# Recruitment Processes of Japanese Sea Bass in the Chikugo Estuary, Japan: Shift from Density-Independence to Density-Dependence During the Early Life Stages

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## ABSTRACT

Japanese sea bass larvae migrate from Ariake Bay, southwestern Japan, into the Chikugo Estuary and inhabit there throughout the juvenile period. Abundance of Japanese sea bass larvae and juveniles in the estuary shows a 40-fold fluctuation, higher than that in adult stock (2-fold). It is likely that a density-independent mechanism seems to influence the survival of larval (pre-immigration) period and that a density-dependent mechanism regulates the survival during the juvenile (post-immigration) period. We tested the hypotheses that physical conditions such as freshwater discharge and temperature influence pre-immigration survival through affecting larval growth rate and that a density-dependent mechanism regulates post-immigration survival of the Japanese sea bass. Mean larval growth rate ($G_{15}$, mm d$^{-1}$) during the pre-immigration period (<15 mm), weight-specific growth coefficient ($G_w$, d$^{-1}$), mortality coefficient ($M$, d$^{-1}$), and relative recruitment potential ($G_w/M$) during the post- immigration period (15–20 mm) were estimated from 1990–2000. Freshwater discharge through the Chikugo River had a significant effect on the temperature of the upper Ariake Bay. The $G_{15}$ varied between 0.04 and 0.10 mm d$^{-1}$ and was significantly correlated with the temperature experienced by the larvae. The $G_{15}$ had a significant effect on the larval and juvenile sea bass abundance, with higher abundance in years with high $G_{15}$. Freshwater discharge seems to be a primary factor for the density-independent control of larval Japanese sea bass survival, influencing water temperature in the upper Ariake Bay and the larval growth. The $G_w/M$ was significantly affected by the Japanese sea bass abundance at 15 mm: lower $G_w/M$ in years of high abundance. Density-dependent regulation seems to operate on the post-immigration Japanese sea bass in the Chikugo Estuary.

*Key words*: density-dependent, density-independent, estuary, fish early life stages, recruitment, survival.

## Introduction

Fish early life stages using estuarine habitats are subject to high variability in physical and biological conditions such as temperature, prey and predator abundance that can affect their survival and recruitment through density-independent process (Secor and Houde, 1995; Limburg *et al.*, 1999; North and Houde, 2003; Yamashita *et al.*, 2003; Shoji *et al.*, 2005). In addition to these environmental conditions, density-dependent regulation has also been considered an important deter-

minant for growth of fish early life stages (Jenkins *et al.*, 1991). However, the mechanisms how density regulates survival of fish early life stages are poorly understood. Comprehensive analyses of the dynamics of fish early life throughout the larval and juvenile stages are indispensable for further understanding of reproductive and recruitment processes of fish stocks.

Japanese sea bass (*Lateolabrax japonicus*) is an estuarine-dependent fish distributed in temperate coastal waters of eastern Asia. In the upper Ariake Bay (Fig. 1),
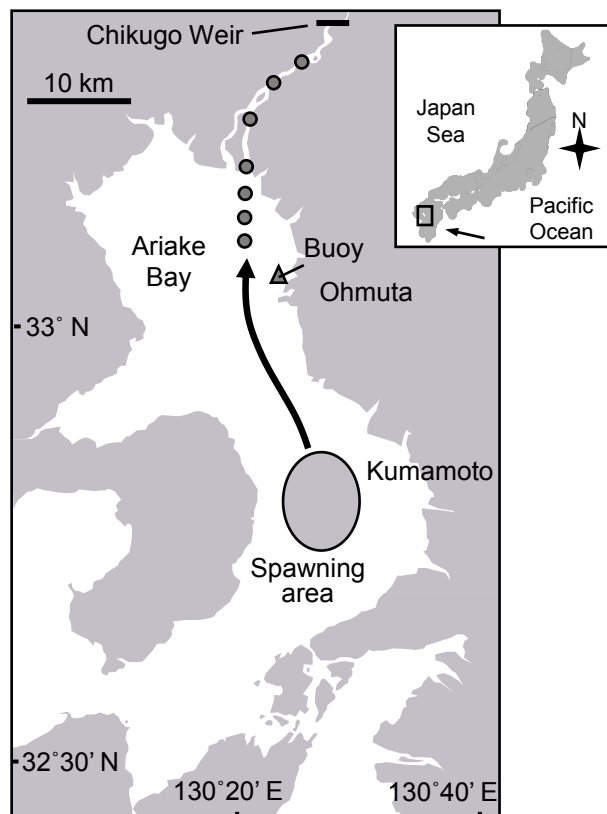
Fig. 1.   Map showing the seven sampling stations in the Chikugo River Estuary, southwestern Japan, where Japanese sea bass larvae and juveniles were collected from 1990 to 2000. Arrow shows the transportation pathway of larval Japanese sea bass from its spawning area off Kumamoto to the Chikugo Estuary.



Fig. 2.   Annual fluctuation in catch of Japanese sea bass in Ariake Bay from 1990 to 2000.

south-western Japan, early life stages of the Japanese sea bass inhabit rivers and brackish-water areas. The Chikugo River Estuary is one of the most important nurseries of the Japanese sea bass in Ariake Bay. Spawning occurs in waters off Kumamoto from November to January and the larvae are transported northward by the anti-clockwise residual current that prevails in the upper Ariake Bay (Hibino *et al.*, 2001; Shoji *et al.*, 2006; Fig. 1). The larvae ascend the Chikugo River in March then inhabit the freshwater areas through spring (Matsumiya *et al.*, 1981).

A 40-fold fluctuation has been reported in the annual abundance of Japanese sea bass larvae and juveniles in the Chikugo Estuary from 1979 to 2000 (Matsumiya *et al.*, 1985; Shoji and Tanaka, 2007a). The high fluctuation in the abundance may be attributed to density-independent survival during the larval period. Although there is no data on adult fish biomass available, the fluctuation in the annual catch of adult fish was minimal: within two-fold fluctuation in Ariake Bay (Fig. 2). The mechanisms
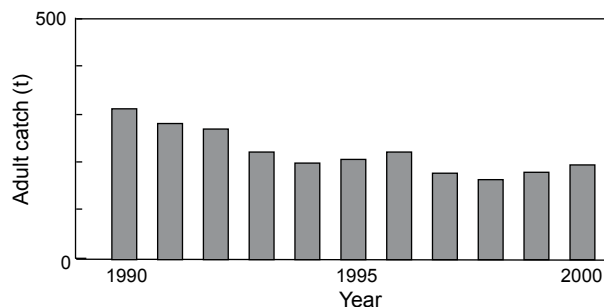
influencing fluctuations in recruitment strength, however, have not been clarified. Variability in freshwater discharge through the Chikugo River influences the water temperature of the estuary (Shoji *et al.*, 2006). In addition, there is a negative correlation between the freshwater discharge and abundance of sea bass larvae and juveniles in the estuary (Shoji and Tanaka, 2007a). Variability in water temperature can significantly affect recruitment of Japanese sea bass through controlling the larval growth rate and consequential larval stage duration (Houde, 1987). Therefore, it is likely that variability in the freshwater discharge may be one of the important determinants for the density-independent recruitment of Japanese sea bass in Chikugo Estuary.

The smaller variability in adult fish catch (2-folds) compared to the high variability in larval and juvenile fish abundance (40-folds) indicates density-dependent regulation exists during the post-immigration stage in Japanese sea bass. Onset of density-dependence in the Japanese sea bass may correspond with migration from Ariake Bay into the Chikugo River, a spatially restricted nursery, since density-dependence becomes evident when competition for space and prey occur among individuals (Jenkins *et al.*, 1991; Watanabe and Nakamura, 1998; Iles and Beverton, 2000).

In the present study, we tested the hypotheses that: 1) freshwater discharge rate through the Chikugo river is a primary factor for the density-independent control of Japanese sea bass survival: the freshwater discharge rate affects water temperature and pre-immigration growth of Japanese sea bass larvae, and 2) density-dependent mechanism affect survival during the post-immigration stage of the Japanese sea bass.

## Materials and Methods

Physical and biological surveys were conducted around the Chikugo River Estuary (Fig. 1) from 1990

to 2000. Seven sampling stations were set at intervals of about 3–5 km along the river and off the river mouth in the upper part of Ariake Bay (Fig. 1). Ichthyoplankton sampling was conducted during spring tide period in late March, which corresponds to the seasonal peak of larval and juvenile Japanese sea bass immigration into the river (Matsumiya *et al.*, 1981). A conical larva-net (1.3 m mouth diameter, 0.33 mm cod-end mesh: Matsumiya *et al.*, 1985) was used for the larval and juvenile fish sampling. Two surface tows for 10 min were conducted at a boat velocity of 2 knots at each station. Fourteen ichthyoplankton samples were obtained for each year. Japanese sea bass larvae and juveniles were sorted and preserved in 95% alcohol on the boat. Surface temperature was measured simultaneously with each sampling.

Japanese sea bass larvae and juveniles were measured in standard length (SL, mm) to the nearest 0.1 mm in the laboratory. Concentration of the larvae and juveniles ($C$, no. m$^{-3}$) was estimated based on the water volume filtered for each surface tow. Matsumiya *et al.* (1981) investigated vertical distribution of the larval and juvenile Japanese sea bass in the Chikugo River Estuary and reported a mean ratio of larval and juvenile concentration (1:0.24) in the upper (<3 m in depth): bottom (>3 m in depth) layers. In the present study, abundance of the larvae and juveniles at each station ($A_s$, no. 100 m$^{-2}$) was calculated according to the ratio of fish concentration in the upper): bottom layers as follows:

$$A_s = 100\left[3C + 0.24C\left(S - 3\right)\right]$$

where $S$ is the depth at each station (m). The average depth of the seven stations was 7.1 m (range: 5.5–9.7 m). Although Japanese sea bass <25 mm SL have been reported to be effectively collected with the larva net in the Chikugo Estuary (Matsumiya *et al.*, 1985), in the present study data on fish >20 mm (3.8% in number of total fish collected) were excluded from the analyses in order to estimate the fish abundance more accurately. In addition, the sample size of fish >20 mm was too small for analysis in several years. Therefore, the mean abundance of fish <20 mm SL from the fourteen tows was used as an index of larval and juvenile sea bass abundance for each year.

Thirty Japanese sea bass of 15–20 mm SL were randomly selected for growth back-calculation for each year. Sagittal otoliths of the larvae and juveniles were removed under a dissecting microscope. The number of daily growth rings was counted and the radius of each ring from the otolith nucleus was measured using a light microscope connected with a video monitor and otolith reading system (ARP/W, Ratoc System Engineering Co. Ltd.). The number of the daily rings and radius of each

ring were recorded. Relationship between SL and otolith radius was expressed by an allometric formula (Shoji *et al.*, 2006). Allometric parameters were determined for each fish by using the biological intercept method (Campana, 1990; Campana and Jones, 1992; Watanabe and Kuroki, 1997). Otolith daily rings start to be deposited at the first feeding stage (day 4) in Japanese sea bass. The SL of first feeding larvae (after ethanol preservation) was fixed at 4.75 mm for the biological intercept of the present species (Shoji *et al.*, 2006). Allometric parameters *a* and *b* were calculated for each larvae by solving the equations:

$$L_{ff} = aR_{ff}^{\ b}$$
$$L_{catch} = aR_{catch}^{\ b}$$

where $L_{ff}$ is SL at the first feeding (4.75 mm), $R_{ff}$ is the measured radius of the first daily ring, $L_{catch}$ is the measured SL at catch, and $R_{catch}$ is the measured radius at catch. Mean of the back calculated SL-at-ages was calculated for fish up to 15 mm at which size Japanese sea bass larvae migrate into the Chikugo River Estuary (Matsumiya *et al.*, 1981). Growth trajectory of Japanese sea bass during the larval period (from the first feeding to immigration into the river) has been reported to be linear (Shoji *et al.*, 2006). Mean somatic growth rate ($G_{15}$, mm d$^{-1}$) during the larval stage (the first feeding to 15 mm SL) was calculated for each year.

Abundance-at-age was estimated for larval and juvenile sea bass at 15–20 mm SL in order to calculate the post-immigration mortality rate as follows. The right sagittal otolith ($n = 50$ per year) was removed under a dissecting microscope. Ages of the larvae and juveniles that were not estimated directly by the otolith-based technique were estimated from the age-length regression (Shoji and Tanaka, 2007a), which was constructed for each year. Instantaneous daily mortality rates of Japanese sea bass during the post-immigration period (15–20 mm) were calculated from the exponential model of decline (Shoji and Tanaka, 2007a):

$$A_t = A_{15}\exp\left(-Mt\right)$$

where $A_t$ is the estimated abundance (no. 100 m$^{-2}$) at age $t$ (days after reaching 15 mm SL), $A_{15}$ is the estimated abundance at 15 mm (no. 100 m$^{-2}$), and $M$ is the instantaneous daily mortality coefficient between 15 and 20 mm. The $A_{15}$ was used as an immigration index of Japanese sea bass for each year. A weight-specific growth coefficient during the post-immigration period (15–20 mm: $G_w$) was estimated for each year as:

$$W_t = W_{15}\exp\left(G_wt\right)$$

where $W_t$ is the weight (mg) at time $t$ (days after reaching 15 mm), $W_{15}$ is the weight at 15 mm, and $G_w$ is the

weight-specific growth coefficient. Relative recruitment potential of the Japanese sea bass during the post-immigration period (15–20 mm) was assessed for each year by examining the ratio of $G_w$ to $M$, which is commonly used as an index of stage-specific survival of fish early life stages (Houde, 1996; Rooker *et al.*, 1999).

Mean daily surface water temperature obtained from a buoy of Fukuoka Prefecture Observing System off Ohmuta (Fig. 1) was considered to represent the temperature that was experienced by the larval Japanese sea bass in the upper Ariake Bay. The daily mean temperature measured by the buoy ($T_b$) was significantly correlated with the mean temperature of the sampling stations ($T_s$) on the same day as the buoy measurement during our winter samplings:

$$T_b = 0.625T_s + 4.68$$

($r^2 = 0.853$, $n = 20$, $p < 0.0001$: Shoji *et al.*, 2006). Therefore, the mean temperature experienced by Japanese sea bass during the larval stage ($T$, °C) was calculated by the use of this equation and was expressed as mean of daily temperatures measured by the Ohmuta buoy from estimated hatch date until estimated date when 15 mm SL was reached for each fish.

## Results

The mean larval growth rate ($G_{15}$) varied between 0.04 mm d⁻¹ (1996) and 0.10 mm d⁻¹ (1995) and was positively correlated with the $T$. Larval and juvenile sea bass abundance seems to be higher and more variable in years with high $G_{15}$ although the relationship between the abundance of larvae <20 mm SL ($A_{<20}$) and $G_{15}$ was not significant (Fig. 3).

The $G_w/M$ ratio was inversely correlated with $A_{15}$ (Fig. 4). The $A_{15}$ varied by a factor of 24 fold (0.078–1.884) for the 11 years (Fig. 5). Mean $A_{15}$ (± standard deviation: SD) and coefficient of variation (CV) for the 11 years was 0.583 (± 0.647) and 33.5%, resepectively (Fig. 5). Variability in the abundance at 20 mm SL larvae ($A_{20}$) was lower than that in $A_{15}$. The $A_{20}$ fluctuated by 9.4 times for the 11 years, ranging between 0.015 (1990) and 0.1423 (2000). Mean (SD) and CV of $A_{20}$ was 0.0485 (±0.0402) and 25.0%, respectively (Fig. 5).

## Discussion

The large fluctuation of larval and juvenile Japanese sea bass abundance and coincidence of high
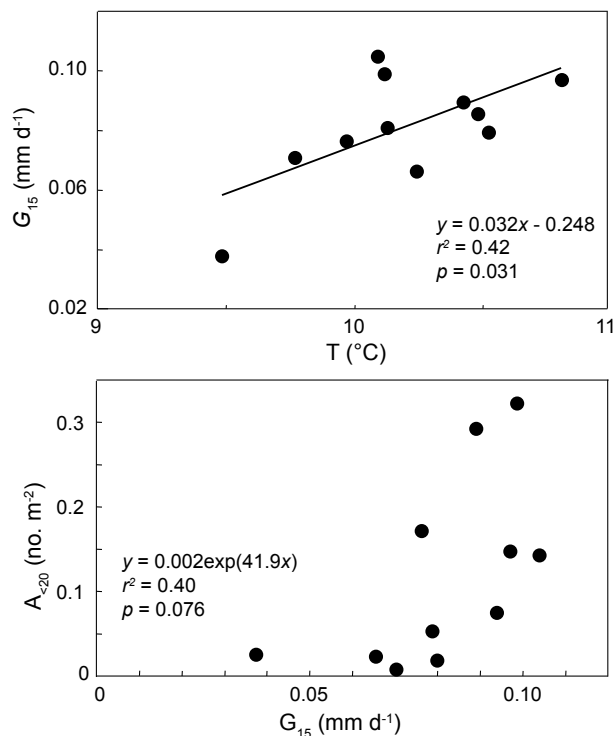


Fig. 3.   Relationships between mean larval growth rate ($G_{15}$, mm d⁻¹) and mean temperature experienced by Japanese sea bass during the larval stage ($T$, °C) from 1990 to 2000 (top) and between abundance of Japanese sea bass <20 mm in standard length ($A_{<20}$) in the Chikugo Estuary to the mean larval growth rate ($G_{15}$, mm d⁻¹) from 1990 to 2000 (bottom).
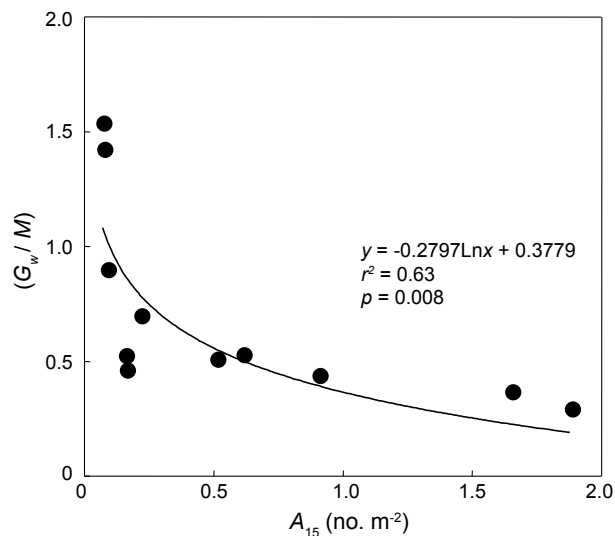


Fig. 4.   Plot of the relative recruitment potential ($G_w/M$) to abundance at 15 mm in standard length ($A_{15}$, no. m⁻²) of Japanese sea bass from 1990 to 2000.
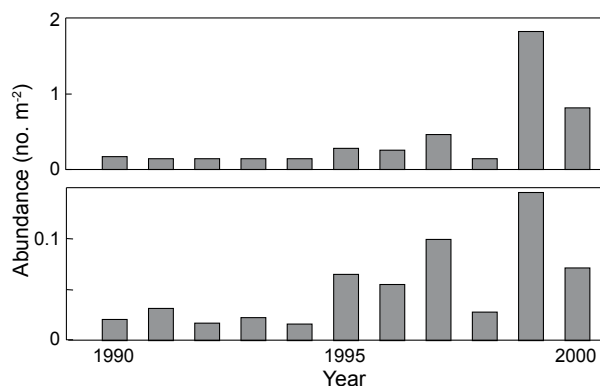
Fig. 5.  Annual fluctuation in abundance at 15 mm ($A_{15}$, top) and 20 mm in standard length ($A_{20}$, bottom) of larval and juvenile Japanese sea bass in Chikugo Estuary from 1990 to 2000.
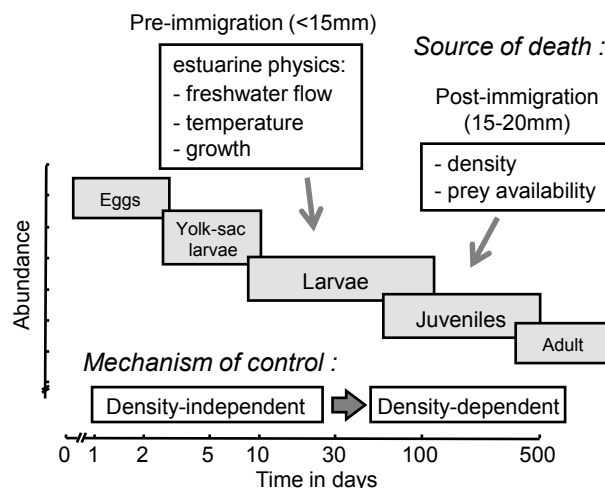


Fig. 6.  Schematic drawings of the survival process in Japanese sea bass with possible mechanism of control for pre- (<15 mm) and post-immigration (>15mm) stages. Physical conditions such as freshwater flow and temperature affect larval growth rate and the larval survival. Density-dependent regulation operates after the immigration into the estuary.

abundance with larval growth rate indicates that a density-independent mechanism controls survival during the larval period as reported in a variety of estuarine fish species and ecosystems (Crecco and Savoy, 1984; Secor and Houde, 1995; North and Houde, 2003; Sirois and Dodson, 2000). A previous study in the upper Ariake and Chikugo Estuary areas showed a significant positive correlation between the freshwater flow through the Chikugo River and water temperature in the upper Ariake Bay during early spring (Shoji et al., 2006). In the present study, water temperature of the upper Ariake Bay had a significant effect on the pre-immigrant sea bass growth rate. Generally, a short larval period due to fast growth is expected to increase survival during the larval stage, when stage-specific cumulative mortality is the highest throughout the life cycle (Houde, 1987). We suggest that physical conditions such as freshwater flow through the Chikugo River, which affects larval growth rate through the variability in ambient temperature, is one of the important determinants for the sea bass larval survival in the upper Ariake Bay (Fig. 6).

The significant effect of sea bass abundance at 15 mm SL ($A_{15}$) on the relative recruitment potential ($G_w/M$) indicates density-dependent control operated during the post-immigration period. Inter- and/or intra-specific predation and competition for prey can be major sources of density-dependent control in fish early life stages (Jenkins et al., 1991; Iles and Beverton, 2000; Kimmerer et al., 2000; Martino and Houde, MS 2004). The highly turbid condition in the Chikugo River would work as predation refuge for the larval and juvenile Japanese sea bass. Water with turbidity >200 NTU prevailed over an area extending up to 10 km from the river mouth during the spring tide period from winter to spring in the Chikugo River (Shoji et al., 2007b). Therefore, predation would

be minimal in the Chikugo River since reaction distance to prey and consumption rate by visual fish predators decrease under conditions with turbidity >200 NTU (Vinyard and O'Brien, 1976; Miner and Stein, 1993). There have not been any possible predators found in the river during winter through spring (Suzuki and Tanaka, unpublished data). Actually, mortality coefficients estimated for the larval and juvenile Japanese sea bass in the Chikugo River for 1990–2000 were lower than 0.1 d$^{-1}$ (Shoji and Tanaka, 2007a, b). It is likely that the mortality from predation is minimal in the Chikugo River.

A shift in habitat from a broad area to a more spatially restricted nursery may correspond with the timing when density-dependent regulation starts to operate in estuarine dependent fish (Watanabe and Nakamura, 1998). In upper Chesapeake Bay, growth and survival of striped bass juvenile is inversely correlated with their recruitment abundance, indicating a density-dependent regulation starts after the immigration to shallow nursery areas and when juveniles begin to feed on benthic prey resources (Martino and Houde, MS 2004) while survival during the larval period is well explained by a density-independent process: due to variability in spring freshwater discharge (North and Houde, 2003). In the present study, increase in the sea bass abundance at 15 mm (immigration stage) caused decrease in the recruitment potential during the post-immigration period (15–20 mm). The variability in abundance decreased as the growth of Japanese sea bass during the larval and juvenile period:

the CV of $A_{20}$ was smaller than that of $A_{15}$. These results indicate that density-dependent regulation starts to operate at the immigration of the Japanese sea bass into the Chikugo River (Fig. 6).

Variability in larval and juvenile fish abundance can control their ingestion and growth by affecting prey abundance (Kiørboe *et al.*, 1988; Jenkins *et al.*, 1991). In the Chikugo River, an estuarine copepod species, *Sinocalanus sinensis*, is almost the exclusive prey species for Japanese sea bass, which composes approximately 99.9% of the number of meso- and macro-zooplankton in the estuary during March (Hibino *et al.*, 1999). Daily consumption by Japanese sea bass larvae and early juveniles is 43.5–60.0% of their body weight (Nanbu, 1977). Their prey requirements would exponentially increase due to the increase in their body weight (Shoji and Tanaka, 2007a) during the post-immigration period. The negative effect of the larval and juvenile Japanese sea bass abundance on their ingestion rate (gut contents weight / body weight) in the Chikugo River (Shoji and Tanaka, 2007a) supports our conclusion that the density-dependence is most likely to be caused by an intra-specific competition for *S. sinensis* since the Japanese sea bass is the most dominant consumer within the ichthyoplankton community in the Chikugo Estuary during spring (Islam and Tanaka, 2006).

In summary, a density-independent, discharge-related control prevails as the primary determinant for pre-immigration, larval Japanese sea bass. Density-dependent process starts to operate as the mechanism of control after the post-immigration stage. Utilization of the riverine area, a spatially-restricted nursery, seems to contribute to the stabilization of the biomass of Japanese sea bass Ariake population through a density-dependent regulation.

## Acknowledgements

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