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Partial migration of juvenile temperate seabass *Lateolabrax japonicus* – a versatile survival strategy

Running title: Partial migration of juvenile seabass

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Abstract

Partial migration describes intrapopulation variation in the migratory behavior i.e. some individuals from a population migrate to low salinity river areas, while others remain in coastal areas. This paper reviews the partial migration pattern of juvenile temperate seabass *Lateolabrax japonicus*, which is a migration pattern not commonly seen in Japan. Seabass spawn offshore, and eggs and larvae are transported to coastal areas. Some of these juveniles then ascend rivers, while others remain in coastal areas. Juveniles efficiently use physical structures in their habitat; they use tidal currents to ascend rivers in macrotidal estuaries, while they use the saltwedge in microtidal estuaries. Once juveniles ascend the river, they can feed on the abundant prey and attain more rapid growth than those remaining in coastal areas. As estuaries are highly productive areas, they play significant roles for juveniles of various fishes as nurseries. However, compared with coastal areas, the relative area of estuaries is considerably smaller and its environmental conditions are more variable. For example, nearly 40% of adult seabass in Tango Bay were estimated to use estuarine areas as a nursery, while the other 60% use coastal areas during their juvenile stage. Using both estuaries and coastal areas through partial migration during the juvenile stage is concluded to contribute to the stabilization and yield of seabass populations.

Keywords: partial migration, juvenile, estuary, river, temperate seabass

Introduction

Most marine animals have complex life cycles and change their habitats according to the development stage, such as spawning area to pelagic nursery ground in early life stages, and feeding ground to spawning ground in adult stages (Secor 2015). There are various spatial scales in fish migration; salmons and eels migrate over an ocean basin scale, while some gobies have amphidromous migration over a river-estuary scale. The ecosystem network linking in coastal areas is regarded as Coastal Ecosystem Complex (CEC), and important for understanding ecosystem structure and functions (Watanabe et al. 2018). In their early life stages, fish are very sensitive to environmental conditions. For example, water that is too cold will delay egg development and hatching, and a lack of suitable food will reduce larval fish growth and survival. Survival during early life stages determines annual recruitments, which control the abundance of fish populations (Houde 1989). The choice of nursery grounds is therefore one of the most important factors for determining recruitment. Larvae or juveniles that are transported to less productive areas would suffer higher mortality rates than those that reach suitable nursery grounds (Cushing 1975). This process is generally essential for fishes, whose nurseries are distant from the spawning areas. During the course of evolution, each species has obtained its own strategy to maximize survival during the early life stage. As a strategy for survival, temperate seabass *Lateolabrax japonicus* makes a partial migration, a term which describes intrapopulation variation in migratory behavior i.e. a fraction of the population migrates and a fraction remains resident within a single habitat during the juvenile stage (Fuji et al. 2011; Islam et al. 2011). Partial migration has been broadly recognized in birds, terrestrial vertebrates and insects, but it has seen limited application to marine fishes (Secor 2015).

Temperate seabass is a euryhaline fish distributed in coastal waters of Japan and the Korean Peninsula (Nakabo 2002). Juveniles of temperate seabass are often dominant in estuaries and coastal areas (Fujita et al. 1988; Islam et al. 2011; Aoki et al. 2014) and thus play an important role in the estuarine and marine ecosystems. This fish is not only popular for sport fishing, but is also commercially important (Islam et al.

66 2011). It is one of a handful of species whose landings have been increasing or have remained in a high
67 level in many Japanese coastal waters (Hibino et al. 2013), in contrast to the declining trend in the
68 landings of other fishes since the 1980s (Fig. 1). Fluctuations in fish stocks are largely dependent on
69 survival during the early life stages (Cushing 1975; Houde 1989; Kasai et al. 2008). Clarification of the
70 ecology of early life of temperate seabass may enable identification and verification of the mechanism of
71 the recent increase in its biomass.

72 Temperate seabass spawn in shelf areas and coastal embayments during the winter season mainly in
73 December and January (Fujita et al. 1988). Larvae of this species hatch offshore and are transported from
74 open waters to coastal areas (Hibino et al. 2007; Islam et al. 2010). The settled larvae and early juveniles
75 move to various shallow environments such as eelgrass beds (Hatanaka and Sekino 1962), sandy beaches
76 (Fuji et al. 2010), tidal flats (Hibino et al. 2002) and estuaries (Matsumiya et al. 1982; Fuji et al. 2010;
77 Iwamoto et al. 2010). The most unique ecological characteristic of temperate seabass is the partial
78 migration pattern in the juvenile stage, e.g., some of the juveniles ascend the river to inhabit the upper
79 estuary, including the freshwater zone (Matsumiya et al. 1982; 1985; Secor et al. 1998; Suzuki et al. 2008;
80 Fuji et al. 2010; 2011; Iwamoto et al. 2010), while others remain and grow in the lower estuary
81 (Matsumiya et al. 1985; Hibino et al. 2002; Fuji et al. 2011) or in the littoral zone (Hibino et al. 2006).
82 The life history of migratory juveniles of temperate seabass in Japan has been particularly investigated in
83 the Ariake Bay – Chikugo River system, and the Tango Bay – Yura River system (Fig. 2). The partial
84 migration of seabass juveniles has been observed in both systems, although their environmental
85 conditions are considerably distinct, which can be attributed to the difference in tidal strength. We review
86 recent findings and examine the partial migration of juvenile temperate seabass in this paper.
87

88 **Overview of partial migration of juvenile temperate seabass**

89 Ariake Bay is located in the southwest of Japan, and the most important characteristic of Ariake Bay is

90 the large tidal range with an amplitude that exceeds 6 m during the spring tide (Fig. 2). The Chikugo
91 River, which is the largest river in Kyushu with a total length of 143 km and a basin size of 2,860 km^2,
92 empties into the northern part of Ariake Bay. The combination of the large tide and sediments transported
93 from the upper stream makes the water extremely turbid in the Chikugo River estuary. Seabass spawn
94 eggs from the center to the mouth of the bay. In early spring, many of juveniles aggregate around the
95 mouth of the Chikugo River. After that juveniles gradually ascend the river (Matsumiya et al. 1982).
96 Some of the juveniles ascend further upstream to ingress into the freshwater area of the estuary (Secor et
97 al. 1998). On the other hand, Hibino et al. (2002) showed that there are many juveniles that grow in the
98 littoral zone (high salinity area). These results indicate variations in migratory pathways for
99 simultaneously occurring juveniles of temperate seabass. Yokogawa et al. (1997) suggested from
100 allozyme data that the temperate seabass in Ariake Bay may be a hybrid of *L. japonicus*, and Chinese
101 seabass *Lateolabrax maculatus*. Nakayama (2002) found genetic differences between the river ascending
102 group and the coastal resident group; the former is more genetically influenced by Chinese seabass than
103 the latter, and suggested that the genetic difference may lead to the partial migration.
104 Tango Bay is a part of the Sea of Japan; as such, the tides are considerably weak (Fig. 2) (Kasai et al.
105 2010). The Yura River empties into the southern part of Tango Bay. The Yura River has a total length of
106 146 km and a basin size of 1,880 km^2. The hydrographic conditions in Tango Bay and the Yura River
107 estuary are distinctly different from those of the macrotidal Chikugo River estuary. The small tides restrict
108 the mixing of seawater and freshwater, and the water thus tends to be stratified in the Yura River estuary
109 (Kasai et al. 2010). Strong turbidity maximum zones are therefore not observed in the estuary, as in the
110 case with microtidal estuaries facing the Sea of Japan. These differences in environmental conditions may
111 lead to different migration patterns of juvenile temperate seabass. Fuji et al. (2010) sampled juvenile
112 temperate seabass along the Yura River estuary and found that juveniles were distributed not only in the
113 shallow coastal zone, but also in the brackish and even in the freshwater zone.

114 The two migratory pathways of early juveniles of the temperate seabass in the Yura River estuary are
115 similar to those observed in the well-mixed Chikugo River estuary (Hibino et al. 2006; Suzuki et al.
116 2008), although the hydrographic conditions of the two estuaries are considerably different (Suzuki et al.
117 2008; Kasai et al. 2010). There is no report that *L. japonicus* is genetically influenced by *L. maculatus* in
118 Honshu (the main island of Japan including the Yura River estuary), as was reported from the Chikugo
119 River estuary (Yokogawa et al. 1997). Therefore, the similarity in migratory pathways in both types of
120 estuaries indicates that the partial migration is ubiquitous and part of the ecology of seabass juveniles.
121
122 **Upstream migration mechanism**
123 Blackhead seabream *Acanthopagrus schlegelii*, yellowfin seabream *Acanthopagrus latus* and Japanese
124 icefish *Salangichthys microdon* are euryhaline and their larvae and juveniles are frequently observed in
125 sandy beaches and tidal flats, but hardly observed in freshwater areas. This indicates that seabass
126 juveniles are not only passively transported to, but actively select estuaries as their habitats (Kinoshita
127 2002). A number of studies have shown that juveniles use 'tidal selective transport' to achieve effective
128 upstream transport. McCleave and Kleckner (1982) investigated the distribution of juveniles of glass eels
129 in the Penobscot River estuary, and showed that they remained on or near the bottom during the ebb tide,
130 but in or below the halocline on the flood tide in stratified portions of the estuary. In tidal freshwater
131 portions of the estuary, glass eels behaved similarly on the ebb tide and moved throughout the water
132 column on the flood tide. These vertical distributions help to gain effective landward transport by
133 selective use of tidal currents. It is also known that many flatfishes exhibit clear tidally-synchronized
134 activity patterns in coastal habitats (Gibson 1997). A similar migratory mechanism has also been reported
135 for seabass juveniles in the Chikugo River estuary (Matsumiya et al. 1985; Islam et al. 2007). On a flood
136 tide, the ascending juveniles concentrate in the middle of the estuary, where the flood tide can assist the
137 upstream progress, while on an ebb tide, they concentrate near the bank, where the low velocity of the

138 stream enables them to resist downstream transport (Matsumiya et al. 1985).

139 In contrast, the tidal range in the Yura River estuary is considerably smaller, so that strong tidal
140 currents do not occur (Kasai et al. 2010). Therefore, juveniles cannot use tidal selective transport in
141 microtidal estuaries, but are able to move into another substantive upstream current, in the following way.
142 The discharge of the Yura River is generally high in winter and early spring due to melting snow. The
143 lower reach of the river is occupied by freshwater until the early spring. However, in late spring, the river
144 discharge gradually reduces and seawater begins to intrude into the bottom layer of the river mouth as a
145 saltwedge. In contrast to the Chikugo River estuary, the water in the Yura River estuary is highly stratified
146 due to the limited mixing by small tidal currents. Fuji et al. (2018) measured the salinity continuously, in
147 addition to a seine net survey of juveniles, in the lower portion of the Yura River. They found that the
148 timing of the salinity increase and appearance of seabass juveniles closely coincided with each other. This
149 indicates that seabass juveniles which have a poor swimming ability can ascend the river using the
150 saltwedge intrusion. This river ascending mechanism is entirely different from that in the well-mixed
151 estuaries, in which the juveniles can use the tidal currents.

152

153 **Productivity in estuaries**

154 The physiological ability to adapt to changing osmotic pressure is essential for migration between
155 seawater and freshwater or brackish water, and the energetic cost would make it difficult to migrate to
156 estuaries and rivers for coastal fishes. There must be reasonable benefit to ascend the river for seabass
157 juveniles, even though they incur a large metabolic cost to control the osmotic pressure. During the
158 juvenile stage, intra- and/or inter-specific competition for prey items is considered to be important for
159 recruitment of fishes because nursery areas and the amount of available prey items are often limited (Van
160 der Veer et al. 2000; Shoji and Tanaka 2008), and prey abundance can be a limiting factor for the growth
161 of juveniles in nursery areas (Beck et al. 2001; Yamashita et al. 2001). Therefore, the abundance of prey

items must be an important reason for seabass juveniles to ascend rivers. As high productivity often generates plenty of prey organisms, estuaries are generally recognized as important nurseries for many fishes (North and Houde 2003; Elliott et al. 2007).

In macrotidal estuaries, the hydrodynamic function of tidal pumping and estuarine circulation maintains high concentrations of suspended solids, forming an estuarine turbidity maximum at low salinities (Suzuki et al. 2007). In the Chikugo River estuary, the estuarine turbidity maximum with turbidity as high as ~4,000 mg l^{-1} is formed ~15 km upstream from the river mouth, although it moves up- and down-stream with the flood and ebb tides. The estuarine turbidity maximum provides a high abundance of copepods and mysids, which are good prey items for juvenile seabass in addition to potential refuges from visual predators (Hibino et al. 1999; Islam et al. 2006; Suzuki et al. 2014). Therefore, juveniles that ascend rivers can receive appropriate nutrition and steadily gain weight. Estuaries with turbidity maximums are considered to be good nurseries not only for seabass, but also for larvae and juveniles of various fishes (North and Houde 2003; Islam et al. 2006).

In contrast, rather than estuarine turbidity maximums, strength of river discharge and associated stratification are keys for production in microtidal estuaries (Kasai et al. 2010). Paerl et al. (2014) showed that changes in freshwater input play an important role in determining the abundance and function of phytoplankton communities in the Neuse and New River estuaries. In the shallow microtidal Patos Lagoon estuary, phytoplankton accumulations occur after marine inflow events, whereas phytoplankton does not accumulate during the high water outflow (Odebrecht et al. 2015). In addition, Friedland et al. (2011) suggested that the transitions in menhaden (*Brevoortia tyrannus*) abundance are closely associated with those in zooplankton abundance in the microtidal York River estuary. Kasai et al. (2010) showed from continuous observations that the productivity in the lower portions of the Yura River increases in spring, which coincides with the season of seabass ascending. Actually in the coastal area of Tango Bay, mysids (*Orientomysis japonica*) are abundant in winter and early spring (Akiyama et al. 2015). They tend

186 to decrease in late spring, instead the other species of mysids (*Neomysis awatschensis*) increase in the
187 Yura River estuary (Fig. 3). Seabass juveniles select highly productive areas and migrate from the coastal
188 area to the estuary. This implies that the prey environments and feeding ecologies of fish differ
189 considerably between macrotidal and microtidal estuaries.
190
191 **Juvenile feeding and growth in estuaries**
192 According to Fuji et al. (2016b), which reviewed studies on various ontogenetic shifts in feeding habits of
193 seabass at the beginning of the juvenile stage, the size of prey items of seabass juveniles enlarges with
194 growth to obtain energy efficiently. This prey shift leads to fast growth and higher survival rate. Hibino et
195 al. (1999) and Islam and Tanaka (2005) showed that species composition of stomach contents and
196 stomach fullness of seabass juveniles reflect the prey abundance in ambient water in the Chikugo River
197 estuary. Ohta (2004) reported that high productivity in the Chikugo River often led to higher growth rates
198 of juveniles in the river than those in the coastal zone. Among various prey items, *Sinocalanus sinensis*
199 that is a semi-endemic copepod in the Ariake Bay plays an important role in fast growth of seabass
200 juveniles in the Chikugo River estuary because of its high production (Suzuki et al. 2012; 2014).
201 Fuji et al. (2016a) analyzed the feeding ecology of juvenile temperate seabass in relation to the
202 abundance and species of prey items in the Yura River estuary. Juveniles mainly fed on copepods and
203 mysids, both in the estuary and in the adjacent coastal area. The dependency on mysids increased as
204 juveniles grew from 15 mm to 25 mm standard length (SL), and the main stomach contents were mysids
205 for juveniles larger than 25 mm SL (Fig. 4a). The mean size of ingested food items increased with the size
206 of the juveniles (Fig. 4b), while the mean number of prey items in each stomach decreased with growth
207 after juveniles reached 22 mm SL. As a result, the stomach content index increased with the size of
208 juveniles (Fig. 4c). These results indicate that the shift to larger-sized prey items (from copepods to
209 mysids) is important for juveniles to obtain energy efficiently. Mysids are larger and more abundant in the

estuaries than in the coastal area. Therefore, the estuary provides better foraging conditions for juvenile temperate seabass than the coastal area.

Foraging ability is one of the most changeable characteristics during the larval and juvenile periods. Thus, leaving or residence in natal food webs would depend on their sizes (Secor 2015). Using $\delta^{13}C$ and otolith analyses, Fuji et al. (2014) compared sizes and growth rates among migration groups. The river ascending group was small and showed lower growth than the surf zone group before river ascending (left half of Fig. 5). However, the former gradually increased the growth rates, and at last, the growth rates of longer resident juveniles in the river caught up with or overcome that of the surf zone group (right half of Fig. 5). It was considered that the juveniles which experienced lower growth rates during the larval and early juvenile stage in the coastal area ascend the river by being displaced from the surf zone by the fast-growing juveniles. However, residence in the estuary enabled juveniles to achieve a similar or even higher growth than residence in the coastal area. This pattern would come from the higher temperature and better ambient prey condition in the estuary than in the coastal area during the juvenile stage (Fuji et al. 2014).

In most cases, the strong influence of body size on reproduction, physiology and behavior can result in differential migration (Secor 2015); smaller individuals with poor growth rates migrate while larger individuals with better growth rates reside. A part of the local population of juveniles of white perch *Morone americana* remain in the freshwater area while juveniles of the other part of the population migrate to brackish water. In this case, juveniles with poor growth migrate to the brackish area (Kraus and Secor 2004a). Kerr et al. (2009) considered that high productivity in the brackish area would lead to higher growth of white perch larvae and juveniles that migrated to the brackish area than those that remained in the freshwater area. 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). Another example of partial migrants is three-spined stickleback *Gasterosteus aculeatus*,

234 which spawns in freshwater ponds and only a subset of the juveniles migrated out to sea (Kitamura et al.
235 2006). Detailed analysis of the body length of fish from this population showed a bimodal distribution,
236 with smaller juveniles migrating and larger fish remaining resident. These examples show that juveniles
237 with higher growth rates remain resident in the natal habitats, while fish with lower growth rates migrate
238 to the other areas (Bujold et al. 2004). The migration pattern of seabass juveniles is similar to these fishes.
239 Migration to the new environment, however, is energetically costly, both in terms of the journey itself
240 and also the physiological changes required to adapt to the different salinity habitat (Chapman et al. 2012).
241 There might be another reason to take this risky strategy. Higher temperature in estuaries would also lead
242 to higher growth rates of juveniles than coastal areas (Hirata 1967; Shoji and Tanaka 2007). Shoji et al.
243 (2006) also described lower abundances of potential predators of larvae and juveniles, including
244 chaetognaths and medusoid jellyfish in the Chikugo River estuary compared to coastal areas. It is likely
245 that smaller individuals migrate to take advantage of the higher growth rates and lower predation with
246 maximizing future fitness returns.
247
248 **Contribution of estuaries as nurseries**
249 Partial migration is the divergence of the population into migratory and resident contingents (Jonsson and
250 Jonsson 1993). Vital rates can vary substantially among habitats. Nursery values can be calculated using
251 the proportion of adult fish from each habitat origin. An adult population is composed of individuals
252 nourished in various nurseries. An understanding of the relative contribution of each nursery area to adult
253 populations is essential to evaluate habitat importance as nurseries (Beck et al. 2001).
254 Much like tree-rings, the layered structure of otoliths can be used to retrospectively study size and age
255 of individual fish (Pannella 1971), and trace elements within otolith layers are reflective of time spent in
256 different habitats (Campana and Thorrold 2001). Recently, otolith microchemistry analysis has been
257 gaining attention as a tool for providing information on the environmental conditions experienced by

258 various juvenile fishes (Secor and Rooker 2000; Gillanders et al. 2003). Single elements and/or
259 combinations of elements have been used as fingerprints of the habitat origins of many fishes (Kraus and
260 Secor 2004b; Fodrie and Levin 2008; Morais et al. 2011). The strontium:calcium ratio (Sr:Ca) of otoliths
261 especially has been reported to be influenced by salinity and is thus used as a natural tag for tracking
262 diadromous migrations (Tsukamoto et al. 1998; Yamashita et al. 2000; Kraus and Secor 2004a; 2004b).
263 Secor et al. (1998) and Ohta (2004) studied the possibility of using otolith Sr:Ca as a natural tag for
264 temperate seabass by culturing juveniles under various salinity conditions, and showed that Sr:Ca
265 decreases significantly in salinities lower than 5. However, a large part of the Chikugo River estuary was
266 occupied by waters with salinity higher than 5. It is thus difficult to estimate the contribution of the
267 estuary as a seabass nursery. Conversely, the Yura River estuary, facing Tango Bay, is classified as a
268 microtidal estuary, and the salinity of most parts of the shallow areas where juveniles are distributed is
269 lower than 5 (Fuji et al. 2010; Kasai et al. 2010). The environmental conditions of the Yura River estuary
270 allow us to use otolith Sr:Ca to evaluate the contribution of estuarine habitats to the adult population of
271 temperate seabass. Fuji et al. (2016b) compared Sr:Ca ratios at the outer edge of the otoliths of seabass
272 juveniles collected from the coastal area in Tango Bay, and brackish estuary and freshwater areas in the
273 Yura River. They showed that the Sr:Ca ratios of juvenile otoliths decreased significantly under lower
274 salinity conditions. These results support the validity of using this method to classify adults into river
275 ascended and coastal resident groups in the juvenile stage. Then the Sr and Ca concentrations of the
276 otoliths of adult seabass were measured linearly along the longest axis of each otolith from the core to the
277 anterior edge. Focusing on the otolith area within 3 mm from the core, which corresponds to the
278 young-of-year period, they found that three typical patterns of fluctuation in Sr:Ca ratios were observed
279 (Fig. 6). The Sr:Ca ratio of one type (thin black line in Fig. 6) declined in the section of the otolith
280 corresponding to c. 0.4–1.0 mm from the core, which represented a standard length of 20 –30 mm,
281 whereas the other types showed consistently high values with growth. The second type (grey line in Fig.

6) showed a declining pattern of Sr:Ca beyond 1.0 mm from the core, corresponding to a standard length over 30 mm. The Sr:Ca ratio of the last pattern (dotted line in Fig. 6) showed a value consistently higher than the criterion within 3.0 mm of the core. These three patterns were considered to represent the early river migrant group, the late river migrant group and the coastal resident group, respectively. Comparing the trajectories of Sr:Ca with the threshold criterion, 39 out of 107, corresponding to 36% of adult seabass were estimated to use the freshwater area (the first and second type) as the nursery during their juvenile stage. Despite the small area covered by estuarine habitats compared with coastal waters, the Yura River estuary contributed considerably to the adult seabass population in Tango Bay. This indicates that estuaries play an important role as nurseries for seabass juveniles, and it should be noted that the estuaries are important nurseries to conserve the stocks of various coastal fishes.

Some studies on flatfishes have also reported high contributions of estuaries compared to other habitats, despite the relatively small areas of estuarine habitat (Kraus and Secor 2004a; Brown 2006). This high contribution of estuaries would be facilitated by the relatively high prey densities and reduced numbers of predators. Azeta (1986) reported that red seabream (*Pagrus major*) juveniles in dominant year classes utilize wider and more various habitats than fish from year classes with lower recruitment levels. Kraus and Secor (2005) also reported that abundant annual cohorts showed different patterns of habitat usage compared to minor annual cohorts. These studies showed the importance of estuaries for the coastal fishes. This means that the degradation of estuarine habitats would lead to significant decrease of fish stocks including temperate seabass. There are many modifications of estuarine environment by human activities, which potentially have considerable effects on the 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). Especially, construction of estuarine weirs would restrict the area of estuarine nurseries, potentially leading to population decrease. We have to take notice of the inter-connectivity of each habitat during early life stages as important nurseries to conserve the stocks of

306 coastal fish.

307

308 **Benefit of partial migration**

309 Density-dependent mechanism is a key to determine the mortality in the juvenile stage of various coastal
310 fishes. Estuaries are generally smaller and thus the density of fish larvae and juveniles is higher than
311 coastal areas (Fuji et al. 2010; Iwamoto et al. 2010). This leads to severe competition and higher mortality
312 in estuaries. Shoji and Tanaka (2007) found that the competition for prey resources causes the density
313 dependent mortality of temperate seabass juveniles in the Chikugo River estuary. The carrying capacity of
314 estuarine nurseries is limited because of the spatially restricted area. This means large concentration of
315 juveniles in estuaries could lead to mass mortality. The partial migration strategy therefore enhances total
316 carrying capacity for juveniles, comparing with the single nursery usage (Kaeriyama 1996; Asami 2004).

317 The environmental conditions of estuaries are more variable than coastal areas. This is true for
318 Japanese estuaries, where the river discharge changes enormously according to heavy rainfall and
319 typhoons. Shoji and Tanaka (2007) investigated the abundance and growth history of seabass juveniles of
320 in the Chikugo River estuary over 11 years. They reported increase in the river discharge has a potential
321 risk to decrease the recruitment of juveniles through the process of downward dispersion, predation due to
322 decreased turbidity and starvation due to decreased zooplankton prey abundance in the estuary.

323 These two characteristics of estuaries (instability and limited area as nurseries) make it a maladaptive
324 strategy for all seabass juveniles to migrate into estuaries. Kerr et al. (2010) showed by the theoretical
325 study that partial migration of white perch stabilizes and maximizes their population. As often happens in
326 unstable environments, a subpopulation sometimes suffers catastrophic damage in a nursery. Even in such
327 an occasion, the other group in the other nursery can survive and support the recruitment, if the
328 population takes partial migration. Temperate seabass is one of the few fishes that can take the partial
329 migration strategy. This might be a reason of relatively steady stocks of seabass in Japanese coastal areas.

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517 **Figure captions**

518 **Fig. 1** Changes in landings of seabass (black line) and coastal fishes (gray line) in Japan.

519 **Fig. 2** Map of the Ariake Bay – Chikugo River system and the Tango Bay – Yura River system

520 **Fig. 3** Density of *Orientomysis japonica* in coastal area of Tango Bay and *Neomysis awatschensis* in the
521 Yura River estuary. Redrawn from Akiyama et al. (2015).

522 **Fig. 4** Ontogenetic shifts of (a) percentage of index of relative importance (%IRI) for all prey items, (b)
523 mean prey size and (c) mean stomach content index (= weight of stomach content / body weight
524 × 100) of seabass juveniles in Tango Bay and the Yura River estuary. ND means no data.
525 Redrawn from Fuji et al. (2016a).

526 **Fig. 5** **(a)** Back-calculated growth rates and (b) standard lengths of seabass juveniles collected in coastal
527 area (white circles) and the Yura River (black circles). Error bars indicate standard deviations.
528 Asterisks indicate significant difference between the two groups (Student's t-tests, $P<0.01$).
529 Redrawn from Fuji et al. (2014). Since seabass ascend the river around age of 90 days, both
530 groups were in the coastal area under 90 day old (left half of the figure), and then separated to
531 river and coastal area over 90 day old (right half of the figure).

532 **Fig. 6** Examples of Sr:Ca ratios of the otoliths of seabass adults. The horizontal line shows the criterion
533 at 4.4×10^{-3}. Redrawn from Fuji et al. (2016b). The thin black line, grey line and dotted line are
534 considered to represent the early river migrant group, the late river migrant group and the coastal
535 resident group, respectively.

536

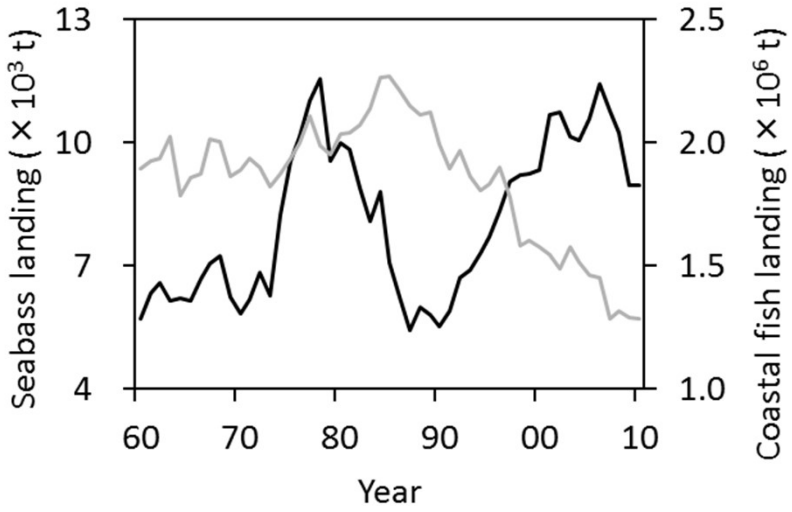


Fig. 1 Kasai et al.

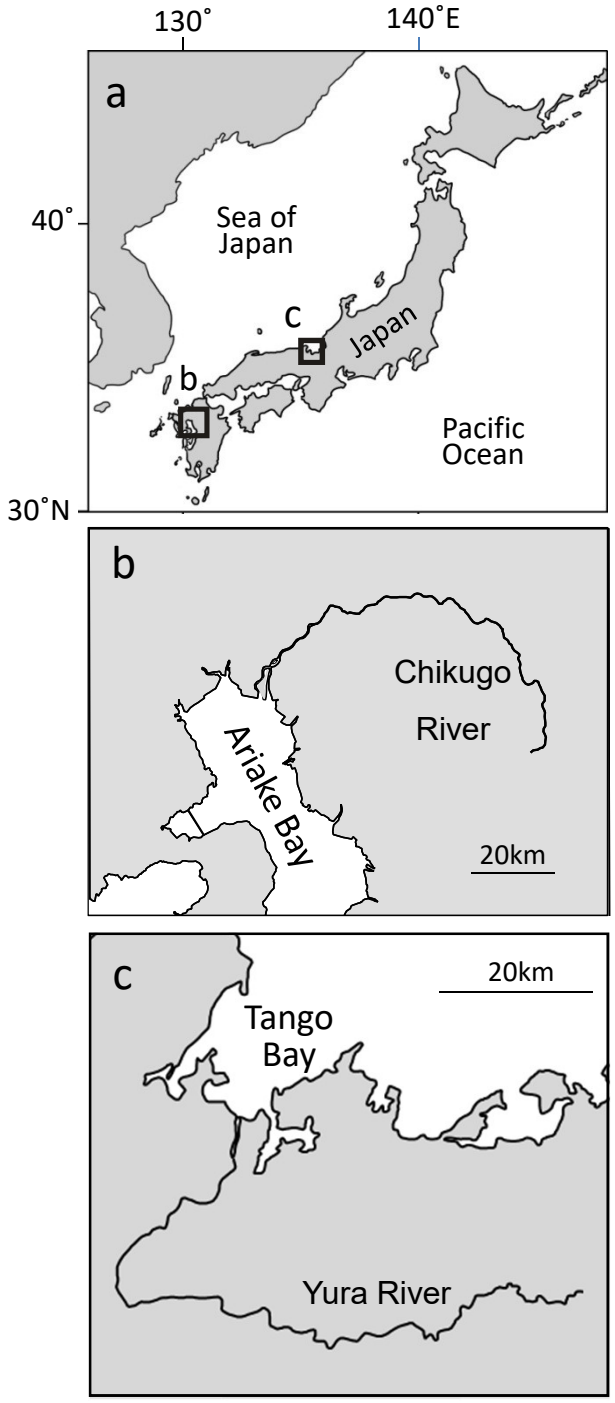
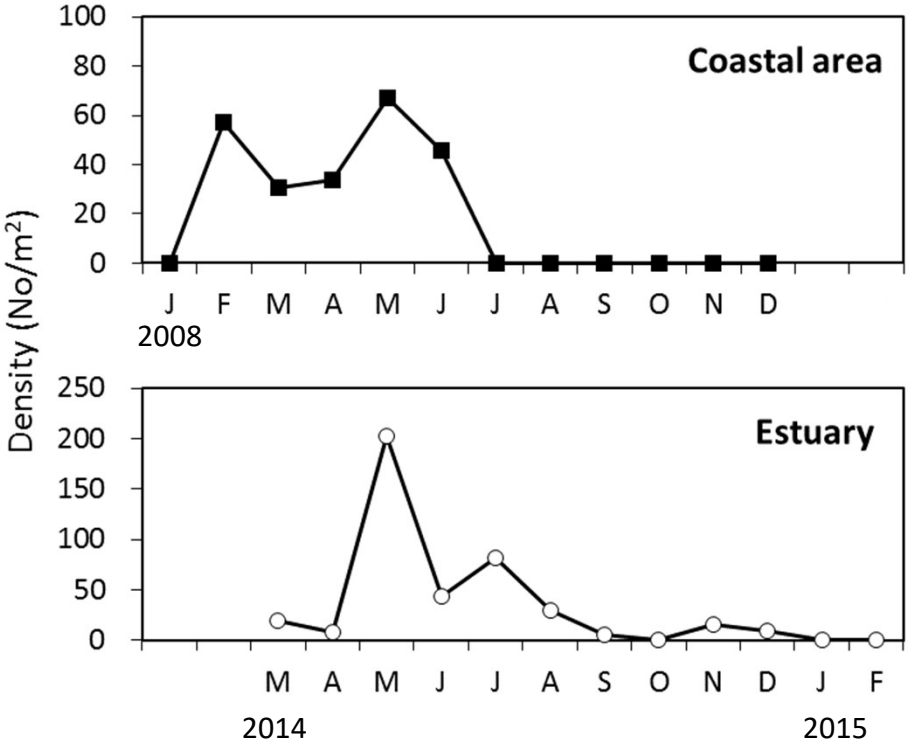


Fig. 2 Kasai et al.



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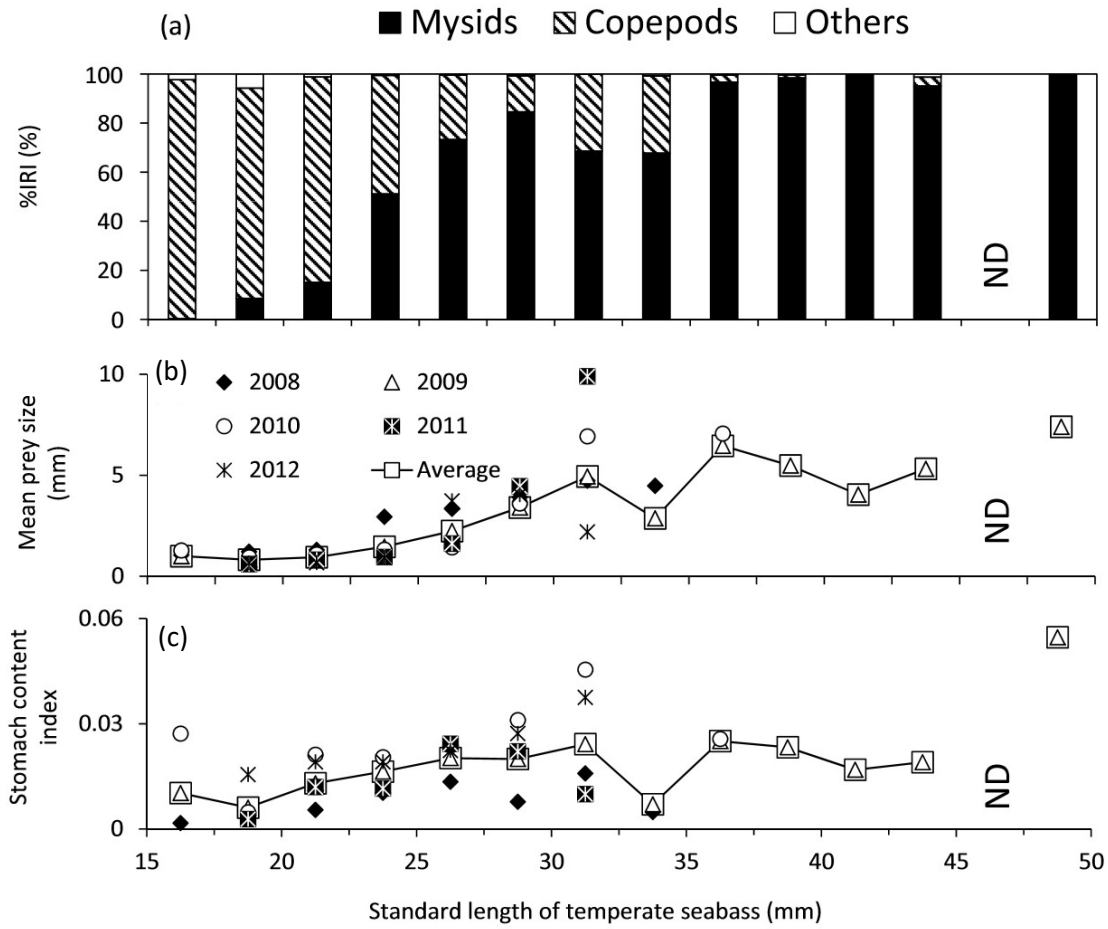
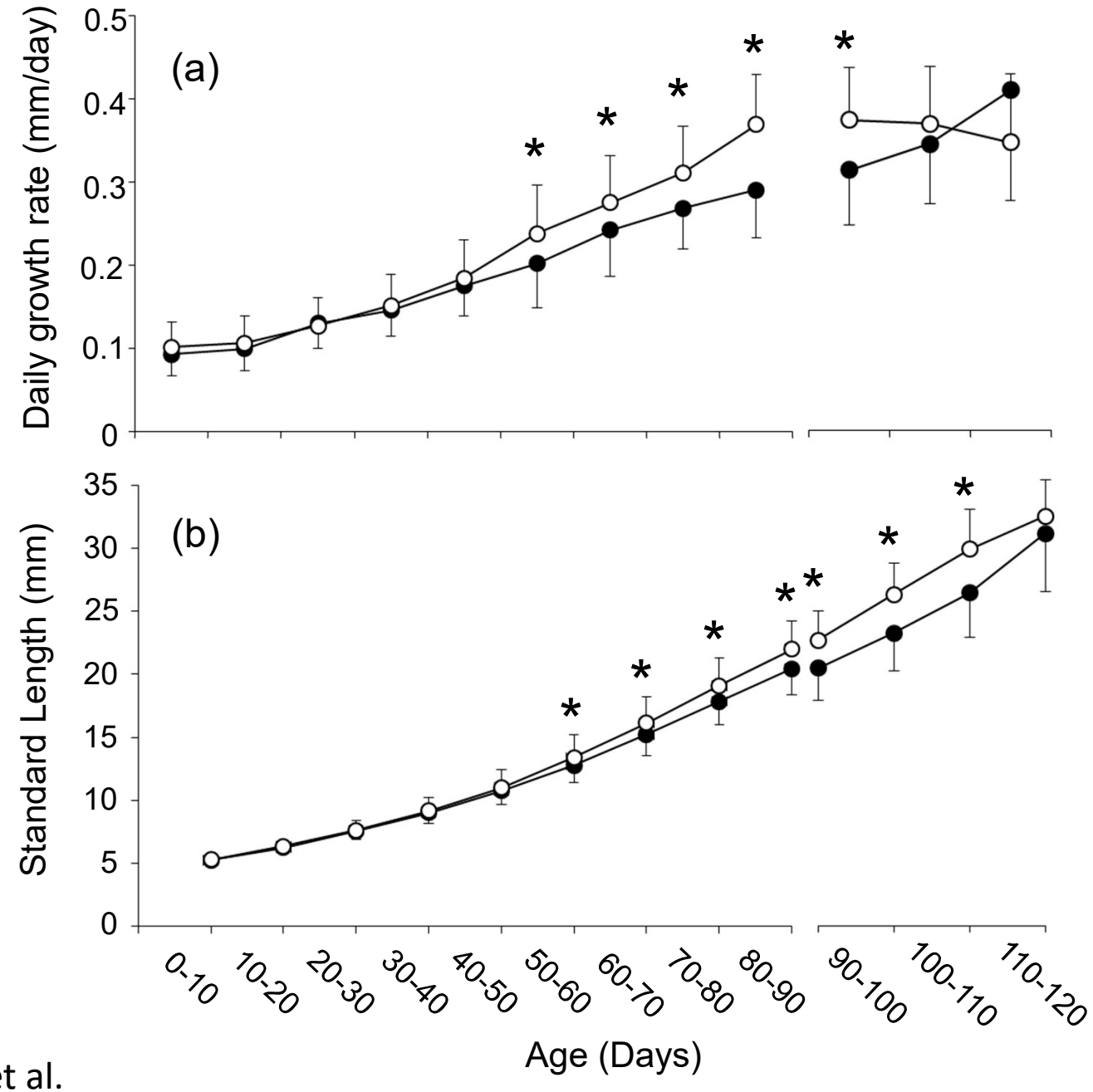


Fig. 4 Kasai et al.



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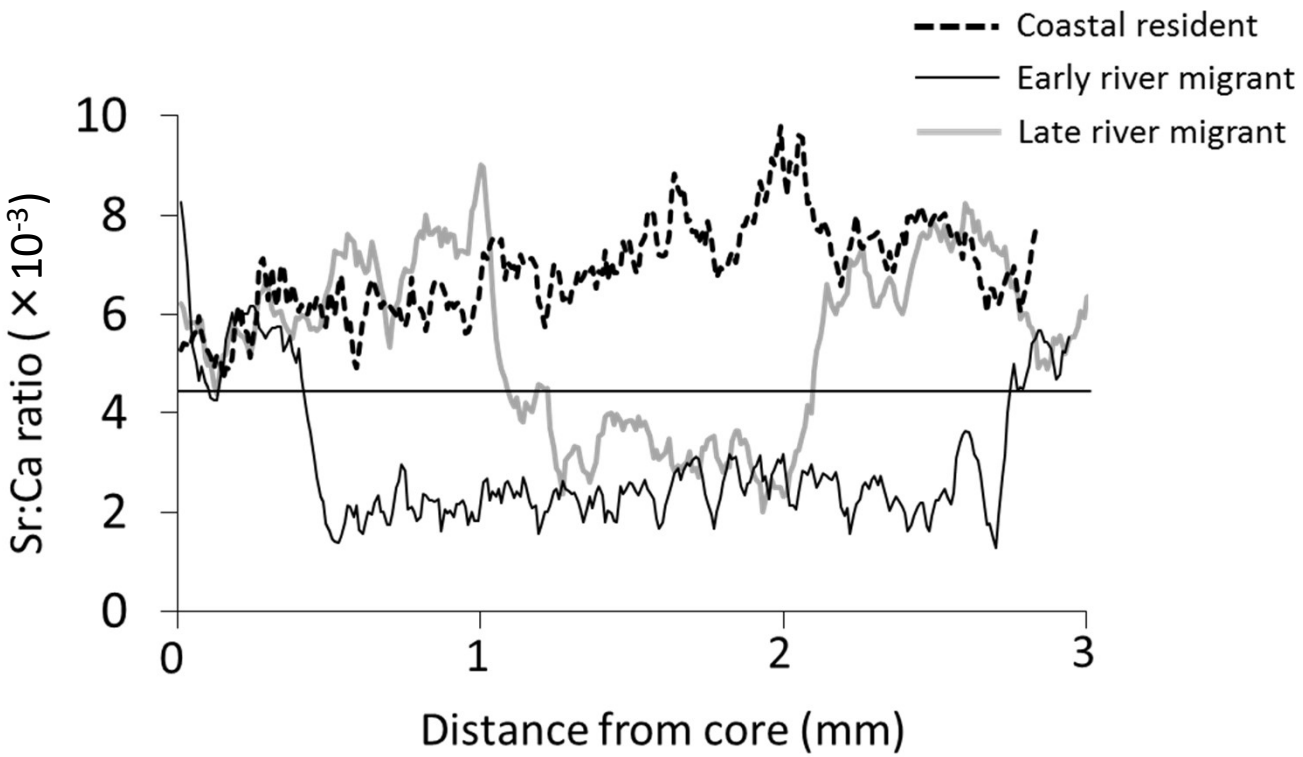

Fig. 6 Kasai et al.