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

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Abstract

Hydrographic conditions and distributions of juvenile temperate seabass *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 saltwedge. In all four studied years, the upstream expansion of their distribution coincided with the timing of the saltwedge intrusion from the lower to upper estuary, indicating that juvenile fish used saltwedge intrusions to ascend the estuary in early spring. However, juveniles sometimes remained in the nearshore area even when the saltwedge intrusion had already occurred, indicating that other triggers are also likely to be necessary. We therefore evaluated the effects of temperature on upstream migration behaviours. The relationship between the mean temperature they experienced from hatchuntil starting the ascent and mean age of each cohort at the upstream migration was fitted in 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: “saltwedge intrusion” “river ascending” “catadromous migration” “juvenile”

Introduction

Temperate seabass *Lateolabrax japonicus* is an important euryhaline species for Japanese coastal fisheries (Shoji et al. 2002). Its utilization of the “coastal ecosystem complex” is characterized as follows; 1) ontogenetic shift of habitats and 2) parallel utilization of various habitats. This fish is known to change its habitats ontogenetically during the early life history as well as other coastal fishes. Temperate seabass 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 there 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 parallel as nurseries after early spring, e.g., seagrass beds (Hatanaka and Sekino 1962, Kinoshita 2002), sandy beach (Fuji et al. 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). Especially, estuaries have been considered as an important nursery for temperate seabass because of its good prey environment (Fuji et al. 2016a) leading to high growth of juveniles (Fuji et al. 2011, Fuji et al. 2014) and high contribution to adult population regardless of its small area relative to other coastal areas (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 would 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 should overcome the river flow regardless of their poor swimming ability. Larvae of some species of fish including temperate seabass 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 that they would use another way to migrate. Saltwedge intrusion is another possible environmental factor which juveniles might use when they ascend 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. However, few researchers have focused on the relationship between juvenile river ascending and saltwedge intrusions.

Second, many studies have 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 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 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).

Hypothesis in this study is that juvenile temperate seabass uses the saltwedge intrusion for ascending the microtidal estuaries. In addition, the relationship between effective cumulative temperature and timing of river ascending was also estimated to confirm that temperature is also an important factor for deciding the timing of river ascending.

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

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 in March, April and May from 2009 to 2012. Three minute tows were performed two times 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 in 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 saltwedge 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 minutes.

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 seabass juveniles of ca. 20 to 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). Age of temperate seabass 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 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 the 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 Japan Meteorological Agency (http://www.data.jma.go.jp/kaiyou/db/tide/suisan/suisan.php).

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 saltwedge, where salinity was 5 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, saltwedge distance and juvenile ascending distance, were compared.

SL - 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 the SL that is 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 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 analysis.

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

$$A_i = N_i - N_{i-1}\ , \qquad (1)$$

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;

$$\%\mathrm{A}_i = \frac{A_i}{\sum A_i}, \qquad (2)$$

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

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

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

$$k = D(T - t), \qquad (4)$$

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 considered as the lower limit below which the biological process will cease (Trudgill et al. 2005). 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 defined by following two ways; first days that individuals started to be collected in the lower or upper estuary (first ascending day) and main ascending days that 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

$$\frac{1}{D} = -\frac{t}{k} + \frac{T}{k}\ . \qquad (5)$$

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 saltwedge intrusion and juvenile river ascending

The fluctuation patterns of river discharge in spring were different among the four years (Fig. 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. The river discharge was low until April and then two heavy floods (over 1000 m^3/s) occurred in the 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 since the beginning 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, the saltwedge intruded into the river up to 6 km upstream from the end of April when the river discharge decreased. The saltwedge then reached 11 km upstream in the beginning of May. In 2011, salinity around the river mouth increased from April, and then the saltwedge reached 11 km upstream in the middle of April and 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 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 movements (Fig. 3). For example, in 2009, juvenile distributions were restricted in the coastal area and the lower estuary during March and beginning of April, when the saltwedge intruded until 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 saltwedge intrusion distance and juvenile ascending distance showed juveniles rarely ascended further than the saltwedge intrusion (Fig. 4). Juveniles went beyond the saltwedge only 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. 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.

In total, ages of 204 individuals with the 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. Hatch date distributed mainly from the mid-January to mid-February (Fig. 6). The peak was at the end of January in 2009, 2010 and 2012, while mid-February in 2011. Samples were categorized into some cohorts (Fig. 6). $\%A_i$ change with time comprised mainly of two phases (Fig. 7); low intensity ascent ($\%A_i$ were mostly lower than 30%) followed by mass ascent ($\%A_i > 50$ %). Different cohorts showed different timing 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 considerably different 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 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 four 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 saltwedge had already intruded (Fig. 10).

Discussion

Juveniles changed their distribution in the Yura River depending on the change of saltwedge intruding distance (Fig. 3). Distances that juveniles ascended the river were within the estimated distances of saltwedge intrusion except for 15 April 2009 and 18 May 2011 (Fig. 4). Although estimated distance of the saltwedge intrusion on 15 April 2009 was 9.3 km, the conductivity logger observed saltwater at 11 km upstream which is the most upstream station juveniles were collected on that date (Fig. 3). This indicates that juvenile distribution on this date was still below the distance of the saltwedge intrusion. On the other hand, both estimated distance of saltwedge intrusion and bottom conductivity logger indicated that the 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 (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 of juveniles ascend the river with the size smaller than 23 mm SL (Fuji et al. 2011), early juvenile temperate seabass utilized the saltwedge intrusion to ascend the Yura River estuary. In the Chikugo River estuary, which is characterized by its large tidal amplitude, juveniles of temperate seabass use tidal selective transport to ascend the river (Islam et al. 2007). 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 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 seabass juveniles are small when they ascend the river (ca. 20 mm SL) (Fuji et al. 2011). Generally speaking, swimming speed of fish is ca. 10 times of their body length and small juveniles have little ability to swim (Tsukamoto and Kajihara, 1973). For example, juvenile red seabream *Pagrus major* at the size of 20 mm

SL can swim at 0.18 m/s at a maximum (Yano and Ogawa 1981). On the other hand, surface water at the Yura River mouth flows downstream at the speed of 0.22 m/s 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 (Kasai et al. 2010). This means that it is difficult for juvenile seabass to ascend the river against the surface water current. In addition, osmoregulatory ability of small juveniles is still not completed and drastic change of salinity of ambient water would be lethal for seabass 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 saltwedge 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 saltwedge intrudes (Dyer 1973). Therefore, it is efficient for juveniles to use the saltwedge intrusion to ascend the microtidal estuary.

The timing of the saltwedge intrusion and that of juvenile river ascending sometimes were mismatched; sometimes no juveniles were found in the river even though the saltwedge intruded into the river, especially during April in 2011 (Fig. 4). We also observed that many cohorts with the insufficient cumulative temperature (< ca. 500 ˚C-days) resided in the coastal area regardless of the saltwedge intrusion (Fig. 10). This means that the saltwedge intrusion is one of the necessary conditions, but not a sufficient condition for juveniles to ascend the river. Saltwedge 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 saltwedge intrudes. This study suggests that temperature would have a decisive influence on the timing of the river ascending.

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 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 in various timings (Fig. 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. 9). The effective cumulative temperature provides a major of “duration” required for the completion of the biological process (Trudgill et al. 2005). Therefore, there could be some biological processes which should be completed before starting the river ascending. The body development which is relating to the river ascending, e.g., ability developments of swimming and osmoregulation, would be biological processes to be completed. 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 seabass juveniles corresponds to the complement of swimming ability and osmoregulation, which are necessary for diadromous migrations (Hirai 2002). This means that larvae under higher temperatures can complete the preparation for diadromous migrations in 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 seabass cease. Makino et al. (2003) reported that no eggs of temperate seabass 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 should be other factors which induce the mass river ascending of juveniles. Tsukamoto et al. (2009) considered 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, stimuli of a wataerfall is the important factor to induce the river ascending behavior (Uchida et al. 1990). Being exposed to river plume in the coastal area might be 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). Main river ascending of most cohorts occurred after flood events (Figs. 2 and 7).

This study suggests that the mechanism of river ascending of juvenile temperate seabass was estimated as follows; juveniles start to ascend the river after at least two conditions were filled; body development, which is indexed by effective cumulative temperature of 514.1 ˚C-days, and saltwedge intrusion. Recruitment to riverine nurseries is important for juvenile temperate seabass because of its good prey environment (Fuji et al. 2016a), which leads to high growth rates (Fuji et al. 2014) and high contribution to its adult population (Fuji et al. 2016b). Therefore, both temperature and saltwedge dynamics could be crucial factors for population dynamics by restricting the river ascending. In the four years in this study, temperature was the main restricting factor of starting the river ascending (Fig. 10), because the saltwedge almost resided in the river during sampling seasons. Low temperature in winter could disturb the river ascending 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 winter-spring season might also restrict the utilization of riverine nursery area. For example, Shoji et al. (2006) considered that high river flow had the potential to decrease the probability of immigration of juvenile seabass into the Chikugo River estuary by increasing juvenile seaward dispersion. Shoji and Tanaka (2006) also argued the reason for 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 saltwedge intrusion could affect the recruitment of temperate seabass in the rivers into Tango Sea or the generality to other rivers in this area. Further study is necessary to confirm this possibility.

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Figure legends

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.

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

Fig. 3 Bottom salinity measured by salinity loggers (lines, left vertical axis) and total number of juvenile temperate seabass *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.

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

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

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

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

Fig. 8 (a) Relationship between the inverse of daily age at 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 at 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). 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.

Fig. 10 Relationships between effective cumulative temperature and estimated distance of the saltwedge 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 2).

Table 1 Regressions for standard length (SL, mm) and age (day) 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

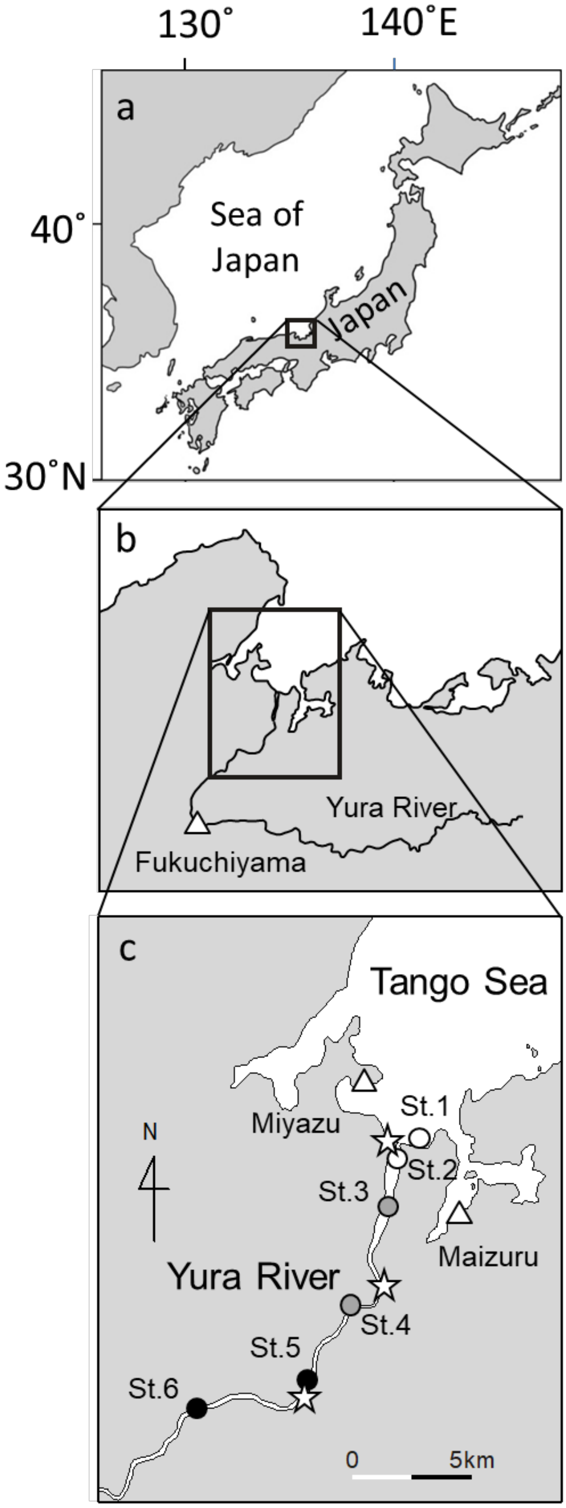
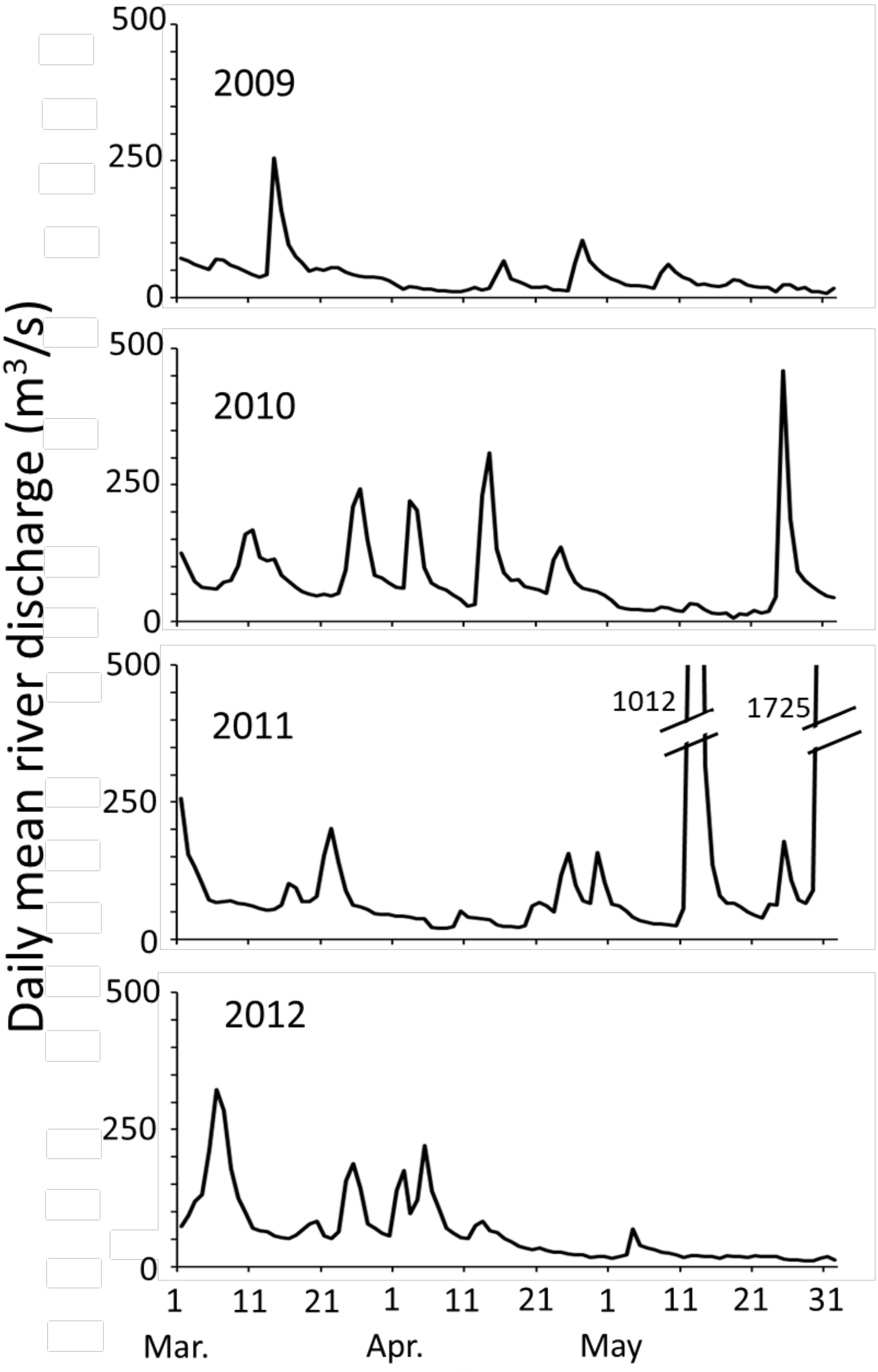


Fig. 1 Fuji et al.



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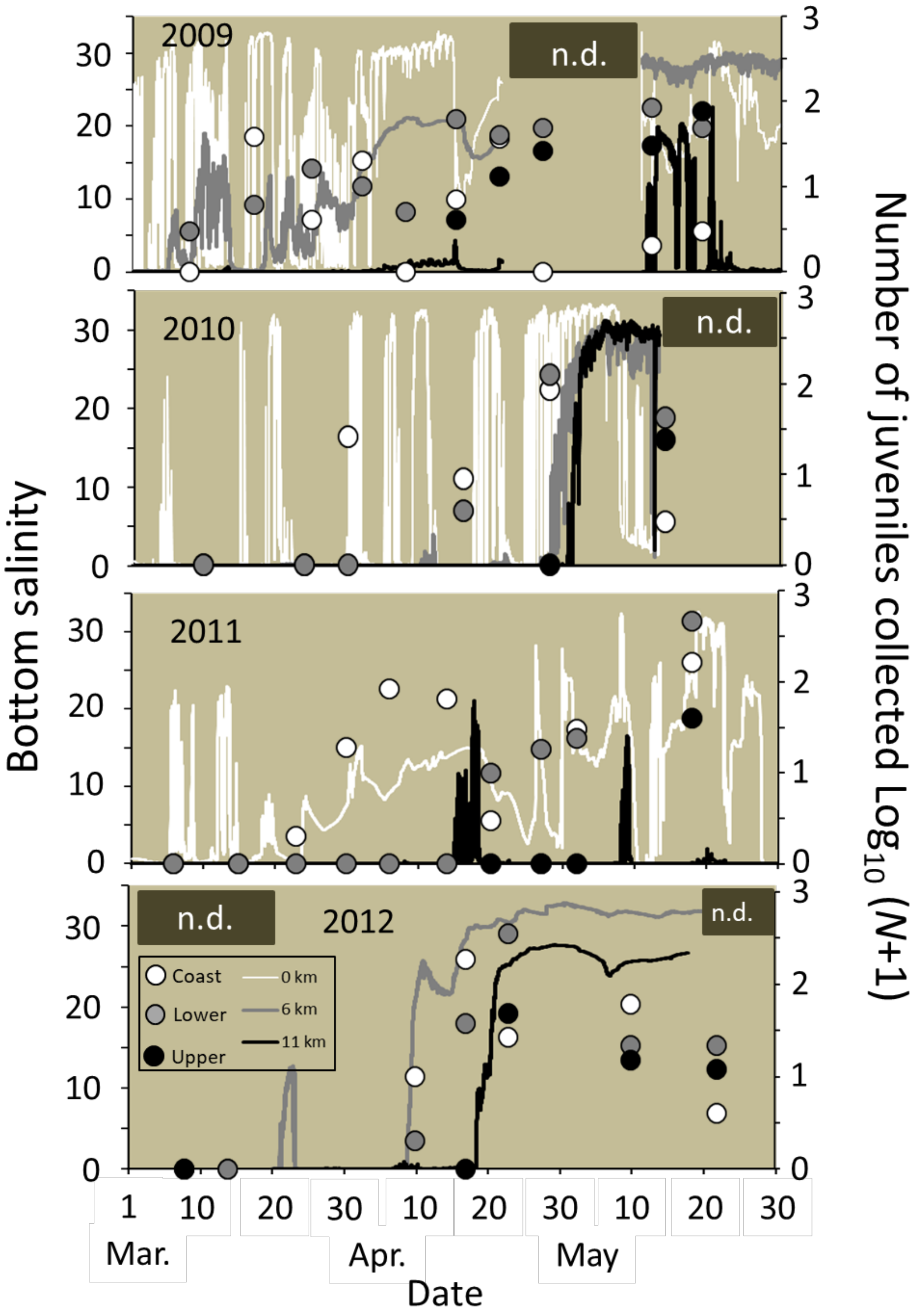

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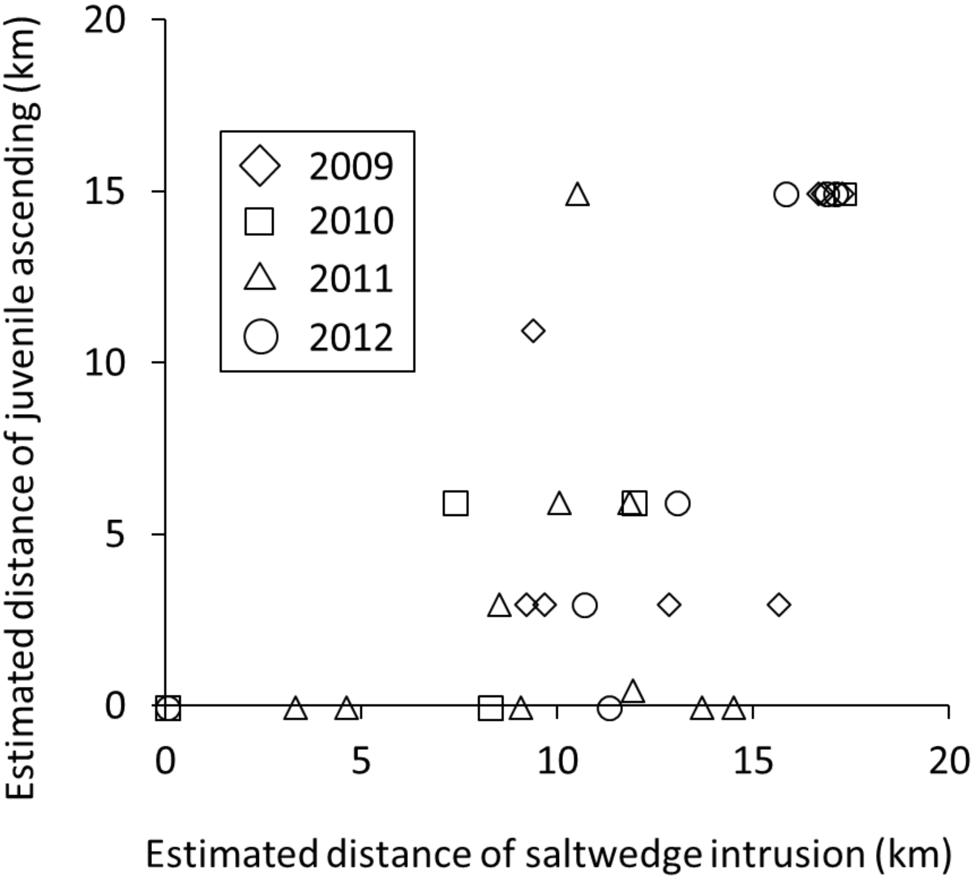

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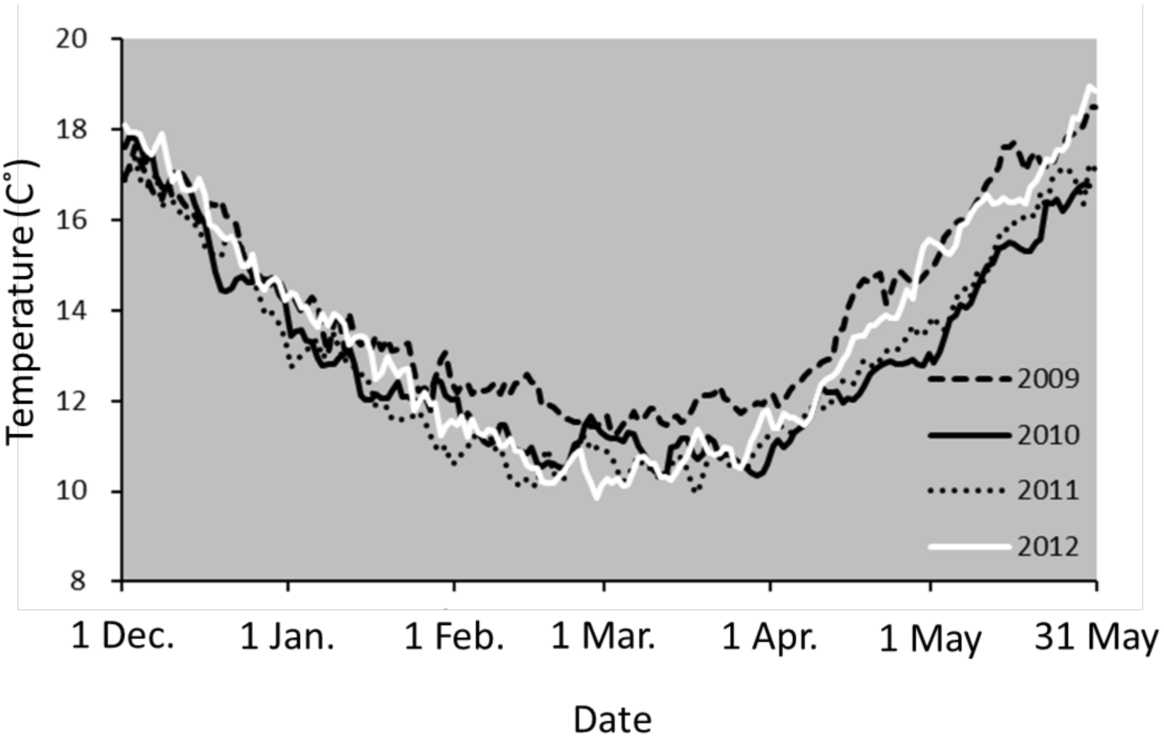

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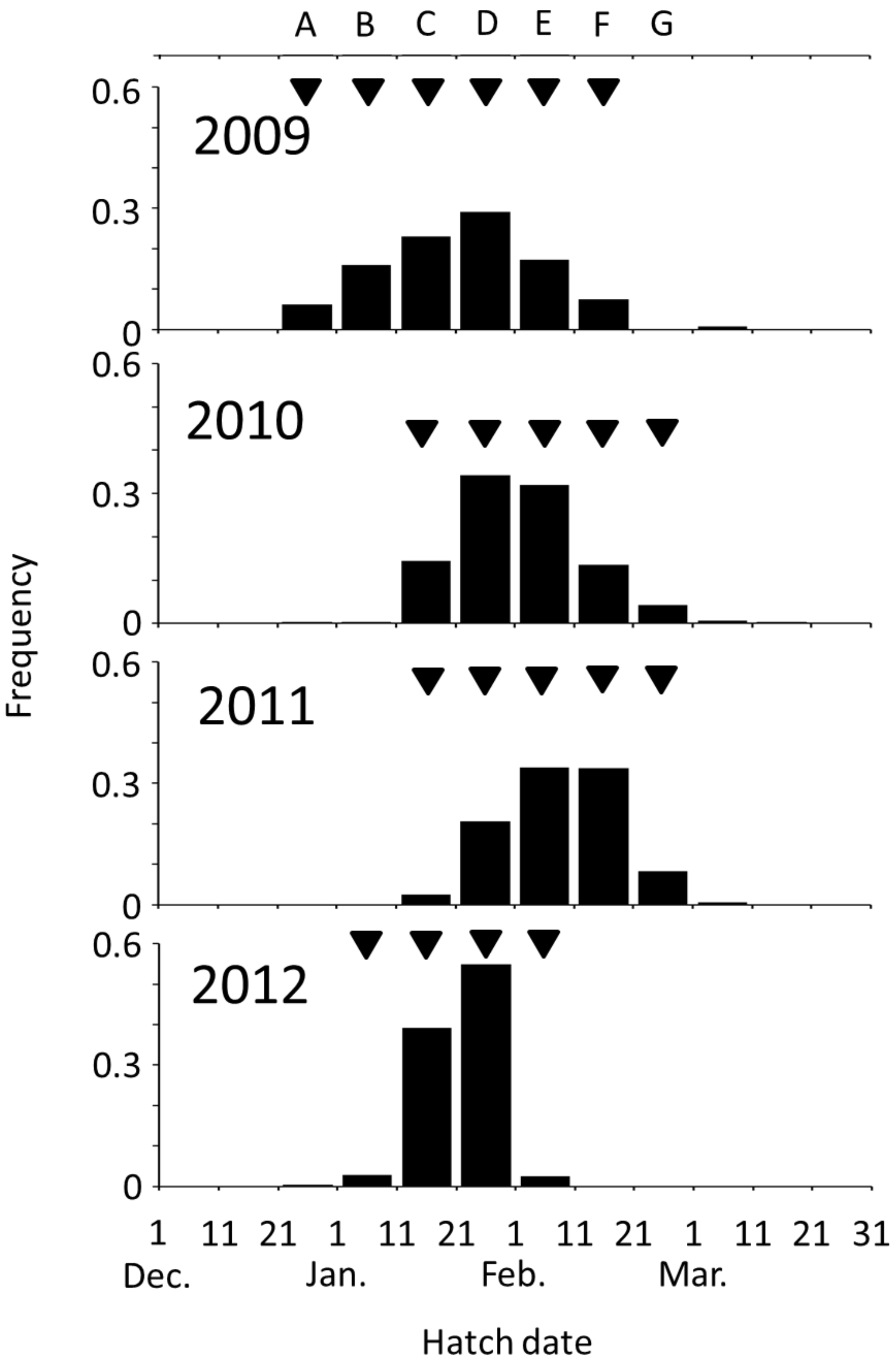

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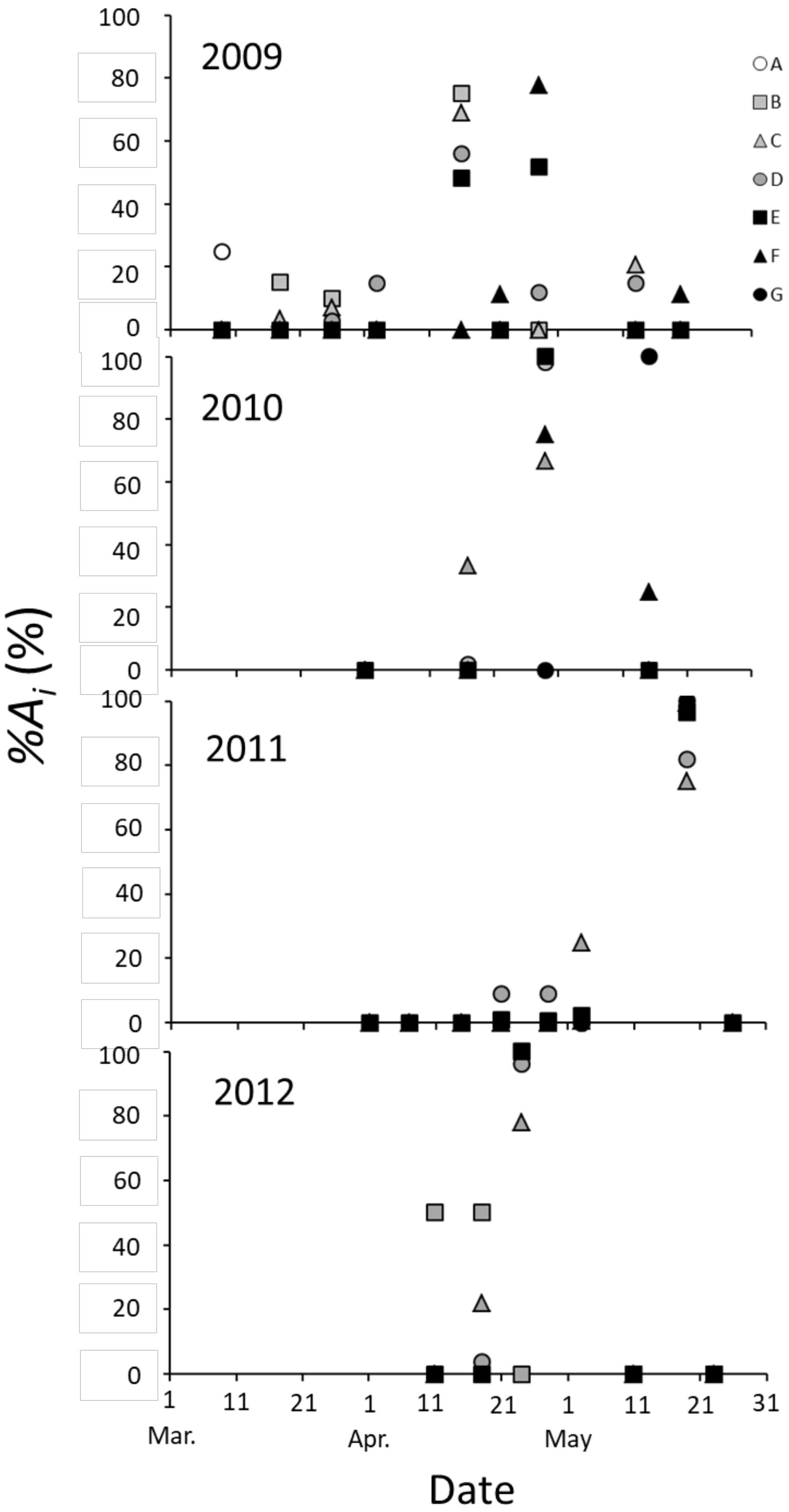

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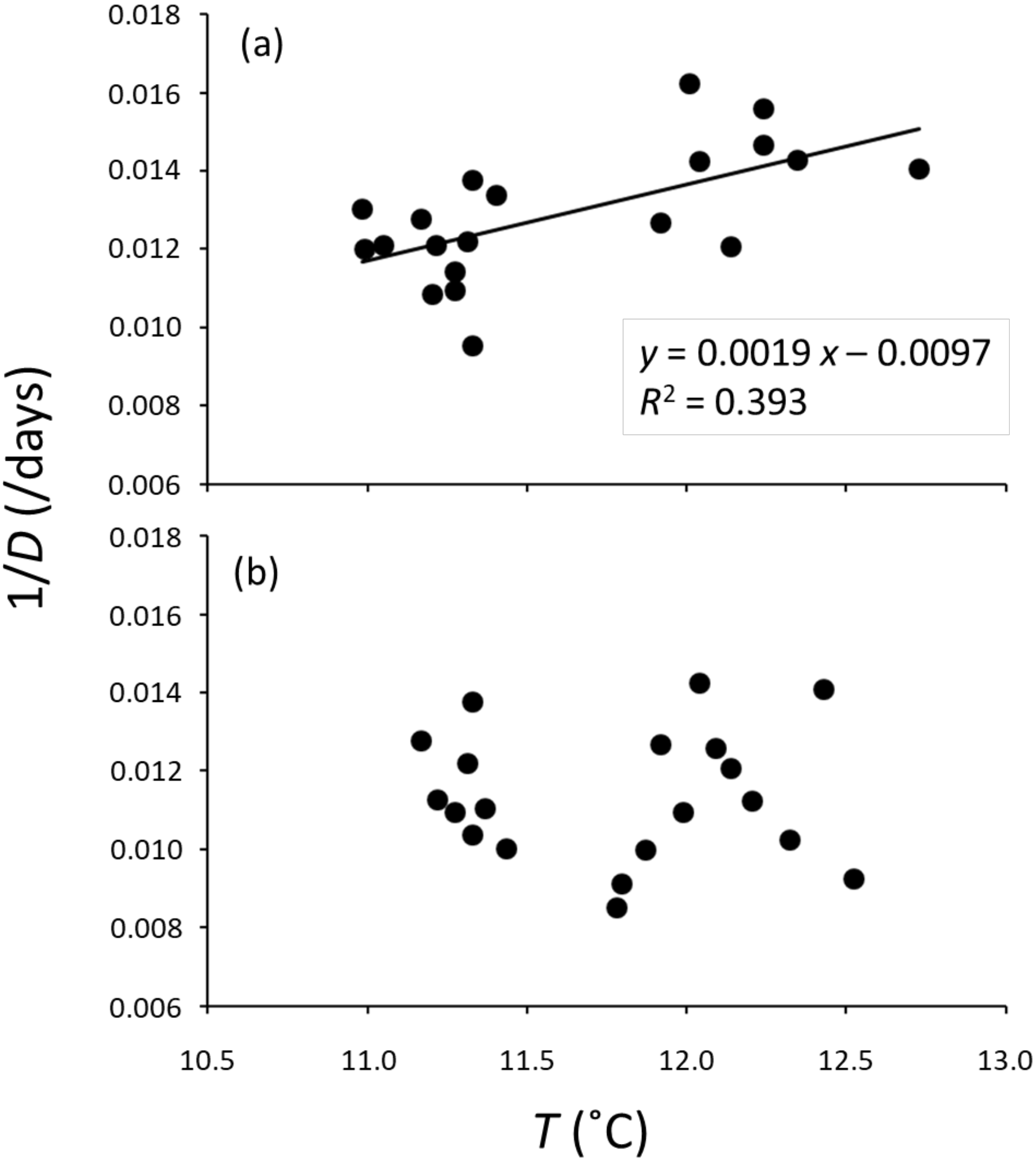

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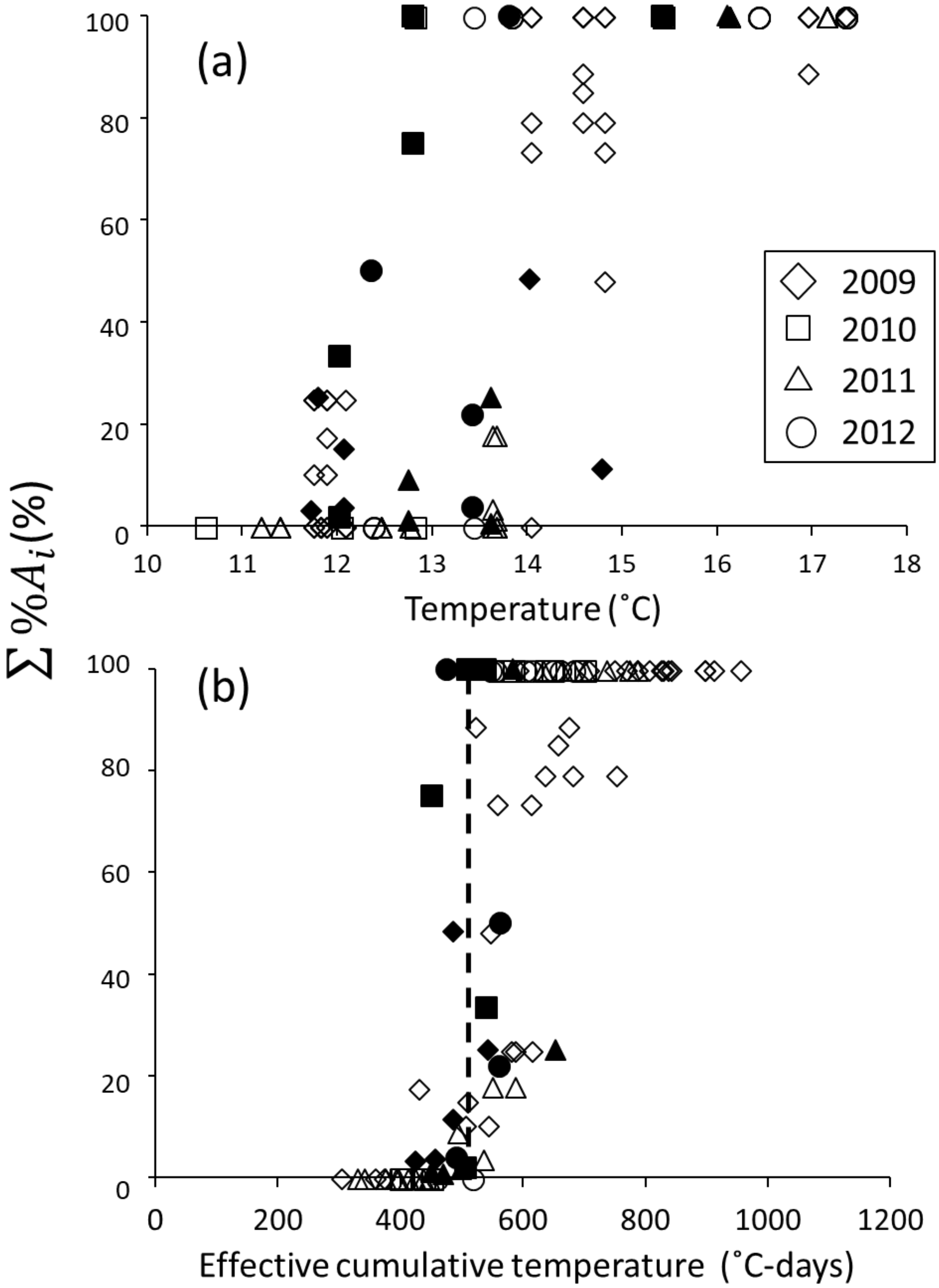

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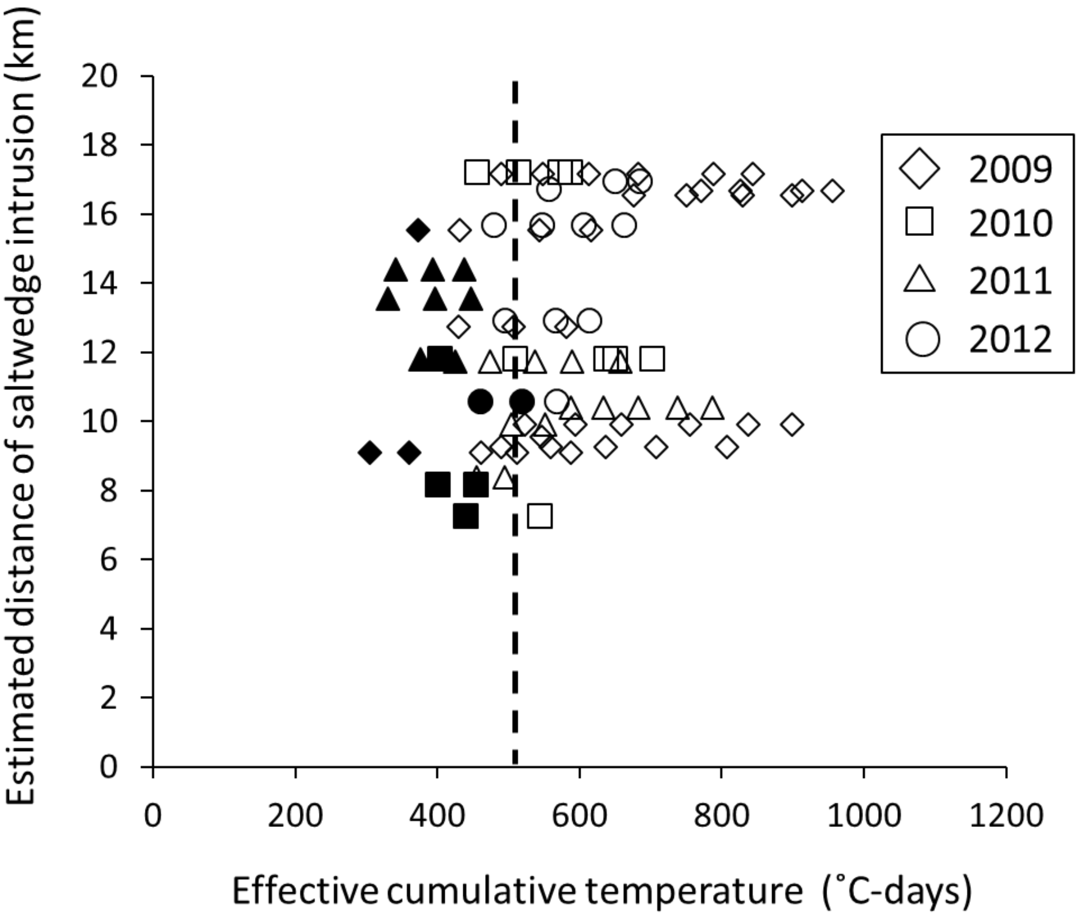

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