Variations in body size of individuals at sexual maturity among local populations of the freshwater prawn *Macrobrachium nipponense* (de Haan), with special reference to freshwater colonization

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**Abstract.**—The body sizes of individuals of the freshwater prawn *Macrobrachium nipponense* at sexual maturity (1-year-old females) were investigated in 23 local populations residing in diverse environments from estuaries to inland fresh waters. The body size of females at maturity was significantly smaller in populations inhabiting fresh waters (37.5 mm in modal body length), owing to the slower growth of individuals, than that found in populations inhabiting brackish-water lakes (57.5 mm) or estuaries (52.5 mm). In the laboratory, however, females from an estuarine population spawned at a body size much smaller (37.5 mm) than observed in nature, and this body size was very close to that observed in freshwater populations under both natural and experimental conditions. The great phenotypic plasticity of body size at maturity in estuarine populations would have played an important role in the colonization, by this species, of inland fresh waters.

Introduction

*Macrobrachium nipponense* (de Haan), a long-armed oriental river prawn, is commonly distributed in estuaries (river mouths) in Japan. In addition, this species occasionally occurs in coastal brackish-water or freshwater lakes (lagoons) of relict-sea origin that were formed after deglaciation in the Holocene (Mashiko, 1992a). Those lacustrine populations are surmised to have immigrated geologically very recently from estuaries (Mashiko & Numachi, 1993). Therein, egg and clutch sizes significantly changed, resulting in a characteristic life-history trait of laying few large eggs in inland fresh waters (Mashiko, 1990a; 1992a). Allozymic and morphometric analyses suggested that such evolutionary changes took place independently in several regions in Japan (Mashiko & Numachi, 2000). In addition to egg and clutch sizes, the body size of individuals at sexual maturity is an important life-history character (Stearns & Koella, 1986) as exactly investigated for decapod crustaceans (e.g., Wenner et al., 1974; Dugan et al., 1991; Ragonese & Blanchini, 1995; Anger & Moreira, 1998). Very intriguing, therefore, is whether the body size at maturity varies among local populations of *M. nipponense* in diverse environments.

To date, the growth of *M. nipponense* individuals has been studied *in situ* at several locations in Japan: Lake Kasumigaura (Okada & Kubo, 1950), Lake Biwa (Kobayashi & Ohno, 1955), Lake Kojima (Sugiyama et al., 1979; Ogawa & Kakuta, 1985), the upper and lower basins of the Sagami River (Mashiko, 1983) and Lake Suwa (Kawabata, 1988). In those locations, females are presumed to grow to approximately 40 to 60 mm in body length by one year after birth, and they lay eggs in that year. Females mostly die after the spawning, while not a few males survive more than one year. Besides, this species is known to have short-span generation in a certain water body of middle Japan:
Fig. 1. The 23 locations for collecting specimens, numbered from south to north on each side of the Pacific and the Sea of Japan.

That is, young females which were born early in the breeding season lay eggs late in that year (Sugiyama et al., 1979). In the present study, the body sizes of individuals at sexual maturity were compared among local populations of *M. nipponense* living in diverse environments from estuaries to inland fresh waters.

Materials and Methods

Individuals were collected from 23 locations in Japan (Fig. 1) from July to August (the climax of the breeding season) during 1983 to 1990. The locality names (with hydrogeographic classification of their habitats - E: estuary; B: brackish-water lake; F: fresh-water lake) are: 1, Oyodo River (E); 2, Shimanto River (E); 3, Lake Kojima (B); 4, Lake Biwa (F); 5, Ibi River (E); 6, Lake Sanaru (B); 7, Sagami River (E); 8, Sagami River (F); 9, Lake Shakuji-i (F); 10, Lake Shinobazunoike (F); 11, Lake Teganuma (F); 12, Lake Kasumigaura (F); 13, Lake Hinuma (B); 14, Ara River (F); 15, Lake Suwa (F); 16, Lake Naganuma (F); 17, Lake Izunuma (F); 18, Lake Shinji (B); 19, Lake Togo (B); 20, Lake Koyama (B); 21, Sendai River (E); 22, Kuzuryu River (E); and 23, Lake Kitagata (B). Out of these 23, the populations in Lake Biwa and Lake Suwa are said to have been transplanted from Lake Kasumigaura many years ago (Fujita, 1936; Kurasawa, 1982).

Collecting was performed with 5.0 mm-mesh trap nets and 5.5 mm-mesh dip nets. Catches by local fishermen were
Fig. 2. Size-frequency distribution in females collected from Lake Kasumigaura (location 12), Lake Sanaru (6) and the Sendai River estuary (21). Shaded bars signify sexually mature individuals; non-shaded bars indicate sexually immature (Lake Kasumigaura) or sex-unidentified (Lake Sanaru) individuals.

Fig. 3. The modal body length of assumptive 1-year-old females in the 23 populations (location number in parentheses). The non-shaded bars indicate freshwater populations, and the bars shaded with dots and with oblique lines indicate brackish-lacustrine populations and estuarine populations, respectively. The arrows on the bar represent the minimal value of ovigerous females (indicated by mid value on 5 mm-interval histogram) in each population (see discussion in the text). Numerals on the histogram: sample size.

used in some localities: Lake Biwa, Lake Kasumigaura, Lake Izunuma, Lake Naganuma, Lake Sanaru, Lake Hinuma, Lake Shinji, Lake Koyama, Lake Togo and Lake Kojima. The fisheries there are usually made by the traditional "Shiba-zuke" (to entrap prawn into a bundle of twigs), or by using seine nets (of nearly the same mesh size with the above). Specimens were preserved in 10% formalin until analysis. In the laboratory, the body length (BL: from the base of the compound eyes to the tip of the telson) of individuals was measured to the nearest 0.1 mm with a slide caliper. Females with deposited eggs and/or broadened brooding cavity on the abdomen were judged to be sexually mature.

Results

Almost all females (over 95%) collected in this study were sexually mature, and the size-distribution of females in popula-
Fig. 4. Growth curve of females for one year after the birth in several locations; a: Lake Kojima (location 3 in Fig. 1, drawn from the data by Ogawa & Kakuta, 1985, but modified according to Mashiko, 1990b and Sugiyama et al., 1979); b: Sagami River estuary (7; Mashiko, 1983); c: Lake Kasumigaura (12; Okada & Kubo, 1950); d: Lake Biwa (4; Kobayashi & Ohno, 1955); e: Lake Suwa (15; Kawabata, 1988); and f: upper basin of the Sagami River (8; Mashiko, 1983). The curves are drawn based on the value of mode on monthly size-frequency histograms. The time on the abscissa indicates the number of month after the climax of the breeding season in each site (usually July; August in curve f).

females in the major group are considered to be one year old, and smaller ones are judged to be "young-of-the-year" (short-span generation). The estuarine population of the Sendai River (location 21) exhibited a bimodal pattern with a predominant peak at 52.5 mm (50.0–55.0 mm in rank) and a subordinate one at 67.5 mm (65.0–70.0 mm). The groups of large females and small females should be composed of 1-year-olds and 2-year-olds, respectively. Thus, 1-year-old females in each population were easily identified by their outstanding peak on the size-frequency histogram, and such females with eggs were very useful to examine the difference of the body size at sexual maturity among populations.

The modal body length of sexually mature 1-year-old females ranged from 37.5 to 47.5 mm (usually 42.5 mm) in the freshwater (lacustrine and riverine) populations, from 42.5 to 52.5 mm (52.5 mm) in the estuarine populations, and from 42.5 to 57.5 mm (57.5 mm) in the brackish-water lacustrine populations (Fig. 3). In general, females in freshwater populations exhibited a significantly smaller body size at sexual maturity than those in estuarine or brackish-water lacustrine populations (P<0.05, Mann-Whitney U-test). There was no significant difference between the groups of estuarine populations and of brackish-water lacustrine populations (P>0.05).
Fig. 5. Body sizes of females which spawned in the laboratory, derived from the estuarine population (upper figure) and the upper-basin population (lower figure) of the Sagami River (locations 7 and 8, respectively). Here, newborn males and females were collected from the field (estuarine population) or obtained by indoor-breeding of parents (upper-basin population), and they had been fed on minced fish meat in aquaria at water temperatures no lower than 15°C even in winter. Most of surviving females laid eggs in the next year, when their body sizes were measured.

Discussion

In this species, 1-year-old females play a substantial role in reproduction (Okada & Kubo, 1950; Sugiyama et al., 1979; Mashiko, 1983). The body size of such females was significantly smaller in freshwater environments than in brackish-wa-

ter (lacustrine and estuarine) environments, this implying that the growth of individuals is slower in freshwater environments. The growth curves of individuals in several populations are shown in Fig. 4. It is apparent that, in fresh waters, the growth of females is significantly depressed and, consequently, females enter into the breeding season, at small body size, one year after the birth.

Of great significance is whether the body size at sexual maturity is intrinsically determined in each population, as is the case with egg sizes (Mashiko, 1992b). Rearing and breeding of individuals in the laboratory should offer a valuable clue on this problem. In a preliminary study by the present author (Fig. 5), females derived from the Sagami River estuarine population (location 7) spawned at the body length of 37.5 mm in mode. This size was significantly smaller than that actually observed in the natural population (52.5 mm; Fig. 3), and very close to the body size of the upper-basin population of that river (location 8) under both natural and experimental conditions (37.5 and 42.5 mm BL, respectively). This means that females in estuarine populations have the potential to sexually mature at smaller body sizes than observed in nature. That is, the difference of body sizes at spawning in a variety of populations of this species is largely due to phenotypic plasticity.

The great phenotypic plasticity of body size can be remarked even from wild populations. The minimal body size of ovigerous females (so-called biological minimal size) in each population is presented in Fig. 3. In a few populations, the data were cited from other authors whenever their measurements were smaller than those obtained in this study: i.e., the populations in Lake Suwa (Kawabata,1988), Lake Kasumigaura (Okada & Kubo,1950), Lake Biwa (Kobayashi & Ohno,1955), and Lake Kojima (Ogawa & Kakuta, 1985). It is
noteworthy that the minimal size of 27.5 mm in Lake Kojima, for instance, was much smaller than the prevalent body sizes of berried females (57.5 mm) there. In addition, this body size recognized in a brackish-water population was very close to those observed in many freshwater populations. This strongly suggests that the minimal body size of this species is around 25.0 to 30.0 mm in spite of seeming differences among populations.

The great plasticity of body size at maturity must have played an important role in the course of colonization from estuaries to inland fresh waters in this species. If the usual body length of 52.5 mm at maturity in estuarine populations were strictly fixed (on genetic basis), females which entered into freshwater habitats would take more than 1 year in order to sexually mature, since they do not usually attain such a large size there by one year after the birth (see Fig. 4). Such a prolongation until reproduction would necessarily lower the survivorship of individuals. Thus, having the capacity to spawn at 25.0-30.0 mm BL in advance must have facilitated estuarine populations to intrude into fresh waters.

Ogasawara et al. (1979) reported that, in *M. nipponense* populations inhabiting fresh waters as well as those inhabiting brackish waters, zoea larvae exhibited the best survivorship in experimental sea water of moderately low salinity. The lower survivorship in fresh water is perhaps due to insufficiently developed osmoregulatory capacity (Mashiko, 1992c). The delay of growth in *M. nipponense* individuals, especially at the early life stage, in freshwater environments may be partly caused by such osmoregulatory stress. Besides, water temperature and food supply should be partly concerned with the different growth rates among populations. However, the precise effects of such environmental factors remain to be investigated hereafter with detailed assessment of environmental factors.

In this study, fishermen's catches were adopted in analysis in addition to the author's own collection. The difference of collecting methods must have scarcely affected the major result in this study, since the collecting methods themselves were essentially irrespective of environmental media.

Acknowledgements


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