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Microdistribution and feeding dynamics of *Coilia nasus* (Engraulidae) larvae and juveniles in relation to the estuarine turbidity maximum of the macrotidal Chikugo River estuary, Ariake Sea, Japan

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Running title. Early life history of *Coilia nasus* (Engraulidae)
ABSTRACT

To evaluate the nursery value of the estuarine turbidity maximum (ETM) for the anadromous engraulid fish *Coilia nasus*, physical and biological samples were collected along the macrotidal Chikugo River estuary, southwestern Japan, from June 2005 to January 2006. Generally, eggs were distributed upstream from the ETM, whereas larvae were distributed in the ETM. The first cohort was washed out of the estuary by a large flood in early July. The second cohort appeared after the flood, gradually extending its distributional area through the estuary and growing to 100 mm in standard length (SL) by December. Larvae and juveniles (20–100 mm SL) fed selectively on copepods, specifically large calanoid species, whereas more developed juveniles fed on mysids. Prey organisms in guts were significantly more abundant and present in greater weights in the ETM (salinity < 10) than in the lower estuary (salinity > 10). The better feeding conditions were primarily attributable to consistently high densities of two large calanoid species, *Sinocalanus sinensis* and *Pseudodiaptomus inopinus*, in the ETM. In contrast, the poor feeding conditions in the lower estuary were likely due to a seasonal decrease in copepod density and the dominance of small copepods such as *Oithona* spp. Given that better feeding conditions contribute positively to the growth and survival of larvae and juveniles, we conclude that the ETM has a significantly higher nursery value for *C. nasus* than other habitats in the Chikugo River estuary.

**Key words:** anadromous fish, Ariake Sea, Chikugo River, *Coilia nasus*, copepod, estuarine turbidity maximum, selective feeding, nursery
INTRODUCTION

Although estuaries generally support high productivity in coastal waters, physical and biological conditions vary drastically even within an estuary. In addition to spatial variations, estuarine conditions fluctuate temporally with the tidal rhythm, freshwater discharge, and seasonal succession. In macrotidal estuaries, the hydrodynamic function of tidal pumping and estuarine circulation maintains high concentrations of suspended solids, forming an estuarine turbidity maximum (ETM) at low salinities (Allen et al., 1980; Uncles et al., 2002). Given that high densities of zooplankton are often associated with the ETM, many studies have suggested that growth and survival of larval and juvenile fish are higher in the ETM than in other areas due to its better feeding conditions (e.g., Dauvin and Dodson, 1990; Martino and Houde, 2010; North and Houde, 2003; Shoji et al., 2005; Sirois and Dodson, 2000). Despite the growing understanding of the nursery value of the ETM, intensive sampling in the ETM has been conducted only in spring and summer when larval and juvenile fish are abundant. Year-round assessment is, therefore, essential to improving our understanding of the nursery value of the ETM in relation to the spatiotemporal dynamics of estuarine conditions.

*Coilia nasus* is an engraulid fish endemic to the innermost part of the Ariake Sea, Japan (Takita, 1967a, 1978; Yamada et al., 2007). This species is important to local fisheries and is defined as an anadromous fish (Takita, 1967b). Congenerous species have a wide distribution in lacustrine, riverine, estuarine, and coastal waters in East Asia (Whitehead et al., 1988). Ecological information about *C. nasus* has been accumulated mainly in the macrotidal Chikugo River estuary, which is the largest estuary flowing into the Ariake Sea. Adults migrate to the tidal freshwater area (> 15 km upstream from...
the sea) to spawn pelagic eggs in summer (Matsui et al., 1986a; Ohmura et al., 2012; Takita, 1967b). Eggs and larvae show high survival rates only at salinities < 10
(Fukunaga and Hamasaki, 1998; Matsui et al., 1986b). Larvae and juveniles feed primarily on cladocerans and copepods, gradually extending their distributional area to
the sea (Matsui et al., 1987). Although such ecological characteristics suggest a great
dependence of *C. nasus* on the estuary, few studies have addressed the feeding, growth,
and survival of *C. nasus* larvae and juveniles in relation to the unique macrotidal
environment, specifically the well-developed ETM (cf., Suzuki et al., 2012a).

In the macrotidal Chikugo River estuary, the ETM develops at salinities < 10
especially during spring tides under usual freshwater discharge levels (Suzuki et al.,
2007, 2009a). A large biomass of copepods is present in the ETM throughout the year
(Suzuki et al., 2013). In contrast, copepod biomass is usually smaller and seasonally
variable in areas outside the ETM (Suzuki et al., 2013). Furthermore, mysid biomass is
larger in the ETM than outside the ETM (Suzuki et al., 2009b). We hypothesize that *C.
nasus* larvae and juveniles benefit from the better feeding conditions in the ETM
irrespective of the season. To test this hypothesis, we examine the feeding dynamics of
*C. nasus* larvae and juveniles from the first feeding to the first overwintering. Physical
and biological samples were collected along the Chikugo River estuary from June 2005
to January 2006. Gut contents of *C. nasus* larvae and juveniles were analyzed in relation
to zooplankton composition in the environment. Our discussion focuses on contrasting
the nursery value of the ETM with that of the lower estuary.
MATERIALS AND METHODS

Study area

The Chikugo River estuary is the largest estuary in the Ariake Sea in terms of both catchment area (2860 km²) and freshwater discharge (annual median of daily averages: 60 m³ s⁻¹). The estuarine environment is characterized by one of the largest tidal ranges in Japan (up to 5 m during spring tides). The tidal reach extends to the Chikugo Weir 23 km upstream from the river mouth (Fig. 1). Strong tidal currents completely mix the water column during spring tides, whereas partial stratification occurs during neap tides (Suzuki et al., 2007). The ETM is usually located 10–20 km upstream from the river mouth at spring high tide, although it is transported back and forth over a 20-km range along the estuary with the semidiurnal tidal cycle between high and low tides. The copepod community of the ETM is overwhelmingly dominated by *Sinocalanus sinensis*, except in summer when *Pseudodiaptomus inopinus* outnumbers *S. sinensis* (Suzuki et al., 2013). The mysid *Hyperacanthomysis longirostris* maintains dominance in and close to the ETM throughout the year (Suzuki et al., 2009b). A description of the dynamics of particulate organic matter in the Chikugo River estuary is published elsewhere (Suzuki et al., 2007, 2009a, 2012a). Overall, physical and biological conditions change clearly with the salinity gradient along the Chikugo River estuary. In the present study, salinity was used to separate the ETM (salinity < 10) from the lower estuary (salinity >10). As *C. nasus* larvae and juveniles are distributed exclusively in the ETM and the lower estuary (Matsui et al., 1987; Takita, 1967b), the tidal freshwater area, which was included in the ETM for convenience, had little influence on comparisons between the ETM and the lower estuary.

Seven regular sampling stations (R1–R7; Fig. 1) were set up at intervals of
1.5–5.5 km along the lower reaches of the Chikugo River; they were located between
the river mouth and the upper limit of the tidal reach (23 km upstream). Three regular
sampling stations (E1–E3; Fig. 1) were set up along the main tidal channel of the river
so that E1 was near the river mouth and E3 was at the edge of the tidal flat (9 km
offshore). Three extra sampling stations (R2.5, R3.5, and R6.5; Fig. 1) were set up in or
close to the spawning area of *C. nasus*. The freshwater discharge was continuously
monitored 26 km upstream and the data were uploaded to the web site
(http://www.qsr.mlit.go.jp/chikugo/data/09-sokuhou/index.html) by the Chikugogawa
River Office. For tidal ranges, water level differences were calculated between low and
high tides in the morning using values that had been predicted for Ohmuta (16 km south
of the river mouth) by the Japan Meteorological Agency (2004).

**Field sampling**

Three sampling methods were used to collect *C. nasus* eggs, larvae, and juveniles (Fig.
2). In *C. nasus*, the transition between the larval and juvenile stages occurs at ca. 30 mm
in standard length (ca. 35 mm in total length; Takita, 1967b). For eggs and larvae, a
small ring net (45 cm mouth diameter, 0.33 mm mesh aperture along the 200 cm conical
body) was towed in the surface water by a boat for 3–10 min at approximately 1 m s^{-1}
against the water currents. The sampling was conducted in or close to the spawning area
of *C. nasus* in the upper estuary (R2.5–R7 including extra stations) 14 times between 8
June and 23 August in 2005. For more developed larvae and juveniles, a large ring net
(130 cm mouth diameter, 1 mm mesh aperture along the 350 cm cylindrical body and
0.33 mm mesh aperture at the 150 cm conical end) was towed as described above.
Sampling was conducted at the 10 regular stations (R1–R7, E1–E3) during spring tides
monthly between August and October 2005. Catches from the small and large ring nets were preserved in 99% ethanol. The sampling was always started at the uppermost station (R7) and finished at the lowermost station (R2.5 or E3) within 4–5 h around high tide in the morning. At each station, zooplankton were sampled by towing a plankton net (45 cm mouth diameter, 0.1 mm mesh aperture along the 100 cm conical body) vertically from the bottom to the surface. Catches from the plankton net were preserved in 5% formalin seawater solution. The volume of water filtered through each net was calculated using digital flow meters that were attached to the respective mouths of the nets. Temperature, salinity, and turbidity were measured in the surface water using an environmental monitoring system (6920 Sonde and 650 MDS Display, YSI, Yellow Springs, Ohio, USA).

Finally, to sample more developed juveniles, Shige-ami fishing (a traditional fishing method used in the Ariake Sea) was conducted at R4 and E1 during spring tides monthly between October 2005 and January 2006. This method of fishing collects fish using a net fixed to the bow of an anchored boat. Fish that swim with water currents are efficiently trapped in the net, especially during the ebb tide. Trapped *C. nasus* juveniles were sampled at 5 min intervals using a dip net and frozen onboard. The frozen specimens were thawed and then preserved in 99% ethanol in the laboratory. Temperature, salinity, and turbidity were measured in the surface water every 10 min. Because the fishing was conducted for 2 h at each station during the ebb tide, salinity decreased with time. This allowed sampling of *C. nasus* from a relatively wide salinity range (usually 5–25 at E1).

*Laboratory analysis*
Eggs, larvae, and juveniles of *C. nasus* were enumerated for samples from each station on each sampling date. The standard length (SL) of all specimens was measured, with the exception of random selection of specimens at stations where the number of specimens far exceeded 100. To obtain a SL frequency distribution for each sampling date, SL frequency distributions at all stations were accumulated after weighted in proportion to the density of *C. nasus* at each station. Comparisons of SL frequency distributions between the three sampling methods revealed a strong bias toward small individuals in samples from the small ring net on 23 August and from the large ring net on 17 October. To minimize the possibility of net avoidance by larger individuals, these samples were not used for further analysis. Sample shrinkage incidental to preservation in ethanol was not considered.

When available, approximately 20 *C. nasus* individuals (larvae and/or juveniles) were randomly picked for each station on each sampling date after 24 July, since when a single large cohort of *C. nasus* occurred continuously (see Results). Under a stereomicroscope, gut contents were removed from the stomach and intestine of larvae and from the stomach of juveniles. Gut contents were enumerated and identified to the lowest taxonomic level possible. Using diagnostic characters (Chihara and Murano, 1997; Mizuno and Takahashi, 2000; Shen and Mizuno, 1984), copepods and mysids were identified to species or genera and other prey organisms to orders or classes. To calculate dry weights, body lengths of the four dominant prey taxa Rotifera, Cladocera, Copepoda, and Mysidacea (see Results) were measured using an eyepiece graticule in the stereomicroscope. The body lengths were converted into dry weights using length-weight relationships devised by Uye (1982) and Pauli (1989).

Zooplankton samples from the environment were processed in the same way as
gut contents. To show spatial patterns of occurrence of dominant zooplankton taxa along the salinity gradient of the Chikugo River estuary, monthly zooplankton data from June 2005 to January 2006 were used (cf., Suzuki et al., 2013). In the present study, the 0.1 mm mesh was used for the plankton net to achieve the maximum sampling efficiency in turbid waters. Although this mesh size is considered fine enough to catch the majority of potential food taxa for *C. nasus*, the density of small zooplankton, such as rotifers and copepod nauplii, might have been underestimated. Given strong vertical mixing in the Chikugo River estuary especially during spring tides (Suzuki et al., 2007, 2009a, 2012a), zooplankton samples obtained from the water column were considered to represent food availability for *C. nasus*.

To evaluate the food preference of *C. nasus* at each station on each sampling date, an electivity index (*E*_i*, Vanderploeg and Scavia, 1979) was calculated as follows:

\[ E_i^* = \frac{W_i - (1/N)}{W_i + (1/N)} \]  
\[ W_i = \frac{r_i/p_i}{\sum (r_i/p_i)} \]

where \( r_i \) and \( p_i \) represent the relative abundance of food types in the gut and the environment, respectively. The number of food types is designated by \( N \). The electivity index \( E_i^* \) changes between plus and minus one with zero indicating random feeding. Although the use of \( E_i^* \) is recommended for evaluating food preferences, the maximum preference value (\( E_i^* = 1 \)) can be attained only under these unrealistic conditions: \( r_i = 1, p_i = 0, \) and \( N = \infty \) (Lechowicz, 1982). It is also important to note that the maximum attainable preference value increases with \( N \). In the present study, \( E_i^* \) was calculated for the above-mentioned four dominant prey taxa. It was also calculated for the six dominant copepod categories *S. sinensis*, *P. inopinus*, *Acartia* spp., *Parvocalanus crassirostiris*, *Oithona* spp., and all copepod nauplii. Ontogenic changes in the food
preference of *C. nasus* were examined using $E_i^*$ and mean SL at each station on each sampling date.
RESULTS

Spatiotemporal occurrence of Coilia nasus

In summer 2005, the daily freshwater discharge remained < 100 m$^3$ s$^{-1}$ until June, with a minimum of < 20 m$^3$ s$^{-1}$ from 17 to 25 June (Fig. 3a). The discharge increased in early July, causing a large flood event from 9 to 14 July with a peak of 1768 m$^3$ s$^{-1}$ on 11 July. Following this flood, the discharge returned to < 100 m$^3$ s$^{-1}$ by late July. Surface water temperature increased gradually from 24 to 28°C before dropping to < 25°C during the flood period (Fig. 3b). Higher temperatures of 25–31°C occurred continuously after the flood period. Surface water turbidity changed clearly with the fortnightly tidal cycle, although it dropped to < 50 NTU (nephelometric turbidity unit) after the flood period (Fig. 3c). Turbidity peaks were found more upstream during spring tides than during neap tides, exceeding 200 NTU at salinity 1. Coilia nasus eggs always showed higher densities (> 10 eggs m$^{-3}$) immediately after neap tides, even during the flood period (Fig. 3d). In contrast, the density of C. nasus larvae did not vary with the fortnightly tidal cycle (Fig. 3e). Although larvae disappeared during the flood period, they reached a maximum density of 600 ind m$^{-3}$ afterward. As for spatial distribution, larvae showed density peaks at salinity 1, whereas eggs were always distributed more upstream (salinity < 1).

Two distinct cohorts of C. nasus were found in the series of SL frequency distributions of specimens sampled using the small ring net (Fig. 4). The first cohort appeared in early June and increased in mean SL from 5.3 mm on 8 June to 18.3 mm on 4 July. This cohort, however, disappeared during the flood period of early July. The second cohort appeared after the flood period and increased in mean SL from 3.3 mm on 19 July to 20.7 mm on 9 August. The second cohort appeared successively in the
series of unimodal SL frequency distributions of specimens sampled using the large ring
net and Shige-ami fishing (Fig. 5). The monthly mean SL of specimens sampled over
the whole estuary were 31, 44, 72, 88, and 102 mm from August to December in 2005
but remained at 100 mm until January 2006. As for spatial distribution, larvae and
juveniles concentrated in the ETM (salinity < 10) in August, whereas in September they
were distributed throughout the estuary. Although the density of juveniles could not be
determined from the non-quantitative Shige-ami fishing samples, the majority of
specimens were sampled in the ETM (except in December). However, significantly
larger specimens (Mann-Whitney test, \( P < 0.05 \)) were always found in the lower estuary
(salinity > 10), with the monthly mean SLs of 40, 52, 104, 106, 105, and 111 mm from
August to January.

Feeding dynamics of Coilia nasus

A typical pattern of the feeding dynamics of \( C. \) nasus was observed in September when
larvae and juveniles occurred at all stations except the uppermost R7. A maximum \( C. \) nasus
density of 0.6 ind m\(^{-3}\) was found in the ETM, where surface water salinity and
turbidity were 0.8 and 481 NTU, respectively (Fig. 6a, b). In the environment, copepods
dominated numerically throughout the estuary, except at R7 where rotifers outnumbered
copepods (Fig. 6c). The density of copepods showed a bimodal pattern along the estuary,
exceeding 50 ind L\(^{-1}\) at R4, R5, and E3. Copepods accounted for > 95% by number of
the gut contents of \( C. \) nasus at each station (Fig. 6d). The number of gut contents per
fish was larger in the ETM than in the lower estuary, even though the SL of \( C. \) nasus
was smaller in the ETM than in the lower estuary (Fig. 6b). Comparisons of the
copepod category composition between the environment and gut contents indicated that
*C. nasus* preferred large copepods such as *P. inopinus* (*E_\text{i}^* = 0.4 to 0.7*) over small copepods such as *Oithona* spp. (*E_\text{i}^* = -1.0 to -0.9*) and nauplii (*E_\text{i}^* = -1.0 to 0*). Among dominant prey taxa excluding copepods, *C. nasus* clearly preferred cladocerans and mysids over rotifers.

The physical and biological environment during spring tides formed similar longitudinal profiles along the estuarine salinity gradient from June 2005 to January 2006. Surface water turbidity exceeded 100 NTU at salinities 0.1–10, with highest values at salinity 1 (Fig. 7a). Rotifers and cladocerans concentrated at salinities < 1, whereas mysids occurred primarily at salinities > 1 (Fig. 7b). The density of copepods always exceeded 1 ind L\(^{-1}\) at salinities 0.1–10, although it often dropped to 0.1 ind L\(^{-1}\) outside this salinity range, especially in the cold season. The dominant oligohaline copepods *S. sinensis* and *P. inopinus* were wholly responsible for the high copepod densities observed at salinities 0.1–10 (Fig. 7c). In contrast, the dominant meso/polyhaline copepods *Acartia* spp., *Parvocalanus crassirostris*, and *Oithona* spp. usually concentrated at salinities > 10. Copepod nauplii occurred throughout the estuary, exhibiting higher densities at salinities 0.1–10.

The electivity index *E_\text{i}^* revealed ontogenetic changes in the food preference of *C. nasus*. Among the four dominant prey taxa, cladocerans were highly selected by *C. nasus* in the SL range of < 60 mm, whereas copepods were generally selected by *C. nasus* in the SL range of 20–100 mm (Fig. 8a). *Coilia nasus* switched its diet from copepods to mysids at 100 mm SL. In contrast, rotifers were usually avoided, even by small larvae (< 20 mm SL). Among dominant copepod categories, the two large copepods *S. sinensis* and *P. inopinus* were selected irrespective of the SL of *C. nasus* (Fig. 8b). In contrast, nauplii and the small copepod *Oithona* spp. were not selected at
all, except by *C. nasus* of < 10 mm SL, which selected nauplii.

The number of prey organisms in the guts of each *C. nasus* was larger in the ETM than in the lower estuary (Fig. 9a), although copepods overwhelmingly dominated the gut contents in both habitats (Fig. 9b, c). Significantly larger numbers of prey organisms were found in the ETM in *C. nasus* SL classes of 50–60, 60–80, 80–100 and > 100 mm (Mann-Whitney test, *P* < 0.05). Prey organisms were always dominated by the two large copepods *S. sinensis* and *P. inopinus* in the ETM, whereas small copepods such as *Oithona* spp. dominated in the lower estuary. Individual dry weights were > 10 times greater for *S. sinensis* and *P. inopinus* compared with *Oithona* spp. As a result, the weight of prey organisms in the guts of each *C. nasus* was greater in the ETM than in the lower estuary (Fig. 10a). Significantly greater weights of prey organisms were found in the ETM in *C. nasus* SL classes of 40–50, 50–60, 60–80, and 80–100 mm (Mann-Whitney test, *P* < 0.05). The two large copepods *S. sinensis* and *P. inopinus* overwhelmingly dominated the gut contents by weight in the ETM (Fig. 10b, c). Although small copepods dominated the gut contents by weight in the lower estuary, mysids outweighed copepods in the *C. nasus* SL classes of > 80 mm.
DISCUSSION

Spatiotemporal occurrence of Coilia nasus

In contrast to other anadromous fish that spawn pelagic eggs for a short period of time (e.g., American shad, Williams and Daborn, 1984; Striped bass, Secor and Houde, 1995), reproduction of C. nasus is characterized by a long spawning season ranging from May to August (Matsui et al., 1986a; Takita, 1967b). In summer 2005, higher densities of C. nasus eggs were observed repeatedly after neap tides irrespective of drastic changes in freshwater discharge and temperature (Fig. 3). This finding agrees closely with previous reports that the spawning migration of C. nasus increases during the neap-spring transition period (Matsui et al., 1986a; Ohmura et al., 2012; Yoshimoto and Kitajima, 1993). Given that the density of copepods generally increases in the Chikugo River estuary during the neap-spring transition period (Suzuki et al., 2012b), newly hatched larvae may be favored by better feeding conditions at this time. In contrast with C. nasus, temperature is a prime determinant of the intensive spawning of American shad (Williams and Daborn, 1984) and striped bass (Secor and Houde, 1995). Although the ecological significance of the fortnightly spawning cycle of C. nasus remains to be studied, it may prove to be a unique strategy for spreading the risk of reproduction failures through its long spawning season.

The spatiotemporal occurrence of eggs and larvae combined with the succession of the SL frequency distribution clearly illustrated the disappearance of the first cohort in the year class of 2005 (Figs. 3, 4). As pelagic eggs of C. nasus hatch 19–21 h after fertilization at temperatures of 24–26°C (Takita, 1967b), eggs and newly hatched larvae can remain within the tidal reach under usual freshwater discharge levels (Hayashi et al., 1994; Matsui et al., 1986b). However, the first cohort was probably
washed out of the estuary by the large flood that occurred in early July. High salinities
would have caused substantial mortality in the sea, as *C. nasus* eggs and larvae are
highly vulnerable to salinities > 10 (Fukunaga and Hamasaki, 1998; Matsui *et al.*, 1986b). In addition, the first cohort possibly suffered from deteriorated feeding
conditions during the flood period when copepods almost completely disappeared from
the estuary (Suzuki *et al.*, 2012b). The second cohort appeared after the flood period
and constituted the majority of the year class (Figs. 4, 5). Having grown to the juvenile
stage (> 30 mm SL), the second cohort survived a large flood in early September (Fig.
2). This indicates that the second cohort had already have gained tolerance to variations
in salinity, food availability, and water currents. The SL frequency distributions of the
second cohort continuously shifted to larger sizes until reaching a ceiling of 100 mm SL
in December. In addition, larger specimens were always sampled in the lower estuary in
each month. Although more developed juveniles likely extended their distributional area
downstream, they remained in the estuary until they grew to 100 mm SL. Previous
studies have suggested that *C. nasus* juveniles begin migration to the sea at a size of 100
mm SL in October at the earliest (Hayashi *et al.*, 2002; Ishida, 1990; Matsui *et al.*, 1987). Overall, prolonged inhabitation in the estuary is considered to be an essential
component in the early life history of *C. nasus*.

**Feeding dynamics of *Coilia nasus***

Ontogenetic changes in the food preference of *C. nasus* were confirmed over a wide
range of SLs (Figs. 6, 8): cladocerans (< 60 mm SL), copepods (20–100 mm SL), and
mysids (> 100 mm SL). In general, food preferences for crustacean zooplankton are
considered common among species in the genus *Coilia* (Chen and Zhu, 2008; Varghese,
1961). The present study is the first to document that *C. nasus* prefers mysids, whereas our other results agree exactly with Matsui *et al.* (1987). However, the preference for cladocerans is still uncertain, as cladocerans are less able to escape planktivorous fish than copepods (Drenner *et al*., 1978). Our further analysis revealed that *C. nasus* selected larger species from copepod communities in the environment, as has been reported for other fishes in estuaries (e.g., Hibino *et al*., 1999; Islam *et al*., 2006a, b; Robichaud-LeBlanc *et al*., 1997). Despite the general categorization of engraulid fishes as filter feeders, anchovies switch their feeding behavior from filtering to biting in response to environmental conditions (James and Findlay, 1989; Leong and O’Connell, 1969). *Coilia nasus* would improve its foraging efficiency (i.e., energy gain per unit foraging effort) by feeding on larger copepods, although the mechanism of the selective feeding by *C. nasus* remains to be studied.

Significantly better feeding conditions for *C. nasus* in the ETM were demonstrated by comparing both number and weight of prey organisms in guts between the ETM and the lower estuary (Figs. 9, 10). Previous studies have reported similar spatial differences in gut contents of other larval and juvenile fishes along the Chikugo River estuary (Hibino *et al*., 1999; Islam *et al*., 2006a, b; Suzuki *et al*., 2008). The better feeding conditions observed in the ETM are primarily attributable to consistently high densities of the two large oligohaline copepods *S. sinensis* and *P. inopinus* (Fig. 7). Moreover, the ETM is considered advantageous for planktivorous fish because high turbidity has less influence on the foraging efficiency of planktivorous fish than on that of piscivorous fish (i.e., predators of planktivorous fish; De Robertis *et al*., 2003). In contrast, the poor feeding conditions observed in the lower estuary were likely due to a seasonal decrease in copepod density and the dominance of small copepods such as
Oithona spp. (Suzuki et al., 2013). Generally, better feeding conditions for larval and juvenile fish in the ETM are considered common in many estuaries (e.g., St. Lawrence River, Dauvin and Dodson, 1990; Sirois and Dodson, 2000; Chesapeake Bay, Martino and Houde, 2010; North and Houde, 2003; Shoji et al., 2005). Nevertheless, it is notable that C. nasus takes advantage of the ETM continuously from summer to winter; previous studies have usually addressed the feeding dynamics of larval and juvenile fish in spring and summer only. Although some C. nasus juveniles migrate offshore to overwinter at higher water temperatures (cf., Hibino et al., 2007), others may stay in the ETM to benefit from better feeding conditions, even in winter.

Implications for the Coilia nasus population

The present study demonstrated the great dependence of C. nasus larvae and juveniles on the ETM (Fig. 11). Eggs are spawned in the tidal freshwater area, whereas newly hatched larvae are distributed in the ETM. During the long spawning season, large floods occasionally strike the estuary. Given the vulnerability of eggs and larvae to high salinities (Fukunaga and Hamasaki, 1998; Matsui et al., 1986b), they usually do not survive far downstream from the ETM. Even after acquiring physiological tolerance, juveniles likely stay in the ETM to utilize the high densities of large copepods. Moreover the dominant mysid H. longirostris occurs abundantly in and close to the ETM (Suzuki et al., 2009b), assuring better feeding conditions for more developed juveniles. Such better feeding conditions in the ETM will contribute positively to the growth and survival of C. nasus from the first feeding to the first overwintering. In addition, potential predators are considered less abundant in the ETM than in the lower estuary (Shoji et al., 2006). Assessment of growth and survival of C. nasus larvae and
juveniles in each habitat is the next issue that needs to be studied. Although direct
evaluation of the contribution of each habitat to adult recruitment is necessary to
identify a nursery (cf. Beck et al., 2001), our overall results indicate that the ETM holds
significantly higher nursery value for *C. nasus* than other habitats in the Chikugo River
estuary.

*Coilia nasus* is one of seven continental relict fishes occurring only in the
Ariake Sea within Japan (Sato and Takita, 2000). Macrotidal estuaries characteristic of
the innermost part of the Ariake Sea are thought to be primarily responsible for the
survival of the relict fish populations after the isolation of the Japanese Archipelago
from the Eurasian Continent by marine transgressions (Hibino et al., 2002; Sato and
Takita, 2000; Yagi et al., 2011). Reproduction of the relict *C. nasus* population depends
greatly on the Chikugo River estuary (Matsui et al., 1986b; Takita, 1967b), although
sporadic reproduction has been observed in other estuaries of the Ariake Sea (Igita,
1986; Yagi et al., 2011). Given high fishing pressure on migrating adults during the
spawning season (Takita, 1967b; Yoshimoto and Kitajima, 1993), effective fishing
regulations are necessary to preserve the relict *C. nasus* population. The present study
indicates that a temporary prohibition of fishing following large floods will facilitate the
occurrence of large cohorts that should constitute the majority of the year class of *C.
nasus*. Furthermore, conservation of the unique macrotidal estuarine environment will
be important to preserve all of the relict fishes, including *C. nasus*. 
ACKNOWLEDGEMENTS

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of the Japanese temperate bass *Lateolabrax japonicus* juveniles with two contrasting copepod assemblages in estuarine nursery grounds in the Ariake Sea, Japan. *J. Fish Biol.* **68**: 569-593.


FIGURE LEGENDS

Figure 1. Study areas and sampling stations along the Chikugo River estuary on the Kyushu Island in southwestern Japan. Filled and open circles represent our regular and extra sampling stations, respectively. The Chikugo Weir is represented by a filled rectangle. Filled and open triangles represent observation points for freshwater discharges and tidal ranges, respectively.

Figure 2. Interrelations among seasonal changes in freshwater discharge and temperature (a), the temporal occurrence of Coilia nasus (b), and schedules of sampling (c) in the Chikugo River estuary from February 2005 to January 2006. Monthly temperature consists of both mean (horizontal line) and range (vertical line) observed in the surface water through the estuary under a monthly sampling program (Suzuki et al., 2012a). Filled triangles represent applications of each sampling method.

Figure 3. Interrelations among daily fluctuations in freshwater discharge and tidal range (a), and spatiotemporal changes in temperature (b), turbidity (c), and the density of Coilia nasus eggs (d) and larvae (e) observed in the surface water along the upper Chikugo River estuary from 8 June to 9 August in 2005. Sampling dates are represented by filled circles in the tidal range plot. The isopleth charts are overlaid with salinity contour lines. Filled triangles represent the locations of the sampling stations. Up- and downward arrows represent the middle of spring and neap tides, respectively.

Figure 4. Frequency distributions of the standard length of Coilia nasus representing each sampling date from 8 June to 9 August in 2005. All specimens were sampled in the estuarine turbidity maximum (salinity <10) using a small ring net (45 cm mouth
diameter, 0.33 mm mesh aperture along the 200 cm conical body). The mean standard
length and the number of specimens analyzed are represented by M and N,
respectively.

Figure 5. Monthly frequency distributions of the standard length of *Coilia nasus* from
August 2005 to January 2006. Filled and open bars represent specimens sampled in
the estuarine turbidity maximum (ETM, salinity < 10) and the lower estuary (salinity
> 10), respectively. Sampling was conducted using a large ring net (130 cm mouth
diameter, 1 mm mesh aperture along the 350 cm cylindrical body and 0.33 mm mesh
aperture at the 150 cm conical end) in August and September, and Shige-ami fishing
from October to January. The mean standard length and the number of specimens
analyzed are represented by M and N, respectively. Information about specimens
sampled in the whole and lower estuary is shown on the left and right sides of each
monthly chart, respectively. Monthly charts are partially magnified in October and
November.

Figure 6. Interrelations among the physical environment (a; salinity and turbidity), the
occurrence of *Coilia nasus* (b; density and frequency distributions of standard length),
zooplankton densities in the environment (c), and prey organisms in the guts of *C.
nasus* (d) observed at the ten regular sampling stations along the Chikugo River
estuary on 19 September in 2005. Major zooplankton categories are represented by
different patterns in the bar charts.

Figure 7. Turbidity (a), the density of dominant prey taxa (b), and the density of
dominant copepod categories (c) observed along the salinity gradient of the Chikugo
River estuary monthly from June 2005 to January 2006 (cf., Suzuki et al., 2013).
Note that all axes are transformed logarithmically.
Figure 8. The electivity index ($E_i^*$, Vanderploeg and Scavia, 1979) of *Coilia nasus* for dominant prey taxa (a) and dominant copepod categories (b) in relation to the mean standard length of *C. nasus*. Each symbol represents $E_i^*$ observed at each station in the Chikugo River estuary from 24 July in 2005 to 16 January in 2006.

Figure 9. The number of prey organisms in the guts of *Coilia nasus* in relation to standard length (a), accompanied by the numerical composition of prey organisms observed in the estuarine turbidity maximum (b; ETM, salinity < 10) and the lower estuary (c; salinity > 10). Each symbol represents individual specimens sampled in the Chikugo river estuary from 24 July in 2005 to 16 January in 2006. The two large copepods *Sinocalanus sinensis* and *Pseudodiaptomus inopinus* constitute Copepoda (large), whereas Copepoda (others) consists mainly of small copepods and unidentified copepods. The number of specimens analyzed is represented by $N$.

Figure 10. The weight of prey organisms in the guts of *Coilia nasus* in relation to standard length (a), accompanied by the weight composition of prey organisms observed in the estuarine turbidity maximum (b; ETM, salinity < 10) and the lower estuary (c; salinity > 10). See Fig. 8 for details.

Figure 11. The early life history of the anadromous engraulid fish *Coilia nasus* in the macrotidal Chikugo River estuary. Adults spawn pelagic eggs in the tidal freshwater area in summer. Larvae are distributed in the estuarine turbidity maximum (ETM, salinity < 10) under usual freshwater discharge levels, whereas they are highly vulnerable to large floods. Although juveniles extend their distributional area through the estuary, they benefit from better feeding conditions only in the ETM where large copepods occur abundantly. Some juveniles migrate offshore to overwinter at higher water temperatures, whereas others stay in the ETM even in winter under the better
feeding conditions.
Fig. 2

(a) Discharge and Temperature

(b) Temporal occurrence of *Coilia nasus*

(c) Schedules of sampling

- Towing of a small ring net in the upper estuary
- Towing of a large ring net through the estuary
- Shige-ami fishing at R4 and E1
Fig. 3

(a) Discharge and tidal range

(b) Temperature

(c) Turbidity

(d) Egg density

(e) Larva density
Fig. 4

- 8 Jun: M=5.3, N=4
- 13 Jun: M=6.3, N=145
- 18 Jun: M=9.2, N=138
- 24 Jun: M=16.6, N=63
- 29 Jun: M=16.0, N=35
- 4 Jul: M=18.3, N=37
- 9, 14 Jul: N=0
- 19 Jul: M=3.3, N=4
- 24 Jul: M=6.2, N=200
- 29 Jul: M=10.3, N=281
- 3 Aug: M=14.5, N=219
- 9 Aug: M=20.7, N=193

Standard length (mm)
Fig. 5

Standard length (mm) sampled in the ETM

<table>
<thead>
<tr>
<th>Date</th>
<th>M</th>
<th>N</th>
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<tbody>
<tr>
<td>23 Aug 2005</td>
<td>31</td>
<td>471</td>
</tr>
<tr>
<td>19 Sep</td>
<td>44</td>
<td>745</td>
</tr>
<tr>
<td>16 Oct</td>
<td>72</td>
<td>220</td>
</tr>
<tr>
<td>14 Nov</td>
<td>88</td>
<td>195</td>
</tr>
<tr>
<td>14 Dec</td>
<td>102</td>
<td>114</td>
</tr>
<tr>
<td>16 Jan 2006</td>
<td>100</td>
<td>106</td>
</tr>
</tbody>
</table>

- M: Mean
- N: Number of samples
Fig. 6

(a) Physical environment

(b) Occurrence of *Coilia nasus*

(c) Zooplankton density (ind. L\(^{-1}\))

(d) Prey organisms (ind. fish\(^{-1}\))

<table>
<thead>
<tr>
<th>Copepoda</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sinocalanus sinensis</td>
<td>Rotifera</td>
</tr>
<tr>
<td>Pseudodiaptomus inopinus</td>
<td>Cladocera</td>
</tr>
<tr>
<td>Acartia spp.</td>
<td>Mysidacea</td>
</tr>
<tr>
<td>Parvocalanus crassirostris</td>
<td>Other zooplankton</td>
</tr>
<tr>
<td>Oithona spp.</td>
<td>Unidentified copepods</td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>Copepod nauplii</td>
</tr>
</tbody>
</table>

Salinity vs. Turbidity (NTU) vs. Density (ind. m\(^{-3}\)) vs. Standard length (mm)
Fig. 7

(a) Turbidity along the salinity gradient

(b) Density of dominant prey taxa along the salinity gradient

(c) Density of dominant copepod categories along the salinity gradient

- **Rotifera**: Cladocera
- **Copepoda**: Mysidacea
- **Sinocalanus sinensis**: Pseudodiaptomus inopinus
- **Acartia spp.**: Parvocalanus crassirostris
- **Oithona spp.**: Copepod nauplii
(a) Electivity index $E_i^*$ for dominant prey taxa

(b) Electivity index $E_i^*$ for dominant copepod categories

Rotifera ▲ Cladocera ○ Copepoda ■ Mysisacea

Sinocalanus sinensis ▼ Pseudodiaptomus inopinus
Acartia spp. □ Parvocalanus crassirostris
Oithona spp. △ Nauplii

Mean standard length (mm)
Fig. 9

(a) Number of prey organisms

(b) Numerical composition of prey organisms in the ETM

(c) Numerical composition of prey organisms in the lower estuary
Fig. 10

(a) Weight of prey organisms

(b) Weight composition of prey organisms in the ETM

(c) Weight composition of prey organisms in the lower estuary
Fig. 11

May    Jun    Jul    Aug    Sep    Oct    Nov    Dec    Jan
Chikugo River

ETM (Salinity < 10)

Lower estuary (Salinity > 10)

Coilia nasus
C. nasus egg
Copepoda

Floods

Better feeding conditions

Worse feeding conditions

Washout

Ariake Sea

Coilia nasus

C. nasus egg

Copepoda