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Author(s)	Suzuki, Keita W.; Nakayama, Kouji; Tanaka, Masaru
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Horizontal distribution and population dynamics of the dominant mysid *Hyperacanthomysis longirostris* along a temperate macrotidal estuary (Chikugo River estuary, Japan)

Keita W. Suzuki^{a,*}, Kouji Nakayama^b, Masaru Tanaka^b

^aDivision of Applied Biosciences, Graduate School of Agriculture, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan

^bField Science Education and Research Center, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan

*Corresponding author.

Tel: 81-75-753-6222. Fax: 81-75-753-6229

E-mail address: keita@kais.kyoto-u.ac.jp

Postal address: Laboratory of Marine Stock-Enhancement Biology, Division of Applied Biosciences, Graduate School of Agriculture, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan

Abstract

The estuarine turbidity maximum (ETM) that develops in the lower salinity areas of macrotidal estuaries has been considered as an important nursery for many fish species. Mysids are one of the dominant organisms in the ETM, serving as a key food source for juvenile fish. To investigate the horizontal distribution and population dynamics of dominant mysids in relation to the fluctuation of physical conditions (temperature, salinity, turbidity, and freshwater discharge), we conducted monthly sampling (hauls of a ring net in the surface water) along the macrotidal Chikugo River estuary in Japan from May 2005 to December 2006. *Hyperacanthomysis longirostris* was the dominant mysid in the estuary, usually showing peaks of density and biomass in or close to the ETM (salinity 1-10). In addition, intra-specific differences (life-cycle stage, sex, and size) in horizontal distribution were found along the estuary. Larger males and females, particularly gravid females, were distributed upstream from the center of distribution where juveniles were overwhelmingly dominant. Juveniles increased in size toward the sea in marked contrast with males and females. The findings suggest a possible system of population maintenance within the estuary; gravid females release juveniles in the upper estuary, juveniles grow during downstream transport, young males and females mature during the upstream migration. Density and biomass were primarily controlled by seasonal changes of temperature, being high at intermediate temperatures (ca. 15-25 °C in late spring and fall) and being low at the extreme temperatures (ca. 10 °C in midwinter and 30 °C in midsummer). High density (up to 666 ind. m⁻³) and biomass (up to 168 mg dry weight m⁻³) of *H. longirostris* were considered to be comparable with those of copepods in the estuary.

Keywords: mysid; *Hyperacanthomysis longirostris*; distribution; population dynamics;

salinity; estuarine turbidity maximum; Japan; Ariake Sea; Chikugo River estuary

1. Introduction

Mysids are especially abundant in coastal and estuarine shallow waters, where they occupy an important position between lower and higher trophic levels (Mauchline, 1980). It is well established that juveniles of various fish species utilize mysid production in coastal and estuarine nursery grounds (Hostens and Mees, 1999; Feyrer et al., 2003; Nemerson and Able, 2004). The distribution and population dynamics of mysids are, therefore, significant in consideration of coastal fish production. In this context, several studies on the ecology of mysids have been conducted in estuaries, emphasizing spatial distribution (e.g. Hulburt, 1957; Baldó et al., 2001) and seasonal production (e.g. Wooldridge, 1986; Mees et al., 1994). However, the mechanism that mysid species use to maintain a population at a certain location within an estuary, where physical conditions drastically change in various spatial and temporal scales, remains unclear. More specifically, extensive research on the different horizontal distributions between sexes and/or life-cycle stages within an estuary has been carried out (Hulburt, 1957; Mauchline, 1970; Orsi, 1986; Hough and Naylor, 1992; Moffat and Jones, 1993; Baldó et al., 2001); however, a comprehensive explanation in terms of population maintenance remains obscure, although mechanisms of position maintenance for respective sexes and life-cycle stages were sometimes discussed in the previous studies.

The Chikugo River estuary, which is located in the innermost part of the Ariake Sea, southwestern Japan (Fig. 1), is a macrotidal estuary with a well-developed estuarine turbidity maximum (ETM). This is one of the most productive fishery areas in Japan, holding a large number of semi-endemic species (i.e. species found only in the Ariake Sea within Japan; reviewed in Sato and Takita, 2000) from several taxonomic groups, such as fish (e.g. *Neosalanx reganius*, Takita, 1996; *Trachidermus fasciatus*,

Cao et al., in press) and crustaceans (e.g. *Sinocalanus sinensis*, Hiromi and Ueda, 1987; *Tortanus derjugini*, Ohtsuka et al., 1995; *Acartia ohtsukai*, Ueda and Bucklin, 2006). The mysid *Hyperacanthomysis longirostris* (Fukuoka and Murano, 2000) is also considered as a semi-endemic species (Chihara and Murano, 1997), found particularly in lower salinities in rivers flowing into the innermost part of the Ariake Sea (Ikematsu, 1963; Suzuki et al., 2008b). Semi-endemic species of the Ariake Sea are considered as continental relicts that presently survive in restricted areas in Japan, being derived from the isolation of the Japanese archipelago from the Eurasian continent by marine transgressions during geological history (Sato and Takita, 2000).

So far copepods have been well studied as an important food for larval and early juvenile fish in the ETM of the Ariake Sea (e.g. Hibino et al., 1999; Shoji et al., 2006; Islam et al., 2006a, 2006b). In addition, several species of mysids recorded from the Ariake Sea (Ikematsu, 1963) have often been found in stomachs of larger juvenile fish of semi-endemic (Kuno and Takita, 1997; Mizutani and Matsui, 2006) and non-semi-endemic species (Takita and Intong, 1991; Suzuki et al., 2008a). For instance, Japanese temperate bass *Lateolabrax japonicus* juveniles exclusively feed on mysids in the ETM, after they ontogenetically change prey categories from copepods (Suzuki et al., 2008a). Although ecological information on mysids is important to understand the ecosystem supporting fish production, particularly semi-endemic fish populations in the Ariake Sea, available data from this sea area is restricted to general descriptions of several mysid species (Ikematsu, 1963; Suzuki et al., 2008b).

The objective of the present study is to investigate the horizontal distribution and population dynamics of dominant mysid species along the Chikugo River estuary, focusing on relationships with physical conditions (temperature, salinity, turbidity, and

freshwater discharge). To characterize seasonal and annual changes, we conducted monthly sampling over the entire tidal area of the estuary for 20 months. We identified biological properties (life-cycle stage, sex, and size) of the dominant mysid *Hyperacanthomysis longirostris* at each station and hypothesized a possible system that would contribute to the population maintenance by comparison of the properties between stations, months, and years.

2. Methods

2.1. Study area

Sampling was conducted along the lower reaches and the tidal channel of the Chikugo River (Fig. 1), the largest river flowing into the Ariake Sea. The Chikugo River estuary is characterized by large tidal ranges, vast tidal flats, and extremely turbid water. Since the water column is almost completely mixed during spring tides (tidal range > 4 m), turbidity exceeds 200 NTU even in the surface water at lower salinities (Shoji et al., 2006; Suzuki et al., 2007). The ETM is transported back and forth over a 20 km range along the estuary with tidal movements between low and high tides (Shirota and Tanaka, 1981), although it is usually located 10 to 20 km upstream from the river mouth at spring high tide (Shoji et al., 2006; Suzuki et al., 2007). As for copepods true estuarine species (i.e. species that complete their entire life cycle within the low salinity areas, *Sinocalanus sinensis* and *Pseudodiaptomus inopinus*) are overwhelmingly dominant in or close to the ETM, whereas common coastal species (e.g. *Acartia omorii*, *Oithona davisae*, and *Paracalanus parvus*) are distributed in the lower estuary (Hibino et al., 1999; Islam et al., 2006a). Among mysids, *Hyperacanthomysis longirostris* is abundant in the upper estuary (Suzuki et al., 2008b), whereas other

species (e.g. *Neomysis japonica* and *Neomysis awatschensis*) are also recorded in the lower estuary (Ikematsu, 1963).

Seven stations (R1-R7; Fig. 1) were set up along the lower reaches of the river, ranging from the river mouth to the upper limit of the tidal area, where the Chikugo Weir is located (23 km upstream). Three stations (E1-E3; Fig. 1) were set up along the tidal channel of the river in such a way that E1 was near the mouth of the river and E3 was at the edge of the tidal flat (9 km offshore). The freshwater discharge is continuously monitored and data uploaded to the web site (<http://www.qsr.mlit.go.jp/chikugo/>) by the Chikugogawa River Office at Senoshita (3 km upstream from the weir).

2.2. Field sampling

Ring-net hauls and environmental surveys were conducted monthly at the ten stations from May 2005 to December 2006. All of the sampling dates (23 May, 24 June, 24 July, 23 August, 19 September, 17 October, 15 November, 15 December 2005, 15 January, 14 February, 16 March, 14 April, 27 May, 30 June, 25 July, 24 August, 22 September, 23 October, 21 November, 22 December 2006) approximately corresponded with spring tides. A ring net (1.3 m mouth diameter, 1 mm mesh aperture along the 3.5 m cylindrical body and 0.33 mm mesh aperture at the 1.5 m conical end) equipped with a digital flow meter was towed in the surface water by a boat for 10 min at approximately 1 m s^{-1} relative to the tidal flow. The duration of towing was sometimes reduced to prevent clogging of the net by excessive zooplankton and suspended matter. Catches from the hauls were preserved onboard in 99 % ethanol. The water volume filtered through the net was estimated using the flow meter. Temperature, salinity,

turbidity were measured from the bottom to the surface at 1 or 2 m intervals with an environmental monitoring system (YSI 650 MDS, YSI, USA). Since the turbidity unit of the monitoring system was sometimes out of order (on 24 July 2005 and 14 February 2006), turbidity was measured with another monitoring system (Compact-CTD, Alec Electronics, Japan) after 16 March 2006. Hauls and surveys were started at the uppermost station (R7) and finished at the lowermost station (E3) within 4-5 h around high tide in the morning. Owing to strong waves, we could not conduct sampling at E3 on 30 June 2006.

To confirm the validity of ring-net hauls in the surface water, mysids were repeatedly collected at three depths (surface, middle, and bottom) with a small conical ring net (45 cm mouth diameter, 200 cm long, 0.33 mm mesh aperture) equipped with a digital flow meter on 24 October 2006. A weight and a buoy were symmetrically tied to the ring of the net. After adjusting the length of the rope between the buoy and the ring, the net was towed at a certain depth for 3 min at approximately 1 m s^{-1} relative to the tidal flow. Temperature, salinity, and turbidity were measured with the Compact-CTD at intervals of 0.1 m and current velocity was measured with a digital flow meter (VR-201, KENEK, Japan) at intervals of 1.0 m at each station. We conducted seven series of sampling between R2 and R5 at intervals of an hour around high tide in the morning, tracking a water mass of approximately salinity 1. The water mass was selected because mysids had been abundantly observed on the previous day (i.e. 23 October 2006).

2.3. Laboratory analysis

Mysid species were identified under a dissecting microscope according to

references (Chihara and Murano, 1997; Fukuoka and Murano, 2000, 2005), before being counted quantitatively for each station every month. As for the dominant mysid *Hyperacanthomysis longirostris*, approximately 100 individuals were randomly picked for classification into four categories (gravid females, non-gravid females, males, and juveniles). On the basis of secondary sexual characteristics, gravid females were defined as those with eggs or larvae in marsupiums; non-gravid females, those with empty marsupiums; males, those with lobus masculina at the antennule peduncle; juveniles, those without secondary sexual characteristics. Additional individuals were analyzed, when juveniles accounted for more than 90% of the first 100 individuals analyzed. The carapace length (from the base of the eyestalk to the posterior mediodorsal margin of the carapace) was measured using an eyepiece graticule in a dissecting microscope. To determine the relationship between carapace length and dry weight, 124 individuals (22 gravid females, 22 non-gravid females, 25 males, and 55 juveniles) collected on 23 May 2005 were dried at 60°C for 12 h after the measurement of carapace length. The juveniles were pooled (up to 13 individuals) by the carapace length class of 0.1 mm (0.7-1.4 mm) to obtain sufficient material for precise measurements of dry weight. After the measurement of dry weight with an electric balance, the following equation was fitted on the data of carapace length (CL) and dry weight (DW):

$$DW = aCL^b, \tag{1}$$

where a and b are constants. At each station where *Hyperacanthomysis longirostris* was collected, the mean dry weight (mg ind.⁻¹) was calculated using both equation (1) and composition of carapace length, to convert density (ind. m⁻³) into biomass (mg m⁻³). Although there is a possibility that some body contents other than

water were extracted from specimens during preservation, the influence of extraction was considered to be minimal, since biomass was compared under the same conditions. To obtain the population structure of *H. longirostris* in each month, the carapace length composition of the four categories (i.e. gravid females, non-gravid females, males, and juveniles) was accumulated monthly in proportion to density at each station.

3. Results

3.1. Physical environment

The daily freshwater discharge was stable and usually less than $100 \text{ m}^3 \text{ s}^{-1}$ in fall and winter (October to March), whereas it drastically changed in spring and summer (April to September), often exceeding $200 \text{ m}^3 \text{ s}^{-1}$ (Fig. 2). In particular, large flood events ($500 \text{ m}^3 \text{ s}^{-1}$) occurred in July, following the minimum discharge ($< 20 \text{ m}^3 \text{ s}^{-1}$) in late June 2005. In 2006, the freshwater discharge was more than $100 \text{ m}^3 \text{ s}^{-1}$ almost all the time from late June to September, since heavy rainfall events occurred repeatedly.

The means of surface temperature observed at the ten sampling stations on each sampling date increased from ca. 10 to 30 °C (spring to summer), before decreasing (fall to winter: Fig. 2). In comparison with seasonal changes, temperature had minimal differences among stations in a specific month of each respective year (range 0.7-3.8 °C). The highest temperature (29.4 °C) was recorded on 24 July 2005, whereas temperature was not so high (22.3 °C) on 25 July 2006 when sampling was conducted during repetitive flood events.

The salinity profiles along the estuary indicated strong vertical mixing through 2005, with the brackish water front of salinity 1 being located at R5 (17 km upstream from the river mouth; Fig. 3). Although the downstream movement and partial

stratification of the front were observed during periods of large freshwater discharges from June to September in 2006, the front was also located close to R5 with strong vertical mixing in the other months in 2006 (Fig. 3).

The ETM was usually found close to the brackish water front of salinity 1, with turbidities more than 100 NTU even in the surface water (Fig. 3). Turbidity was relatively low from April to August in 2006, being less than 100 NTU through the estuary in June 2006. Given that ring-net hauls were usually conducted at the surface of well-mixed water columns (especially in and close to the ETM), surface salinity was used as an approximate criterion for ambient salinity in the further analyses.

3.2. Species composition and horizontal distribution of mysids

Five mysid species, *Hyperacanthomysis longirostris*, *Neomysis awatschensis*, *Neomysis japonica*, *Orientomysis aspera* (Fukuoka and Murano, 2005), and *Rhopalophthalmus orientalis*, occurred in the estuary, showing respective patterns of horizontal distribution in relation to salinity (Fig. 4). *H. longirostris* was overwhelmingly dominant (up to 100%) in the upper estuary in 2005 and the second half of 2006, although its dominance was observed only close to the brackish water front of salinity 1 in the first half of 2006. *N. awatschensis* was occasionally dominant at the uppermost stations (R6 and R7, salinity < 1), whereas *N. japonica*, *O. aspera*, and *R. orientalis* were often dominant at lower stations, never found upstream from the front of salinity 1. Among the latter three species, *O. aspera* and *R. orientalis* tended to occur more downstream than *N. japonica*.

The density of the dominant mysid *Hyperacanthomysis longirostris* is separately presented from the other mysids (Fig. 5). The highest density of *H.*

longirostris in a specific month of each respective year was usually observed between salinity 1 and 10, being considerably shifted downstream owing to repetitive flood events in the summer of 2006. *H. longirostris* was abundantly ($> 10 \text{ ind. m}^{-3}$) collected at a station in the estuary in May, June, and October to December 2005, and May, July, October, and November 2006, with the maximum of $666.0 \text{ ind. m}^{-3}$ at R5 on 24 June 2005. Generally, density was low in midsummer (August) and winter to spring (January to April). In comparison with *H. longirostris*, the other mysids were less abundant throughout the estuary all the year around except at lower stations in March and April 2006.

The relationship between carapace length and dry weight of *Hyperacanthomysis longirostris* was well represented by equation (1) ($a = 0.035$, $b = 3.530$, $N = 77$, $R^2 = 0.952$). Spatial and temporal changes in biomass of *H. longirostris* closely coincided with those in density (Fig. 5). Biomass was relatively large ($> 5 \text{ mg m}^{-3}$) at a station in the estuary in May, June, October to December 2005, and May, July, and October 2006, being largest at R4 on 23 May and 24 June 2005 (164.9 and 168.3 mg m^{-3} , respectively).

3.3. Life-cycle stage, sex, and size of *H. longirostris*

The composition of life-cycle stage, sex, and size of *Hyperacanthomysis longirostris* was compared among stations in each month of the respective years (Fig. 6). Larger individuals, which for the most part consisted of gravid females, were always distributed at upper stations, gradually decreasing in frequency downstream. In contrast, larger juveniles were found at lower stations, whereas smaller juveniles were usually dominant at or close to the peak density of *H. longirostris* on each sampling date.

A typical pattern of size differences was observed on 23 May 2005; the mean \pm standard deviation of carapace length of juveniles being 1.1 ± 0.3 (number of specimens analyzed; N = 26), 1.0 ± 0.3 (N = 75), 1.4 ± 0.3 (N = 58), 1.8 ± 0.3 (N = 22), 1.9 ± 0.3 (N = 25), and 1.9 mm (N = 1) from R5 to E1, whereas that of the other individuals being 2.8 ± 0.3 (N = 99), 2.6 ± 0.4 (N = 72), 2.5 ± 0.4 (N = 45), 2.0 ± 0.4 (N = 52), 2.2 ± 0.3 (N = 82), 2.2 ± 0.3 (N = 80), and 2.3 ± 0.3 mm (N = 7) from R6 to E1. Similar patterns clearly occurred along the estuary in months when *H. longirostris* was abundant, being found at least partially in the other months of both years (even in July 2006 when the largest freshwater discharge was recorded).

The population structure of *Hyperacanthomysis longirostris* changed seasonally with a little difference between years (Fig. 7). The smallest juveniles (carapace length < 1.0 mm) were sampled throughout the year except in midsummer (July and August) and midwinter (January and February). Males and non-gravid females were sampled every month, whereas gravid females almost disappeared from the samples from December to February. In addition, gravid females were very scarce or absent in April and June 2006, respectively. The monthly means of carapace length (excluding juveniles) decreased from May to July (2.5 to 2.1 mm), increasing gradually from July to January (2.1 to 3.5 mm), before reaching a maximum size from January to March (ca. 3.5 mm). In comparison with 2005, juveniles were overwhelmingly dominant in June, while almost absent in August 2006.

As for the vertical distribution, *Hyperacanthomysis longirostris* was always collected in the surface between 2.5 h before and 3.5 h after the high tide, being more abundant than in the bottom (Fig. 8). The other mysid species were seldom collected on both 23 and 24 October 2006. The water mass that we tracked on 24 October

corresponded exactly with the ETM, as was indicated by low salinities (0.2 to 2.5) and high turbidities (256 to >1000 NTU) observed. The current velocity ranged from 13 to 104 cm s⁻¹, showing a tendency to be faster in the surface than in the bottom during both flood and ebb tides. Although females and males of *H. longirostris* were abundantly (> 5 inds. m⁻³) collected mainly in the surface water through the series of sampling, juveniles were abundantly (> 5 inds. m⁻³) collected only at lower stations (R2 and R3, Fig. 8).

4. Discussion

4.1. Inter-specific distribution of mysids

We conducted monthly sampling under a regular condition (around high tide in the morning during spring tides) each month over a 20 month period, making it possible to analyze seasonal and annual changes. A large number of specimens were successively collected along the Chikugo River estuary, although the methods did not allow sampling of mysids over the entire water column. The lack of information about the bottom distribution of mysids proved to be not critical, since mysids were collected in the surface more abundantly than in the bottom (Fig. 8) at least in the ETM around high tide under normal freshwater discharge. The distribution of mysids is likely to be mixed vertically by the strong tidal currents particularly during spring tides. In addition, the estuary is relatively shallow and extremely turbid (depth mostly < 6 m, turbidity often > 100 NTU; Fig. 3), conditions which possibly minimize the concentration of mysids near the bottom. Consequently, in the following sections, we confidently discuss the horizontal distribution and population dynamics of the dominant mysid in relation to the physical conditions along the estuary.

Through the course of the sampling period, *Hyperacanthomysis longirostris* was dominant close to the brackish water front of salinity 1 in the Chikugo River estuary, the distribution of which usually corresponded with the ETM (Figs. 3, 5). Among the other mysids, *Neomysis japonica* has been reported to be one of the most dominant estuarine mysids not only in the Ariake Sea (Ikematsu, 1963) but also in the Pacific coasts of Japan (Yamada et al., 1994; Chihara and Murano, 1997). Although *N. japonica* was often dominant in the lower Chikugo River estuary (salinity > 10), the density of *N. japonica* did not exceed that of *H. longirostris* except in spring (Figs. 4, 5). *Orientomysis aspera* and *Rhopalophthalmus orientalis* sometimes occurred more downstream than *N. japonica* (Fig. 4), having a preference for higher salinities. In contrast, *Neomysis awatschensis* was sometimes dominant at lower salinities in the upper estuary (salinity < 1; Fig. 4). These species are likely to have different salinity preferences, although they are generally considered as estuarine and coastal species (Yamada et al., 1994; Chihara and Murano, 1997).

As for well-known estuarine mysids in the world (e.g. *Neomysis americana*, Hulburt, 1957; Laprise and Dodson, 1994; *Neomysis integer*, Cattrijsse et al., 1994; Mees et al., 1994; *Mesopodopsis slabberi*, Moffat and Jones, 1993; Cattrijsse et al., 1994), salinity is considered as the primary determinant of horizontal distribution, although turbidity is not always considered as an important factor. However, estuarine mysids probably include several groups of mysids which have different salinity preferences, namely different levels of dependence on estuarine environments (e.g. low salinity, high turbidity, and seaward residual current). In the present study, *Hyperacanthomysis longirostris* was solely distributed in a close relation to the ETM (salinity 1-10), which indicates that *H. longirostris* is a true estuarine species that is

totally dependent on estuarine environments. In addition, *H. longirostris* is a semi-endemic species in the Ariake Sea (Chihara and Murano, 1997), probably having been isolated from the original population on the Eurasian continent during geological history (a continental relict; Sato and Takita, 2000). There are no other estuaries with well-developed ETM in Japan other than the Ariake Sea, which might account for the restricted geographic distribution of *H. longirostris* in Japan.

4.2. Intra-specific distribution of *H. longirostris*

Freshwater discharge, which is considered as one of the most important determinants in estuarine environments, is stable in fall and winter, whereas it drastically fluctuates in spring and summer in the Chikugo River estuary every year. During the last ten years (1997-2006), freshwater discharge was the second smallest in 2005 (daily mean = $91 \text{ m}^3 \text{ s}^{-1}$) in marked contrast to the second largest in 2006 ($150 \text{ m}^3 \text{ s}^{-1}$). As a result, lower temperatures, salinities, and turbidities were observed along the estuary in the spring and summer of 2006 (Figs. 2, 3). Consequently, it is possible to reveal both seasonal and annual changes in horizontal distribution and population dynamics of *Hyperacanthomysis longirostris* by examination of similarities and differences between the contrasting years.

The horizontal distribution of *Hyperacanthomysis longirostris* was different between sexes and life-cycle stages (Fig. 6), the pattern of which was usually found despite the fluctuation of physical conditions. Females, particularly gravid females, were distributed upstream from the center of distribution where small juveniles were overwhelmingly dominant. In addition, juveniles were larger at lower stations, whereas the other individuals were larger at upper stations. Similar patterns of

distribution have been reported at least partially for several estuarine mysids (Hulburt, 1957; Mauchline, 1970; Orsi, 1986; Hough and Naylor, 1992; Moffat and Jones, 1993; Baldó et al., 2001). These authors, however, tended to consider the intra-specific distribution pattern as an incidental result of tidal and/or circulation currents rather than as a significant mechanism of population maintenance, partly because the pattern was not so clear in the previous studies compared to the present study.

For an understanding of the intra-specific distribution pattern, we hypothesize a possible system of population maintenance within an estuary: gravid females release juveniles in the upper estuary, juveniles grow during downstream transport, young males and females mature during the upstream migration. Although this hypothesis comprehensively connected the intra-specific distribution pattern with population maintenance in an estuary, several points remain to be tested. The first question is about the consistency in time scales between the growth period of mysids and the speed of downstream transport. The speed of the residual current in the Chikugo River estuary is estimated at 9.6 km day^{-1} (11.1 cm s^{-1}), as the river is approximately 300 m in width and 3 m in depth with a freshwater discharge of $100 \text{ m}^3 \text{ s}^{-1}$ on average. On the other hand, rearing experiments have shown that the period for sexual differentiation depends largely on temperature, being shorter at higher temperatures: 6-22 days at 10-25 °C for *Oriomysis robusta* (Sudo, 2003; Fukuoka and Murano, 2005) and 14-42 days at 8-25 °C for *Neomysis integer* (Fockedey et al., 2005). Assuming that juvenile *Hyperacanthomysis longirostris* has been transported over a 20 km range along the estuary (R6 to R1; Figs. 1, 6) until sexual differentiation, the speed of downstream transport is estimated at $0.5\text{-}3.3 \text{ km day}^{-1}$ ($0.6\text{-}3.8 \text{ cm s}^{-1}$), being much slower than the residual current. The result of the test calculation strongly suggests that juveniles have

to minimize downstream transport to develop within the estuary. The second question is about the mechanism of upstream migration, since the swimming ability of mysids was lower than 10 cm s^{-1} even in the adult stage (*N. integer*; Roast et al., 1998). Selective transport in strong tidal currents rather than estuarine circulation is most likely to occur in the macrotidal Chikugo River estuary, as was suggested for several estuarine mysids (Orsi, 1986; Hough and Naylor, 1992; Kimmerer et al., 1998). In the present study, females and males of *H. longirostris* were observed to move upstream with the ETM during the flood tide, while juveniles seemed to remain downstream (Fig. 8). To understand the processes controlling the downstream transport as well as upstream migration, it is, however, necessary to investigate the horizontal and vertical distribution of mysids and currents at least over a tidal cycle.

The optimal salinity ranges for estuarine mysids are known to be different between life-cycle stages (Greenwood et al., 1989; Fockedey et al., 2005, 2006). In the case of *Neomysis integer*, embryos survived and developed well at salinities of 14-17, whereas juveniles matured only at salinities of 5-15 (Fockedey et al., 2005, 2006). In this context, the intra-specific distribution pattern has to be considered in relation to the optimal salinity ranges of the respective life-cycle stages of *Hyperacanthomysis longirostris*. Although there is need for behavioral and physiological information about *H. longirostris*, the intra-specific distribution pattern would contribute to the population maintenance within the estuary probably through the hypothesized system.

4.3. Population dynamics of *H. longirostris*

The density and biomass of *Hyperacanthomysis longirostris* were relatively

high at intermediate temperatures, being low at the lowest and highest temperatures (Figs. 2, 5). Although either gravid females or juveniles were found in most months, both were almost absent in January and February (Fig. 7), which indicates that reproduction was interrupted in midwinter. Minimal growth and reproduction at the lowest temperatures (ca. 10 °C) were responsible for the low density and biomasses in the overwintering generation, as was reported for mysid species in temperate coasts and estuaries (reviewed in Mauchline, 1980). In midsummer, the density and biomass of *H. longirostris* were also low in July, August 2005, and August 2006 when the three highest temperatures were recorded, whereas they were relatively high in July 2006 when temperature dropped owing to repetitive flood events (Figs. 2, 5). Rearing experiments of temperate mysids revealed that the mortality of juveniles was higher at 25 °C than at lower temperatures (Sudo, 2003; Fockedey et al., 2005). In addition, these experiments showed the influence of temperature on growth, sexual maturity, and reproduction as well as mortality. Small juveniles were almost absent in July 2005 and August 2006 despite high proportions of gravid females (Fig. 7), which possibly suggests high mortalities of juveniles at the highest temperatures (ca. 30 °C). In summary, it is likely that recurring recruitments of juveniles support high density and biomass of *H. longirostris* at intermediate temperatures (ca. 15-25 °C) in late spring and fall, whereas reproduction is interrupted or diminished at the extreme temperatures in midwinter and midsummer. Although it is necessary to conduct more frequent sampling to know the exact number of generations, on the basis of monthly changes in carapace length composition (Fig. 7), *H. longirostris* has at least one generation other than the overwintering generation which lives at most from November to May.

Freshwater discharge had various complex effects on the population dynamics

of *Hyperacanthomysis longirostris*, although it clearly shifted the horizontal distribution of *H. longirostris* (Fig. 5) as well as salinity and turbidity (Fig. 3). The most notable difference of density and biomass between years was found in June (Fig. 5). Density and biomass were the largest during the sampling period under the smallest freshwater discharge ($< 20 \text{ m}^3 \text{ s}^{-1}$) in June 2005, in marked contrast to one of the lowest density and biomass under repetitive flood events ($> 1000 \text{ m}^3 \text{ s}^{-1}$) in June 2006. The large freshwater discharge not only shifted the salinity front downstream but also toned down the ETM in June 2006 (Fig. 3), conditions of which may have reduced the population of *H. longirostris*. The population was, however, not always diminished by flood events, since relatively high density and biomass were observed in a turbid water similar to the ETM offshore from the river mouth in July 2006 (Figs. 3, 5). The ETM was reported to be especially abundant in copepods and detritus in the Chikugo River estuary (Shoji et al., 2006; Islam et al., 2006a; Suzuki et al., 2007), potentially providing abundant foods for mysids (Mauchline, 1980; Takahashi, 2004). There is a possibility that environmental conditions, including temperature, salinity, turbidity, and food, would be temporarily improved for *H. longirostris* all over the innermost Ariake Sea owing to repetitive flood events in July 2006. As for the true estuarine copepods *Sinocalanus sinensis* and *Pseudodiaptomus inopinus* in the Chikugo River estuary, Ueda et al. (2004) inferred from high frequency sampling during flood events that adult copepods could survive just above the bottom and that they could replace the loss of population through reproduction. *H. longirostris* might also have a specific strategy to survive flood events in addition to the hypothesized system to maintain the population under ordinary conditions.

5. Conclusions

The present study demonstrated the horizontal distribution and population dynamics of the dominant and semi-endemic mysid *Hyperacanthomysis longirostris* under the fluctuation of physical conditions along the macrotidal Chikugo River estuary. As a next step, it is necessary to investigate the population dynamics of *H. longirostris* in relation to biological conditions (e.g. food, predator, and competitor) as well as physical conditions. The biomass of *H. longirostris* was often as large as the copepod biomass (up to 100 mg m⁻³ on average in the Chikugo River estuary, Islam et al., 2006a). Ecological studies on *H. longirostris* will lead to a better understanding of the food web in the ETM, which has been considered as an important nursery for both semi-endemic and non-semi-endemic fish species in the Ariake Sea (Hibino et al., 1999; Shoji et al., 2006; Islam et al., 2006a, 2006b; Suzuki et al., 2008a, 2008b).

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Figure captions

Fig.1. Study area and sampling stations (open circles) along the Chikugo River estuary of the Ariake Sea, Kyushu Island, Japan. The observatory for freshwater discharge is represented by a closed circle.

Fig. 2. Daily freshwater discharge (solid line) and monthly temperature (open diamonds) in the Chikugo River estuary from May 2005 to December 2006. Monthly temperature is the mean of surface temperature observed at the ten sampling stations on each sampling date.

Fig. 3. Profiles of salinity and turbidity along the Chikugo River estuary from May 2005 to December 2006. Closed triangles under the horizontal axes represent the locations of the ten sampling stations.

Fig. 4. Numerical composition of the mysid species collected at the ten sampling stations along the Chikugo River estuary from May 2005 to December 2006. Solid and dashed vertical lines represent surface salinity 1 and 10, respectively.

Fig. 5. Density (closed circles) and biomass (dashed lines) of the dominant mysid *Hyperacanthomysis longirostris* collected along the Chikugo River estuary from May 2005 to December 2006. Total density of the other mysid species is represented by open triangles. Solid and dashed vertical lines represent surface salinity 1 and 10, respectively.

Fig. 6. Carapace length composition of the dominant mysid *Hyperacanthomysis longirostris* collected at each sampling station in the Chikugo River estuary from May to December in 2005 (a) and 2006 (b). Sampling stations are arranged from the uppermost R7 (left) to the lowermost E3 (right). Four categories of the mysid (i.e. gravid females, non-gravid females, males, and juveniles) are represented by

different patterns in bar graphs. Closed triangles represent stations where the highest density was observed on each sampling date. N, number of specimens analyzed.

Fig. 7. Monthly changes in population structure of the dominant mysid *Hyperacanthomysis longirostris* in the Chikugo River estuary from May 2005 to December 2006. Four categories of the mysid (i.e. gravid females, non-gravid females, males, and juveniles) are represented by different patterns in bar graphs. Closed triangles represent the means of carapace length in each month (excluding juveniles).

Fig. 8. Hourly changes in vertical distribution of *Hyperacanthomysis longirostris* observed in the estuarine turbidity maximum of the Chikugo River estuary around high tide on 24 October 2006. All individuals (top) consist of females and males (middle), and juveniles (bottom). Vertical lines represent the time of high tide.

Fig. 1

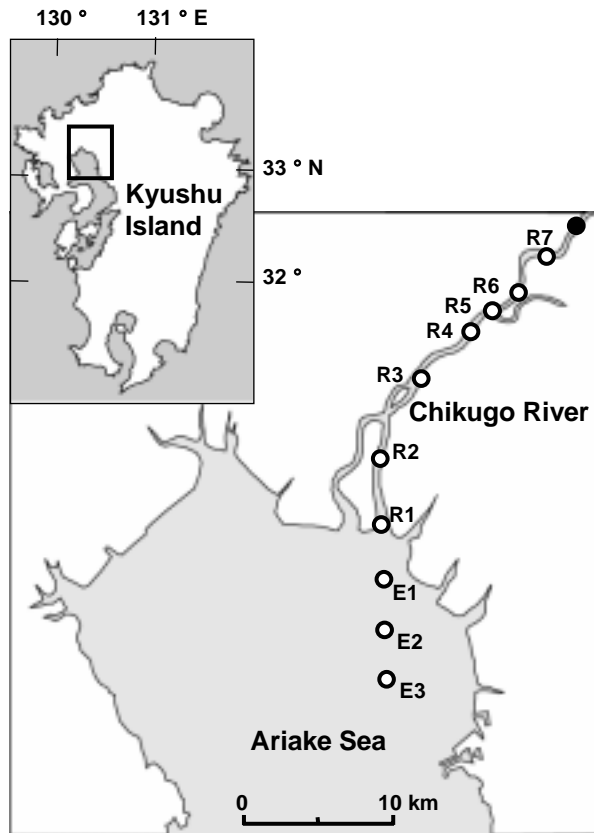


Fig. 2

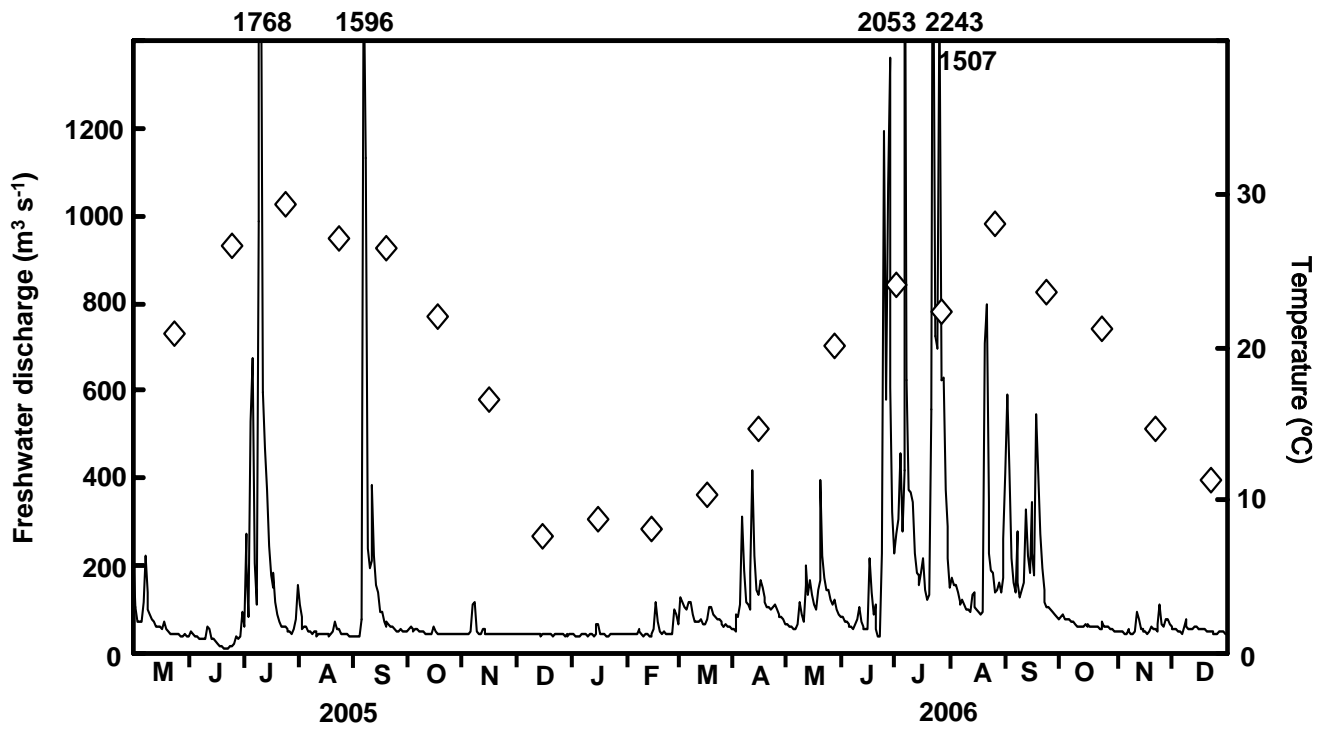


Fig. 3

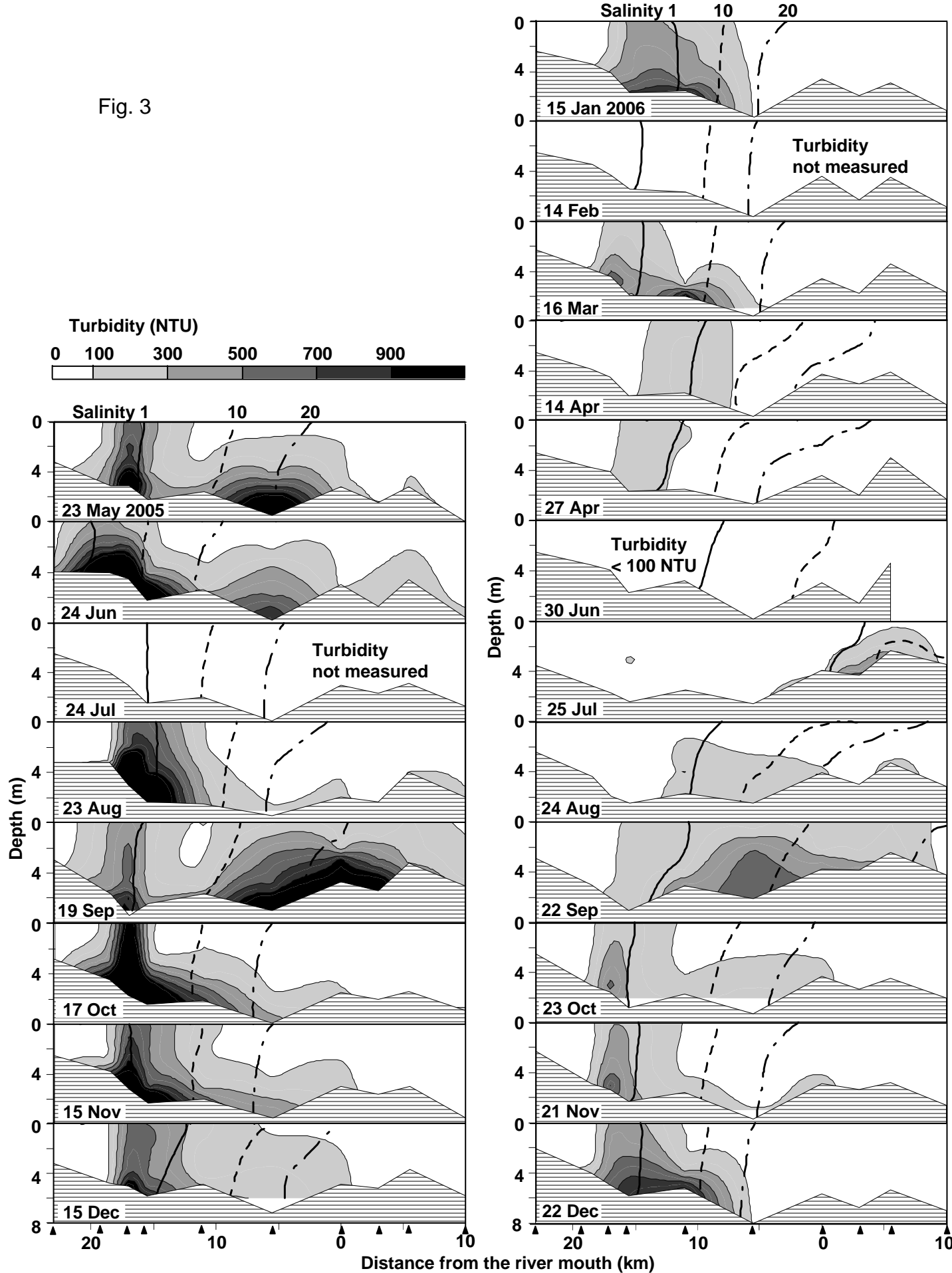


Fig. 4

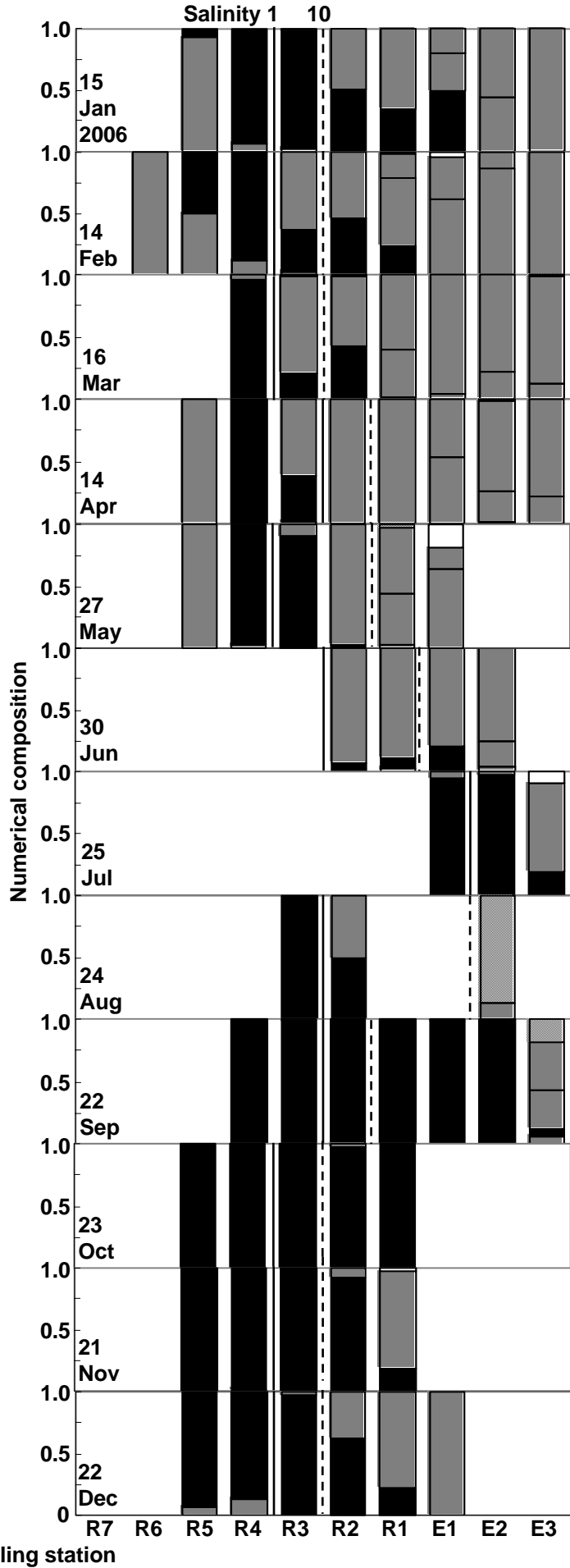
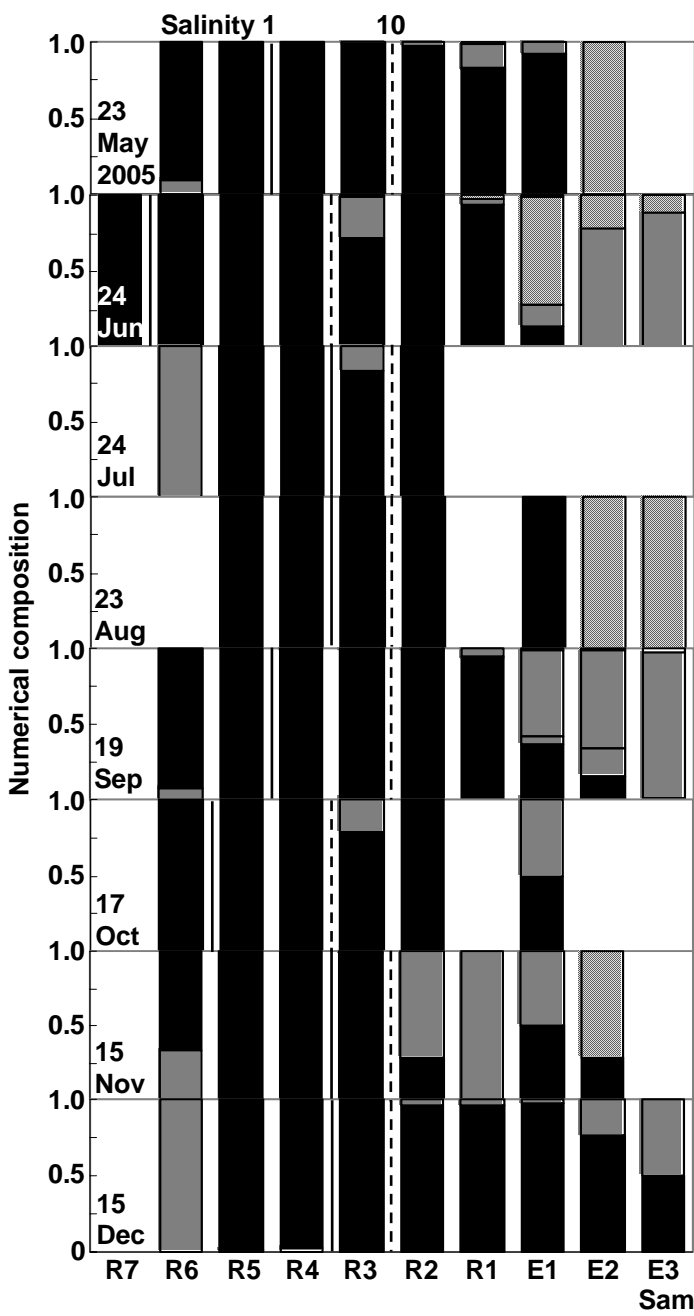
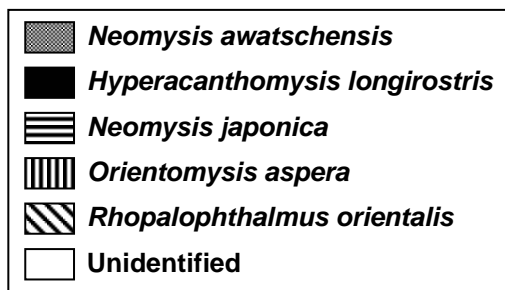


Fig. 5

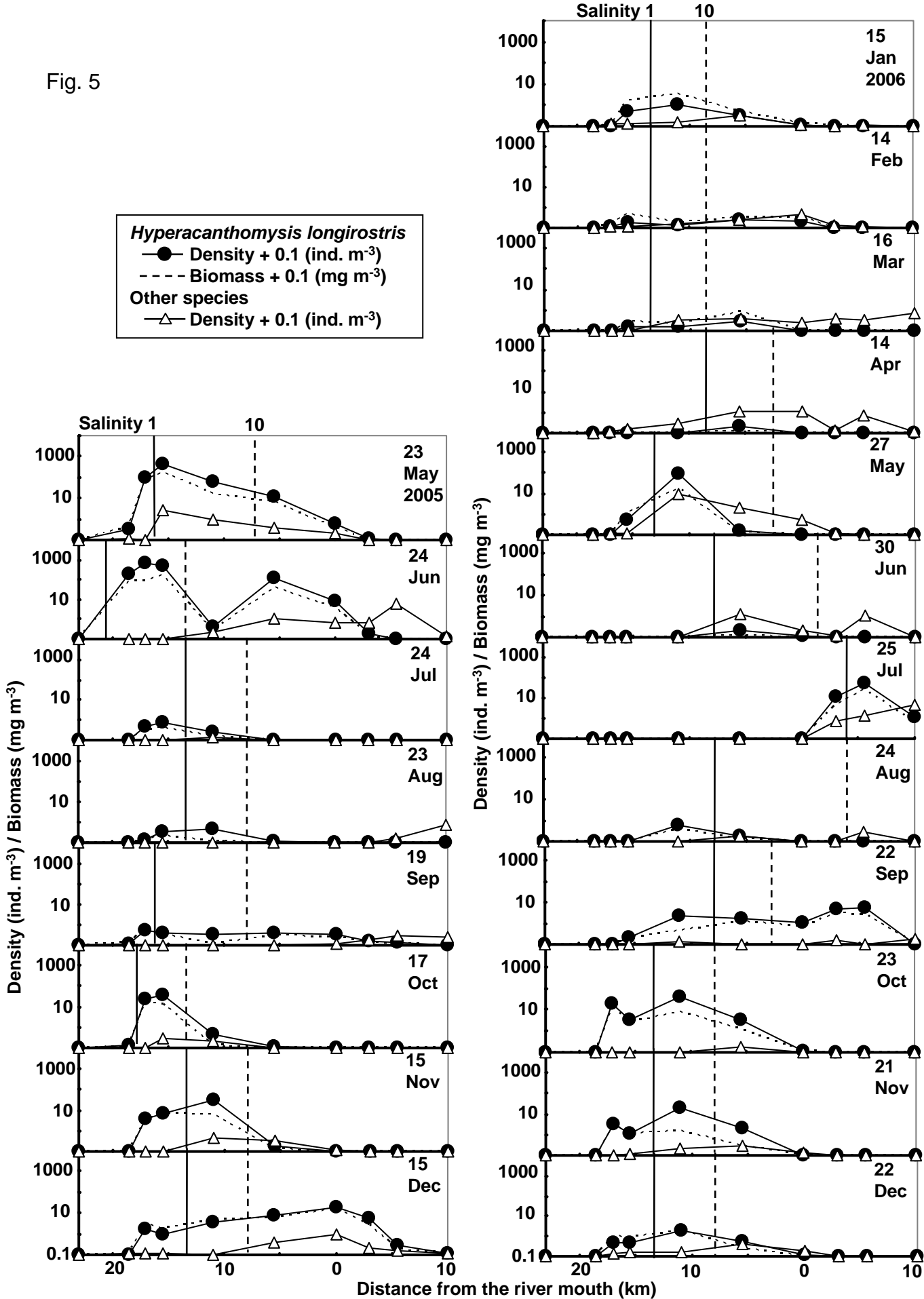
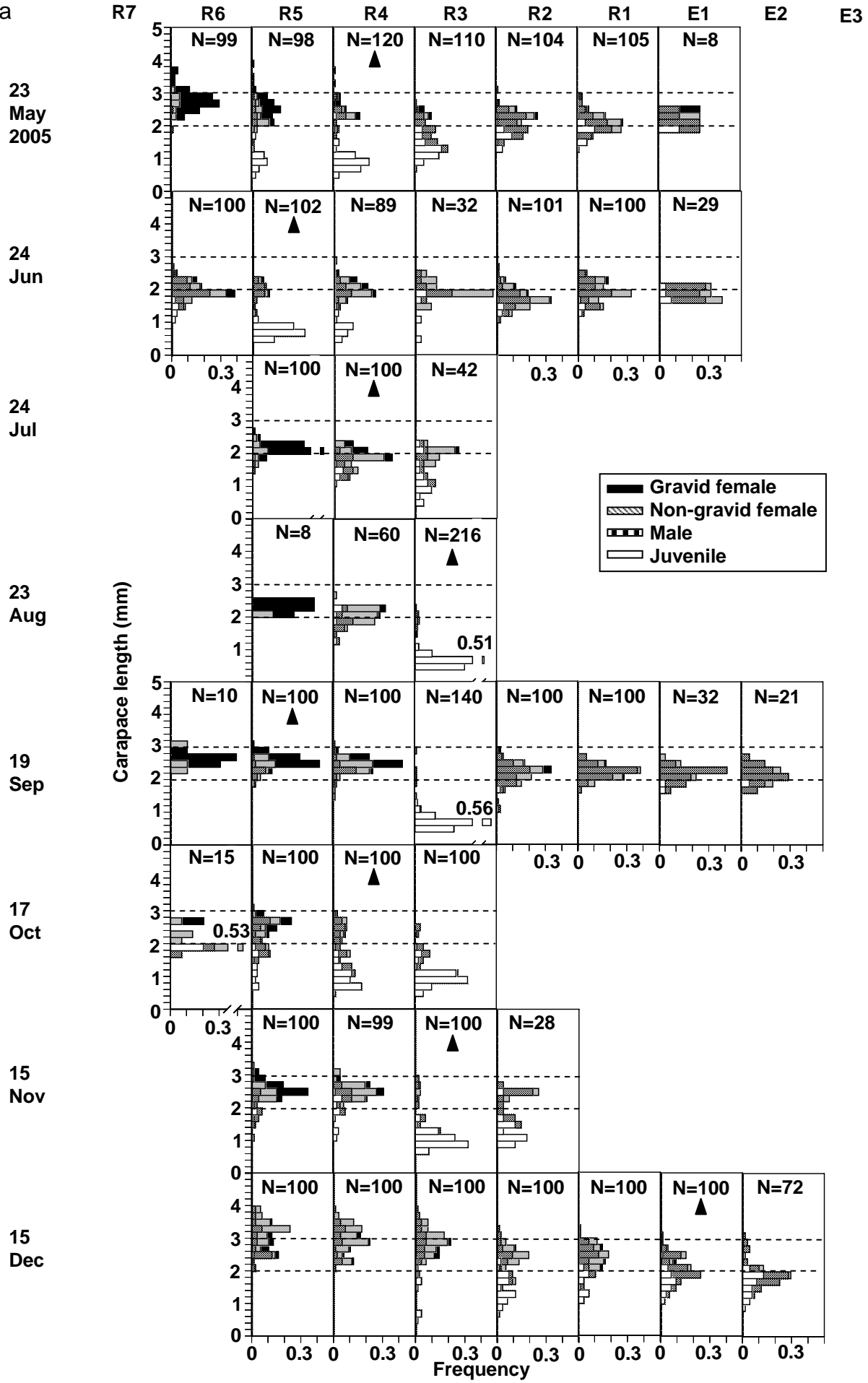


Fig. 6a



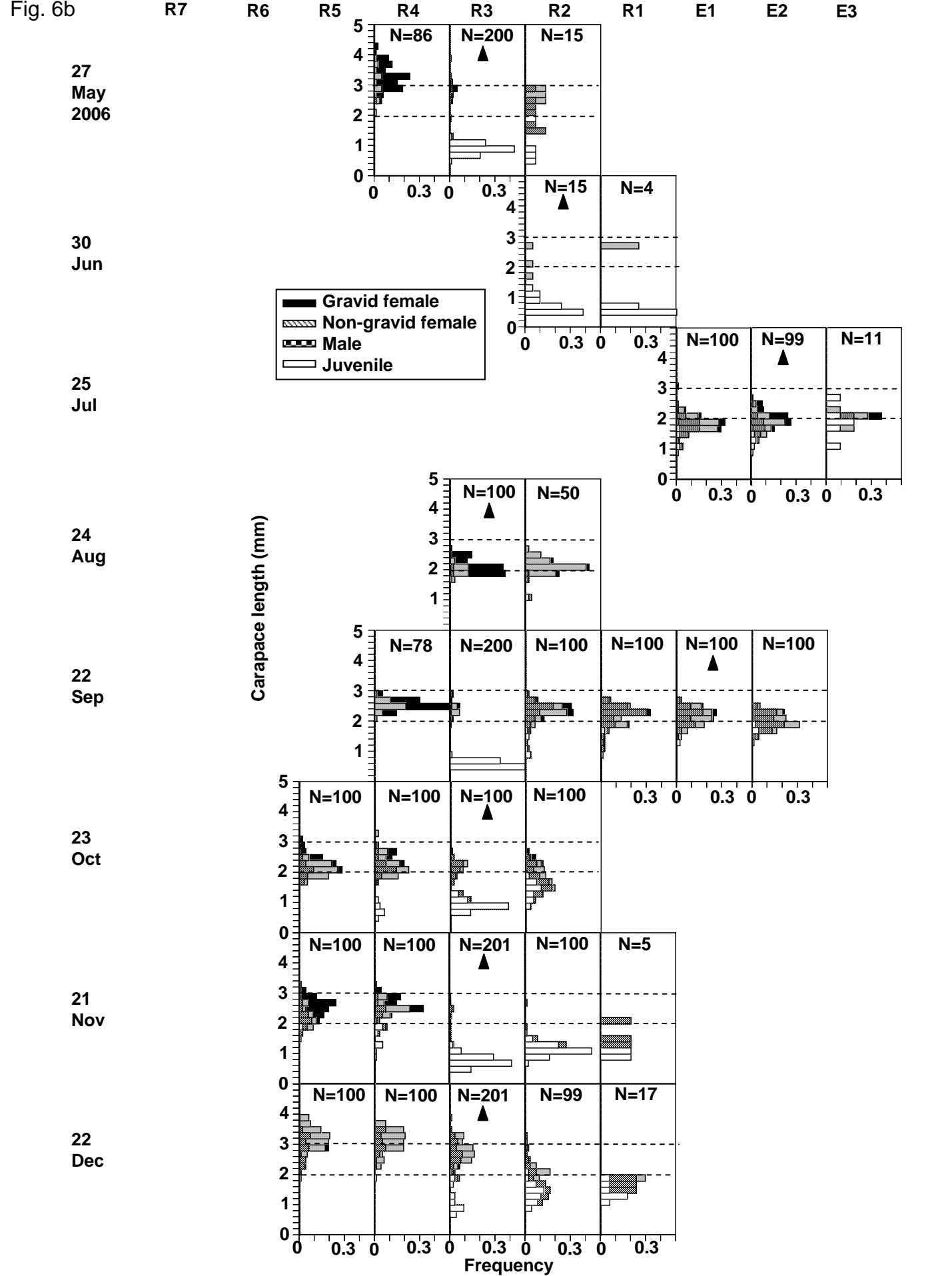


Fig. 7

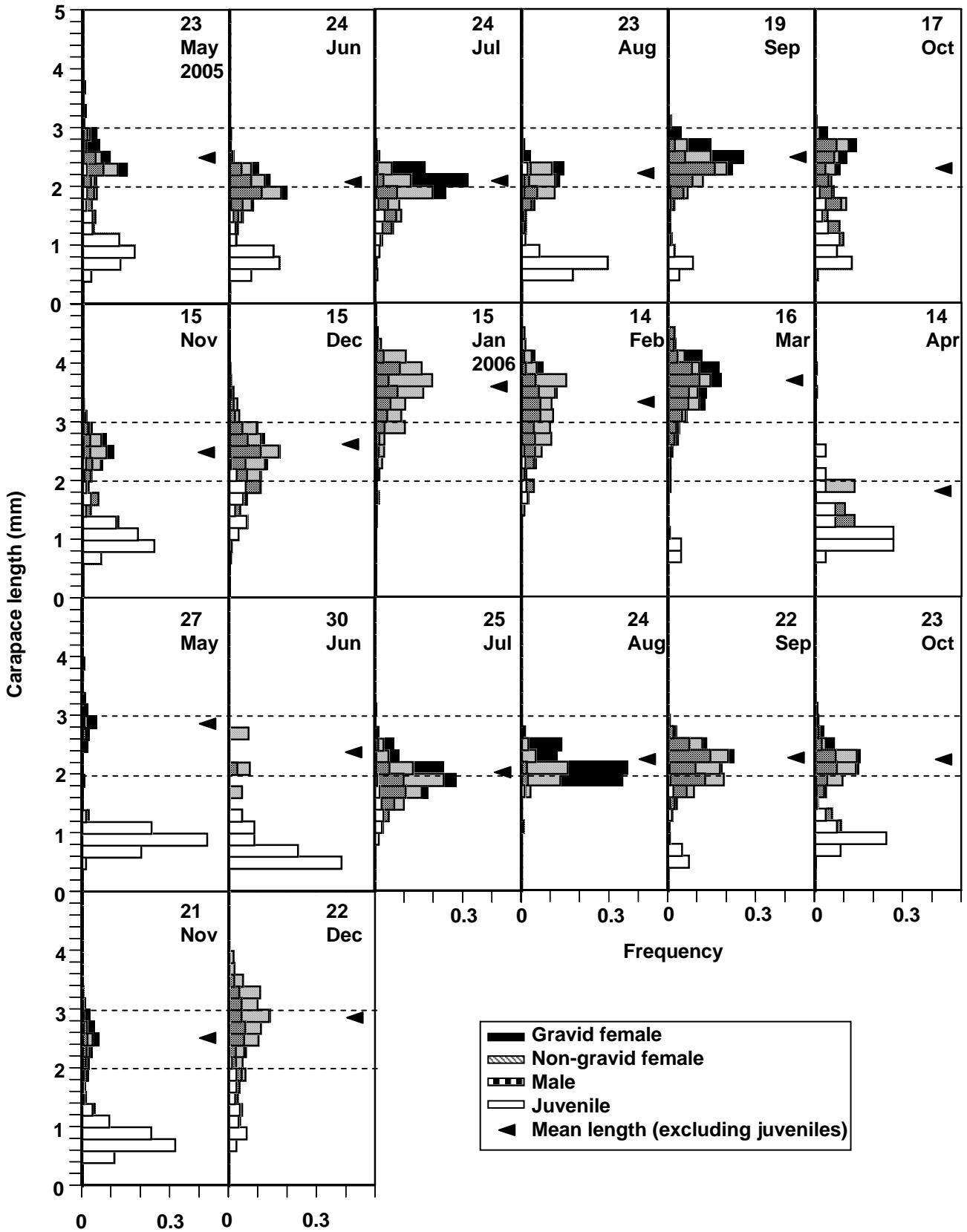


Fig. 8

