39$, $P \leq 0.05$), while no significant relationship was obtained for the main river ascending day ($P > 0.05$, Fig. 8b). Base temperature (t) and effective cumulative temperature (k) were estimated as 5.0 °C and 514.1 °C–days

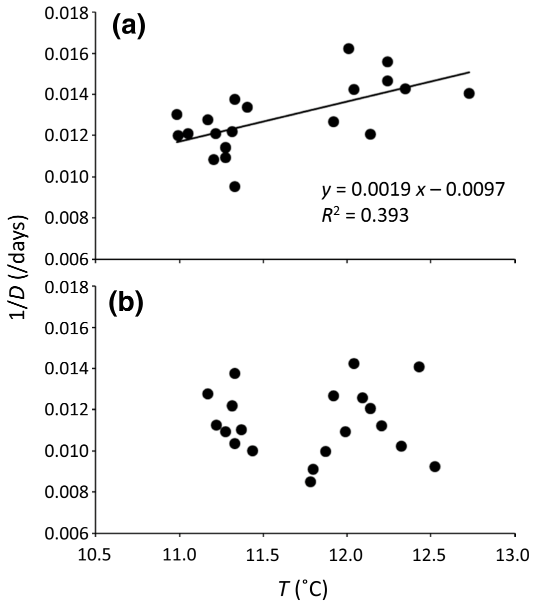

Fig. 8 **a** Relationship between the inverse of daily age on first river ascending day (D) of juveniles for each cohort and mean experienced temperature (T: °C) until ascending. **b** Relationship between the inverse of daily age on the main river ascending day for each cohort and mean experienced temperature until the main ascending day

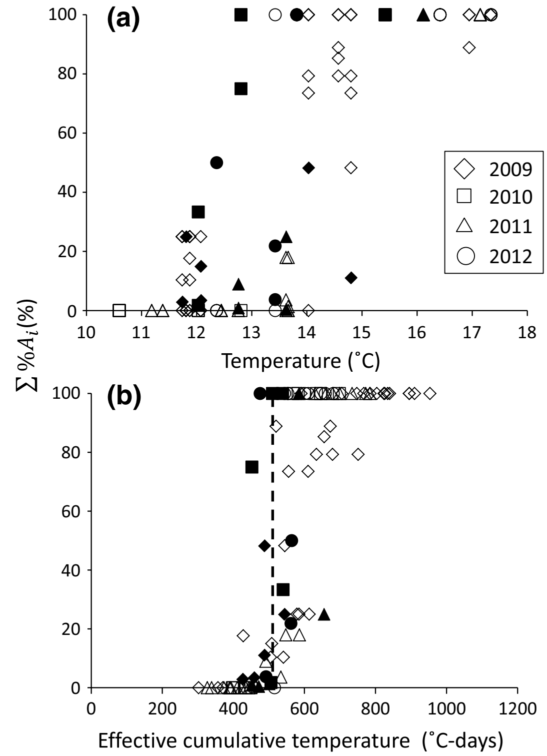

Fig. 9 Relationships between cumulative river ascending index (A_i) and **a** temperature and **b** effective cumulative temperature. *Broken line* indicates the effective cumulative temperature estimated for the first ascending day (514 °C–days). The first day that individuals for each cohort started to be collected in the lower or upper estuary (first ascending day) are shown by *filled plots*

for the first ascending day. Temperature on the first day of ascending was not a specific level or value, but varied, ranging from 11.7 to 16.1 °C (Fig. 9a). However, all cohorts in all 4 years showed a similar pattern of cumulative A_i trajectories against effective cumulative temperature (Fig. 9b). Most of the cohorts started to ascend the river at the ca. 500 °C–days. Many cohorts that did not attain the effective cumulative temperature distributed only in the coastal area, even though the salt wedge had already intruded (Fig. 10).

Discussion

Juveniles changed their distribution in the Yura River depending on the change of salt wedge intruding distance (Fig. 3). Distances that juveniles ascended the river were within the estimated distances of salt wedge intrusion except for 15 April 2009 and 18 May 2011 (Fig. 4). Although estimated distance of the salt wedge intrusion on 15 April 2009 was 9.3 km, the conductivity logger observed saltwater at 11 km upstream, which was the most upstream station juveniles were collected at on that date (Fig. 3). This indicates that juvenile distribution on this date was still less than the distance of the salt wedge intrusion. On the other hand, both estimated distance of salt wedge intrusion and bottom conductivity logger indicated that the salt wedge remained around 11 km upstream, while juveniles went further on 18 May 2011. Only larger individuals (> 23 mm SL) reached

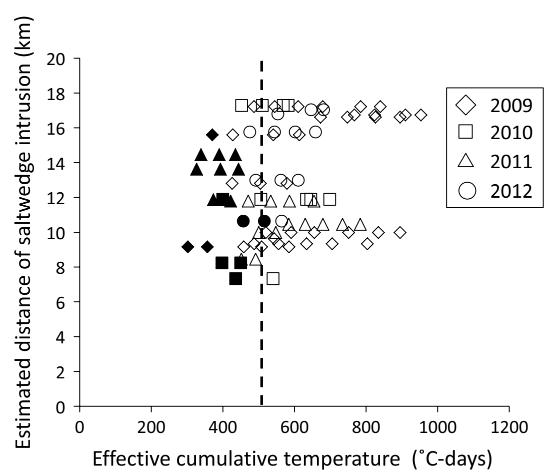

Fig. 10 Relationships between effective cumulative temperature and estimated distance of the salt wedge intrusion for each cohort. *Broken line* indicates the effective cumulative temperature estimated for the first ascending day (514 °C–days). *Filled plots* show the days that juveniles were collected only in the coastal area (St. 1 and St. 2)

15 km upstream (St. 6), while smaller ones (< 23 mm SL) remained at 11 km upstream (St. 5) on 18 May 2011. This would mean that only larger juveniles have enough osmoregulatory and swimming ability to ascend the river against the freshwater flow. Given the information that most juveniles ascend the river with the size smaller than 23 mm SL (Fuji et al. 2011), early juvenile temperate sea bass utilized the salt wedge intrusion to ascend the Yura River estuary. In the Chikugo River estuary, which is characterized by its large tidal amplitude, juveniles of temperate sea bass use tidal selective transport to ascend the river (Islam et al. 2007). Not only temperate sea bass 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 strong water currents (Yamashita et al. 1996; Gibson 1997; Islam et al. 2007). However, in the Yura River estuary, there is no strong tidal upstream current because of small tidal amplitude (Kasai et al. 2010). This means that juveniles cannot use the tidal selective transport in this area. The temperate sea bass juveniles are small when they ascend the river (ca. 20 mm SL) (Fuji et al. 2011). Generally speaking, the swimming speed of fish is ca. 10 times their body length/s, and small juveniles have little swimming ability (Tsukamoto and Kajihara 1973). For example, juvenile red seabream *Pagrus major* at a size of 20 mm SL can swim at a maximum of 0.18 m/s (Yano and Ogawa 1981). On the other hand, surface water at the Yura River mouth flows downstream at a speed of 0.22 m/s in summer, the lowest river discharge season during the year (Yamazaki et al. 2005). It is expected that this current speed increases in winter and spring when the river discharge is higher than summer because of snow melting (Kasai et al. 2010). This means that it is difficult for juvenile sea bass to ascend the river against the surface water current. In addition, the osmoregulatory ability of small juveniles is still not completed and a drastic change of salinity of ambient water would be lethal for sea bass juveniles (Hirai 2002). Around the Yura River mouth the salinity of the surface water in spring drastically changes from ca. 30 to almost 0 within a small spatial range (ca. 1 km) (Kasai et al. 2010). On the other hand, there is a stable broad brackish layer between the salt wedge and the surface layer in the Yura River estuary (Kasai et al. 2010) in which juveniles can physiologically adjust to lower salinity. In addition, water flows upstream in the bottom layer when the salt wedge intrudes (Dyer 1973). Therefore, it is efficient for juveniles to use the salt wedge intrusion to ascend the microtidal estuary.

The timing of the salt wedge intrusion and that of juvenile river ascending were sometimes mismatched; sometimes no juveniles were found in the river even though the salt wedge intruded into the river, especially during April in 2011 (Fig. 4). We also observed that many cohorts with insufficient cumulative temperature (< ca. 500 °C–days) resided in the coastal area regardless of the salt wedge intrusion (Fig. 10). This means that the salt wedge intrusion is one of the necessary conditions, but not a sufficient condition for juveniles to ascend the river. Salt wedge intrusion would be like opening a gate: juveniles can enter the estuary only when the gate opens. However, it does not mean that juveniles always ascend the river when the salt wedge intrudes. This study suggests that temperature has a decisive influence on the timing of river ascent.

Some previous papers reported that there are temperature thresholds for initiating fish migration (Kusuda 1963; Solomon 1978). On the other hand, cumulative temperature is known to be a 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 (Fig. 9). Former studies did not consider the effects of hatch dates and only focused on the first ascending day in a year. The present study showed many cohorts ascended the river with various timings (Fig. 7). This means that the temperatures at which they started ascending were different among cohorts and that there is no temperature threshold initiating migration behavior (Fig. 9). The effective cumulative temperature provides an indicator of the duration required for the completion of biological processes (Trudgill et al. 2005). Therefore, there may be some developmental biological processes which have to be completed before starting the river ascent; for example, ability to swim and osmoregulation. Higher 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 sea bass juveniles corresponds with the completion of swimming ability and osmoregulation, which are necessary for diadromous migrations (Hirai 2002). This means that larvae at higher temperatures can complete the preparation for diadromous migrations at a younger age. This enables them to ascend the river at younger ages (Fig. 8a). Base temperature (t) estimated in this study (5.0 °C) means the temperature at which body development of larval temperate sea bass ceases. Makino et al. (2003) reported that no eggs of temperate sea bass hatched out at 5 °C.

On the other hand, the effective cumulative temperature was not a good indicator for the main river ascending days (Fig. 9). There must be other factors which induce the mass river ascending of juveniles. Tsukamoto et al. (2009) thought that fish start to migrate by receiving a trigger from particular endogenous or exogenous factors after filling necessary conditions, e.g., age or body size. After filling the necessary 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, the stimulus of a waterfall is the important factor for inducing river ascending behavior (Uchida et al. 1990). Being exposed to a river plume in the coastal area might be one of the potential triggers for juvenile temperate sea bass to start river ascending behavior, because juvenile temperate sea bass start to change the structure of their gills to adjust to lower salinity water after they experience lower salinity water (Hirai et al. 1999). The main river ascending of most cohorts occurred after flood events (Figs. 2, 7).

This study suggests that the mechanism of river ascent by juvenile temperate sea bass is as follows; juveniles start to ascend the river after at least two conditions are met: body development, which is indexed by an effective cumulative temperature of 514.1 °C–days, and salt wedge intrusion. Recruitment to riverine nurseries is important for juvenile temperate sea bass because it is a good environment for prey (Fuji et al. 2016a), which leads to high growth rates (Fuji et al. 2014) and high contribution to the adult population (Fuji et al. 2016b). Therefore, both temperature and salt wedge dynamics could be crucial factors for population dynamics by restricting river ascent. Over the 4 years of this study, temperature was the main restricting factor in starting the river ascent (Fig. 10), because the salt wedge almost resided in the river during sampling seasons. Low temperature in winter could disturb river ascent and extend the period for stay in the coastal area, where higher mortality would be caused by many predators. On the other hand, high river discharge during the winter-spring season might also restrict the utilization of the riverine nursery area. For example, Shoji et al. (2006) thought that high river flow had the potential to decrease the probability of immigration of juvenile sea bass into the Chikugo River estuary by increasing juvenile seaward dispersion. Shoji and Tanaka (2006) also argued that ascending would lead to lower mortality, because there are more predators in the high salinity environment, e.g., jellyfishes and arrow-worms. Annual variation of the salt wedge intrusion could affect the recruitment of temperate sea bass in the rivers into the Tango Sea. Further study is necessary to confirm this possibility.

Acknowledgements We would like to express our sincere gratitude to Dr. Masahiro Ueno for his creative comments and help with samplings. This study was partly supported by the Coastal Ecosystem Complex Project of the Ocean Resource Use Promotion Technology Development Program, MEXT of Japan.

References

Arayama K, Imai J, Kanou K, Kohno H (2002) Ichthyofauna of surf zones in the outer Tokyo Bay. La mer 40:59–70 **(in Japanese with English abstract)**

Benoît HP, Pepin P, Brown JA (2000) Patterns of metamorphic age and length in marine fishes, from individuals to taxa. Can J Fish Aquat Sci 57:856–869

Bohlin T, Dellefors C, Faremo U (1993) Timing of sea-run brown trout (*Salmo trutta*) smolt migration: effects of climatic variation. Can J Fish Aquat Sci 50:1132–1136

Boubée JA, Mitchell PC, Chisnall BL, West DW, Bowman EJ, Haro A (2001) Factors regulating the downstream migration of mature eels (*Anguilla* spp.) at Aniwhenua dam, Bay of Plenty, New Zealand. New Zeal J Mar Fresh Res 35:121–134

Dyer KR (1973) Estuaries: a physical introduction. Wiley, London

Fuji T, Kasai A, Suzuki KW, Ueno M, Yamashita Y (2010) Freshwater migration and feeding habits of juvenile temperate seabass *Lateolabrax japonicus* in the stratified Yura River estuary, the Sea of Japan. Fish Sci 76:643–652

Fuji T, Kasai A, Suzuki KW, Ueno M, Yamashita Y (2011) Migration ecology of juvenile temperate seabass *Lateolabrax japonicus*: a carbon stable-isotope approach. J Fish Biol 78:2010–2025

Fuji T, Kasai A, Ueno M, Yamashita Y (2014) Growth and migration patterns of juvenile temperate seabass *Lateolabrax japonicus* in the Yura River estuary, Japan—combination of stable isotope ratio and otolith microstructure analyses. Environ Biol Fish 97:1221–1232

Fuji T, Kasai A, Ueno M, Yamashita Y (2016a) The importance of estuarine production of large prey for the growth of juvenile temperate seabass (*Lateolabrax japonicus*). Estuar Coasts 39:1208–1220

Fuji T, Kasai A, Ueno M, Yamashita Y (2016b) Importance of estuarine nursery areas for the adult population of the temperate seabass *Lateolabrax japonicus*, as revealed by otolith Sr:Ca ratios. Fish Oceanogr 25:448–456

Fujita S (2004) Ecological study on larvae and juveniles of the two sea basses and the three sparines occurring in the Shimanto Estuary, Japan. Bull Mar Sci Fish Kochi Univ 23:1–57 **(in Japanese with English abstract)**

Fujita S, Kinoshita I, Takahashi I, Azuma K (1988) Seasonal occurrence and food habits of larvae and juveniles of two temperate basses in the Shimanto Estuary, Japan. Jpn J Ichthyol. 35:365–370

Gibson RN (1997) Behavior and the distribution of flatfishes. J Sea Res 37:241–256

Hatanaka M, Sekino K (1962) Ecological studies on the Japanese seabass, *Lateolabrax japonicus*—1. Feeding habit. Nippon Suisan Gakkaishi 28:851–856 **(in Japanese with English abstract)**

Hayashi B, Kiyono S (1978) Ecological studies on the Japanese sea bass, in the western Wakasa Bay—2. The food habitat and growth of Japanese seabass in yearling. Rep Kyoto Inst Ocean Fish Sci 2:109–116 **(in Japanese)**

Hibino M, Ohta T, Kinoshita I, Tanaka M (2002) Fish larvae and juveniles occurring in the littoral zone of a tidal flat, in the bottom of Ariake Bay, Japan. J Ichthyol 49:109–120

Hibino M, Ohta T, Isoda T, Nakayama K, Tanaka M (2007) Distribution of Japanese temperate bass, *Lateolabrax japonicus*, eggs and pelagic larvae in Ariake Bay. Ichthyol Res 54:367–373

Hirai N (2002) Physiology of osmoregulation. In: Tanaka M, Kinoshita I (eds) Temperate bass and biodiversity. Koseisha-koseikaku, Tokyo, pp 103–113 **(in Japanese)**

Hirai N, Tagawa M, Kaneko T, Seikai T, Tanaka M (1999) Distributional changes in branchial chloride cells during freshwater adaptation in Japanese sea bass *Lateolabrax japonicus*. Zool Sci 16:43–49

Hoffman JC, Limburg KE, Bronk DA, Olney JE (2008) Overwintering habitats of migratory juvenile American shad in Chesapeake Bay. Env Biol Fish 81:329–345

Ichthyological Society of Japan (2003) Guidelines for the use of fishes in research. The Ichthyological Society of Japan, Japan. http://www.fish-isj.jp/english/guidelines.html

Islam MS, Hibino M, Tanaka M (2007) Tidal and diurnal variations in larval fish abundance in an estuarine inlet in Ariake Bay, Japan: implication for selective tidal stream transport. Ecol Res 22:165–171

Islam MS, Ueno M, Yamashita Y (2009) Otolith microstructure of Japanese seabass larvae and juveniles: interpretation and utility for ageing. J Appl Ichthyol 25:423–427

Iwamoto Y, Morita T, Shoji J (2010) Occurrence and feeding habits of Japanese seabass *Lateolabrax japonicus* larvae and juveniles around the Ohta River estuary, upper Hiroshima Bay, Seto Inland Sea. Nippon Suisan Gakkaishi 76:841–848 **(in Japanese with English abstract)**

Iwata M, Tsuboi H, Yamashita T, Amemiya A, Yamada H, Chiba H (2003) Function and trigger of thyroxine surge in migrating chum salmon *Oncorhynchus keta* fry. Aquaculture 222:315–329

Jansen T, Gislason H (2011) Temperature affects the timing of spawning and migration of North Sea mackerel. Cont Shelf Res 31:64–72

Kaeriyama M (1989) Development and growth of the genus *Oncorhynchus* 1. Concepts and effective accumulative temperature on development and growth. Tech Rep Hokkaido Salmon Hatch 158:22–28

Kasai A, Kurikawa Y, Ueno M, Robert D, Yamashita Y (2010) Salt-wedge intrusion of seawater and its implication for phytoplankton dynamics in the Yura Estuary, Japan. Estuar Coast Shelf Sci 86:408–414

Kinoshita I (2002) Diversity of the early life history. In: Tanaka M, Kinoshita I (eds) Temperate bass and biodiversity. Koseisha-koseikaku, Tokyo, pp 79–90 **(in Japanese)**

Kusuda R (1963) An ecological study of the anadromous "ayu" *Plecoglossus altivelis* T. et S.—2. Seasonal variations in the composition of the anadromous ayu schools in the river Okumo, Kyoto. Nippon Suisan Gakkaishi 29:822–827 **(in Japanese with English abstract)**

Kuwatani Y (1962) The comprehensive study for fish banks related to the ecology of temperate seabass. Ann Rep Kyoto Prefect Fish Exp 8:1–124 **(in Japanese)**

Makino N, Matumaru Y, Tanaka M (2003) Effects of temperature and salinity on egg development of the Japanese sea bass, *Lateolabrax japonicus*. Aquac Sci 51:55–64 **(in Japanese with English abstract)**

Matsumiya Y, Mitani T, Tanaka M (1982) Changes in distribution pattern and condition coefficient of the juvenile Japanese sea bass with the Chikugo River ascending. Nippon Suisan Gakkaishi 48:129–138 **(in Japanese with English abstract)**

McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 55:77–92

Nakamura T, Kasuya K (2004) Forecasting of the first ascending day and the number of ascending schools of amphidromous ayu *Plecoglossus altivelis* in the Naka River, Tochigi Prefecture, central Japan. Nippon Suisan Gakkaishi 70:288–296 **(in Japanese with English abstract)**

Nakane Y, Suda Y, Sano M (2010) Food habits of fishes on an exposed sandy beach at Fukiagehama, South-West Kyushu Island, Japan. Helgol Mar Res 65:123–131

North EW, Houde ED (2001) Retention of white perch and striped bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. Estuaries 34:756–769

Ohmi H (2002) Juvenile ecology in Yura river estuary in Wakasa Bay. In: Tanaka M, Kinoshita I (eds) Temperate bass and biodiversity. Koseisha-koseikaku, Tokyo, pp 44–53 **(in Japanese)**

Shoji J, Tanaka M (2006) Influence of spring river flow on the recruitment of Japanese seaperch *Lateolabrax japonicus* into the Chikugo estuary, Japan. Sci Mar 70S2:159–164

Shoji N, Sato K, Ozaki M (2002) Distribution and utilization of the stock. In: Tanaka M, Kinoshita I (eds) Temperate bass and biodiversity. Koseisha-koseikaku, Tokyo, pp 9–20 **(in Japanese)**

Shoji J, Ohta T, Tanaka M (2006) Effects of river flow on larval growth and survival of Japanese seaperch *Lateolabrax japonicus* (Pisces) in the Chikugo River estuary, upper Ariake Bay. J Fish Biol 69:1662–1674

Solomon DJ (1978) Migration of smolts of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) in a chalk stream. Env Biol Fish 3:223–229

Suzuki KW, Kasai A, Ohta T, Nakayama K, Tanaka M (2008) Migration of Japanese temperate bass *Lateolabrax japonicus* juveniles within the Chikugo River estuary revealed by $\delta^{13}C$ analysis. Mar Ecol Prog Ser 358:254–256

Tamura Y, Moteki M, Yokoo T, Kohno H (2013) Occurrence patterns and ontogenetic intervals based on the development of swimming- and feeding-related characters in larval and juvenile Japanese sea bass (*Lateolabrax japonicus*) in Tokyo Bay. La mer 51:13–29

Trudgill DL, Honek A, Li D, Van Straalen NM (2005) Thermal time—concepts and utility. Ann Appl Biol 145:1–14

Tsukamoto K, Kajihara T (1973) Swimming speed and ability of fish. Fish Eng 10:31–36

Tsukamoto K, Miller MJ, Kotake A, Aoyama J, Uchida K (2009) The origin of fish migration: the random escapement hypothesis. In: Haro AJ, Smith KL, Rulifson RA, Moffitt CM, Klauda RJ, Dadwell MJ, Cunjak RA, Cooper JE, Beal KL, Avery TS (eds) Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society Symposium vol 69, Bethesda, pp 45–61

Uchida K, Tsukamoto K, Kajihara T (1990) Effects of environmental factors on jumping behavior of the juvenile ayu *Plecoglossus altivelis* with special reference to their upstream migration. Nippon Suisan Gakkaishi 56:1393–1399

Watanabe T (1965) Ecological distribution of eggs of common sea bass, *Lateolabrax japonicus* (Cuvier) in Tokyo Bay. Nippon Suisan Gakkaishi 31:585–590 **(in Japanese with English abstract)**

Watanabe Y, Kawamura T, Yamashita Y (2018) Introduction: the coastal ecosystem complex as a unit of structure and function of biological productivity in coastal areas. Fish Sci 84. https://doi.org/10.1007/s12562-018-1176-7

Yamashita Y, Tsuruta Y, Yamada H (1996) Transport and settlement mechanisms of larval stone flounder, *Kareius bicoloratus*, into nursery grounds. Fish Oceangr 5:194–204

Yamazaki Y (2002) Effectiveness of hatchery-raised juveniles released to a brackish lake Hinuma. In: Tanaka M, Kinoshita I (eds) Temperate bass and biodiversity. Koseisha-koseikaku, Tokyo, pp 32–43 **(in Japanese)**

Yamazaki T, Watanabe T, Taga M (2005) Current observations at the mouth of Yura River. Tech Bull Hydrogr Oceanogr 23:112–118 **(in Japanese)**

Yano I, Ogawa Y (1981) Swimming speeds of larvae and juvenile of red sea bream, *Chrysophrys major*. Bull Natl Res Inst Aquac 2:49–54 **(in Japanese with English abstract)**

Zydlewski GB, Haro A, McCormick SD (2005) Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. Can J Fish Aquat Sci 62:68–78