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Protogynous Hermaphroditism in the Brackish and Freshwater Isopod, *Gnorimosphaeroma naktongense* (Crustacea: Isopoda, Sphaeromatidae)

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ABSTRACT—Protogynous sex change in *Gnorimosphaeroma naktongense,* inhabiting brackish water and freshwater bodies, was examined by culturing precopulatory guarding pairs. The transitional stages of masculinizing of a female were observed clearly after releasing juveniles from a female marsupium. About forty percent of the females cultured showed direct evidence of sex change to males in the outer morphology at the end of laboratory experiments. As histological observations were not done to make clear the processes of gonad changes, the possibility of protogynous sex change was strongly suggested. Precopulatory mate guarding may be a primary selective pressure favoring protogyny in *G. naktongense.*

INTRODUCTION

Sequential hermaphroditism has evolved among many phylogenetically different animals and plants (Ghiselin, 1969; Manning, 1975). In crustaceans, protandorus sex change, from male to female, is predominant, but only 17% of 63 sequentially hermaphroditic species showed protogynous sex change, from female to male (Brook *et al.*, 1994). Protogynous sex change has been reported in only marine species, 3 species of anthrids, 5 species of tanaids and 3 species of sphaeromatids (Brook *et al.*, 1994). There is no species showing protogyny in the crustaceans inhabiting both brackish water and freshwater bodies.

Gnorimosphaeroma naktongense Kwon and Kim was found from brackish waters, upstream of rivers and some freshwaters near coasts (Kwon and Kim, 1987; Abe and Fukuhara, in preparation). There are no records of ecology and reproductive biology of this species. The species has a period of active precopulatory mate guarding in April-May and July-August, and the population increases in June and September-October by departing juveniles from female marsupia at the mouth of the River Agano (Abe and Fukuhara, in preparation).

We began to consider the possibility of protogynous sex change of this species in the course of the life cycle study in brackish and freshwater bodies. Because protogynous sex change is uncommon in crustaceans, especially among freshwater species (Ghiselin, 1969; Sadovy and Shapiro, 1987), sex change in this species is of particular interest for sex change theory in animals. In this paper, examination of protogyny in *G. naktongense* is conducted experimentally, and the possibility of sex change from female to male is strongly suggested from the observation of outer morphological characters of reproductive organs.

MATERIALS AND METHODS

Animals were collected in April, 1992 and 1994 at the mouth of the River Agano, Niigata Prefecture, showing minimum and maximum electric conductivity of 0.06–1.98 mS/cm during 1993–1994. Pairs of male and female in precopulatory guarding were cultured separately in petri dishes (9 cm diameter) filled with water and provisioned with pieces of dead *Zizania latifolia* collected at the sampling site. Animals in petri dishes were incubated at room temperature under natural light condition in 1992 and 15°C under 12L-12D in 1994. Each pair was cultured during about 80 days after the end of guarding by male. Changes of external morphology and molting were noted at appropriate intervals. Gravid females and sex-changed males (sex change from female to male), fixed in 8% formalin solution, were observed in the usual way under SEM for external morphological characteristics of their reproductive organs. The inner reproductive organs of sex-changed males were also observed under a dissecting microscope.

For evidences of sex change in the field, animals were sampled randomly in April, July and August 1994, and fixed in 8% formalin solution. After grouping into juveniles with no sexual characters, females with nonfunctional oostegites or large oostegites and males with only penes, the head width (outer distance between eyes) was measured as an indicator of body size.

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RESULTS

The results of the sex change experiment are shown in Table 1. All the pairs in precopula guarding separated by the beginning of May in 1992 and by the end of May in 1994. All the females released their broods at the end of May in 1992. But in 1994, half of the females which had embryos within marsupium, died before releasing juveniles. This indicates that cultured females had matured thoroughly. All the males died in the course of experiments.

Females molted within about one week after release of brood. They molted progressively two or three times by the end of experiments.

About one half of the females that released their broods died in the course of the experiments. Females which died in brooding had already very small penes. More developed penes were observed in females that died after release of broods (Fig. 1A). All the females remaining alive at the end

Table 1. Results of protogynous sex change experiments in *Gnorimosphaeroma naktongense* collected at the mouth of the River Agano, Niigata. Each pair in precopulatory guarding was cultured in a petri dish at room temperature in natural light in 1992 experiment and 15°C and 12L-12D in 1994.

Pairs cultured	Dead females before releasing broods	Females releasing broods	Dead individuals after releasing broods	Females changing sex	Period of culture
13	0	13	11	2	23 Apr. - 12 Jul. 1992
30	14	16	1	15	30 Apr. - 8 Aug. 1994

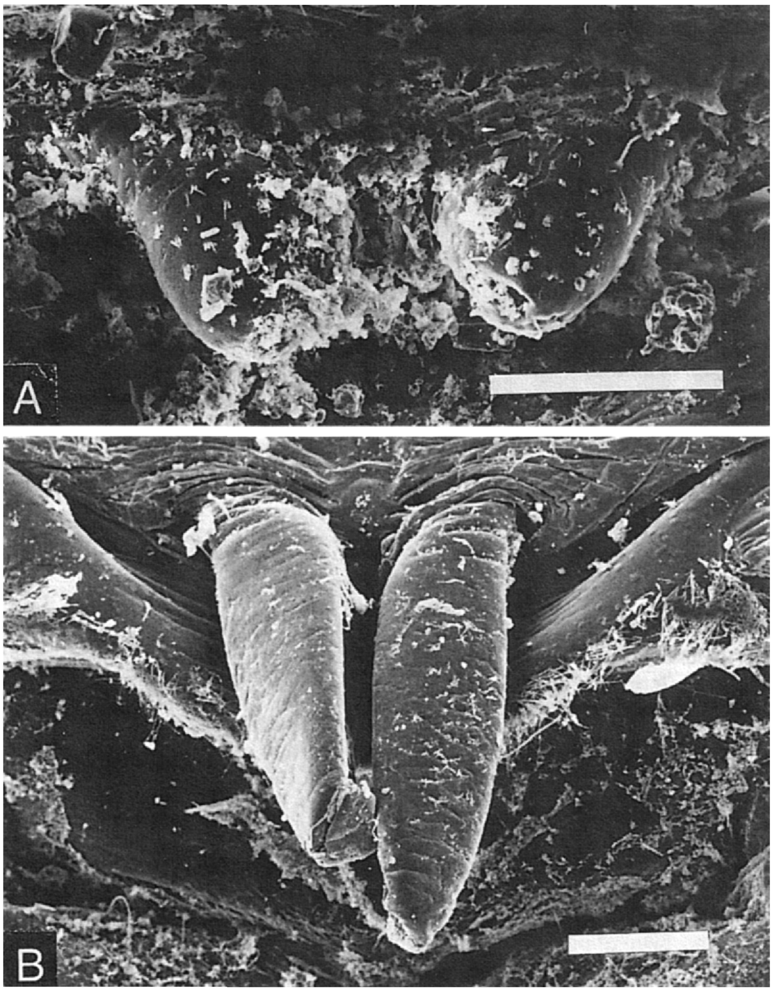

Fig. 1. Scanning electron micrographs illustrating the development of penes in the process of sex change in *Gnorimosphaeroma naktongense.* Materials for 1994 experiment in Table 1 were used for observations. Each pair in precopulatory guarding was cultured in a petri dish under the condition of 15°C and 12L-12D in 1994. (A) Intermediate stage from female to male with small penes. A female cultured 9 days after releasing juveniles, but no molting was observed. (B) A sex-changed male with fully developed penes, cultured 58 days and molted three times after releasing juveniles. The bar represents 100 µm.

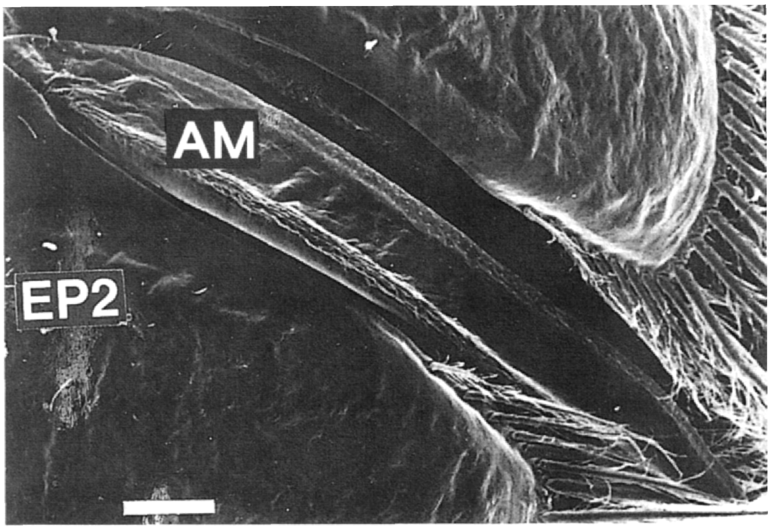

Fig. 2. Scanning electron micrograph illustrating a fully developed appendix masculina of a sex-changed male of *Gnorimosphaeroma naktongense*. The same animal in Fig. 2B was used. AM: Appendix masculina; EP2: endopod of plepod 2. The bar represents 100 μm.

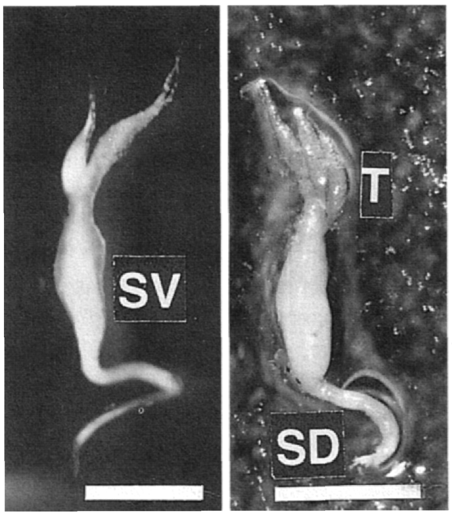

Fig. 3. Male reproductive tracts of *Gnorimosphaeroma naktongense*. Right: left gonad (viewed from abdomen) of a sex-changed male (head width of 2.2 mm) with fully developed penes. Specimen from sex-change experiment conducted in 1994 was killed and dissected 75 days (after four times molting) after releasing juveniles. Left: left gonad (viewed from abdomen) of a male (head width of 2.0 mm) guarding a female. Specimen was collected on 21 May 1995 at the mouth of the Agano River. T: testis; SV: seminal vesicle; SD: seminal duct. The bar represents 1 mm.

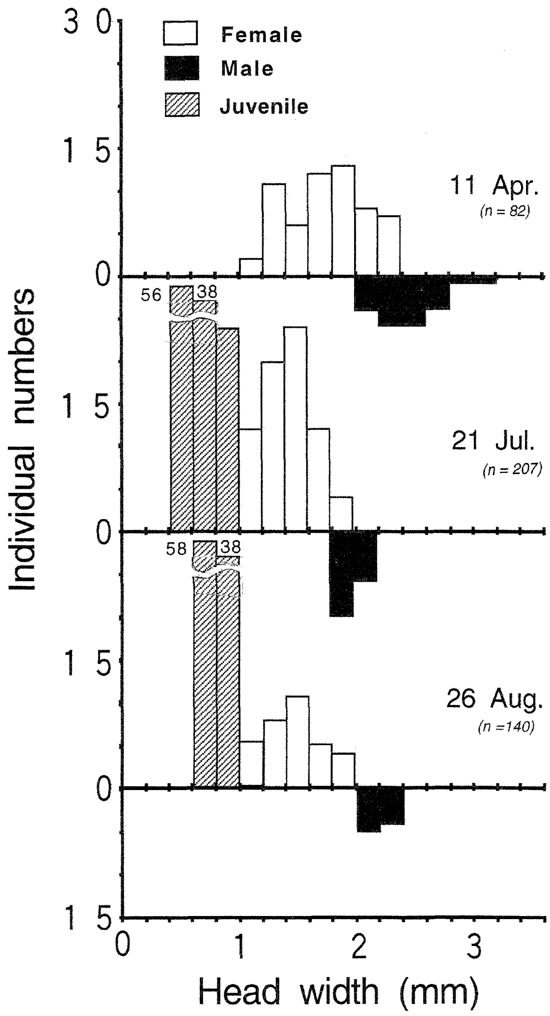

Fig. 4. Body size (head width; outer distance between eyes) distributions of *Gnorimosphaeroma naktongense* sampled randomly in April, July and August in 1994 at the mouth of the Agano River. See text for detailed explanation.

of the experiments showed direct evidence of sex change into males. The sex-changed males had one pair of fully developed penes (Fig. 1B) and appendix masculina (Fig. 2). These were the same organs in external morphology that precopulatory guarding males had. Transitional developmental stages of penes appearing in the process of protogynous sex change were observed in the tidal isopod *Gnorimosphaeroma oregonense* (Brook *et al.*, 1994).

One pair of fully developed male reproductive tract, testis, seminal vesicle and seminal duct which were organs quite similar to those of guarding males, was observed in a sex-changed male (Fig. 3).

Marked sexual dimorphism in size was evident among males and females, and males were larger than females (Fig. 4). In April, females indicated bimodal distribution in size, small and large groups, whereas males indicated only one group (Fig. 4). The small female group was born last October, and the large one last June. There were no males in a generation released from broods of females in October. Members of the large female and male groups disappeared in the July collection after release of their broods, and many juveniles of the new generation appeared in the field. Also males smaller than those in April but nearly equal to or larger in size than the large female group in April, were collected in July and August. There is a strong possibility that these males were sex-changed from constituents of the large female group found in April, since there is no small male group associated with the small female group in the April samples. There was no observation suggesting social structure in these populations in the field.

DISCUSSION

The external changes in the reproductive organs of *Gnorimosphaeroma naktongense* females indicate protogynous sex change under culture condition. Data also showed a possibility of sex change in the field population (Fig. 4). As histological observations were not done to clarify the processes of gonad changes, the possibility of protogynous sex change was strongly suggested. Though our experimental animals were sampled from brackish sites, females from a freshwater spring also showed transitional stages of male characters, indicating their sex reversal (Abe and Fukuhara, in preparation). *G. naktongense* may be the first species reported, which inhabits also freshwater bodies and undergoes a protogynous sex change in crustaceans.

Brook *et al.* (1994) categorized protogynous *G. oregonense* into seven reproductive stages: juveniles, receptive females with or without penes, mature females with or without penes, immature males with nonfunctional penes and matured males. In our study, though outer morphological changes in masculinizing were not yet observed in detail, similar changes occurred in *G. naktongense.* Histological changes of gonadal structure during and following sex change have been investigated in protogynic and protandric fishes (Sadovy and Shapiro, 1987), or protandric shrimp (Boddeke *et al.*,1991). Histological investigations to reveal the differentiation of reproductive organs should be the subject of future study in protogynous *G. naktongense* as well as a more detailed description of the outer changes in organs during sex change.

After Ghilselin's size advantage model (SAM) (Ghiselin, 1969), sequential hermaphroditism will evolve by selection when the relative reproductive success of a male or female differs with size or age. Factors which favor the evolution of protogyny are those which tend to depress male fecundity values at early ages, such as inexperience, territoriality, or female mate selection (Sadovy and Shapiro, 1987; Warner, 1988). Sexual dimorphism in size (Fig. 4) and active precopulatory guarding behavior is acknowledged in *G. naktongense*. Larger males tend to guard larger females which have a positive correlation with brood size (Abe and Fukuhara, in preparation), giving a higher relative reproductive success to larger males than smaller ones. Precopulatory mate guarding in *G. naktongense* may be a primary selective pressure favoring protogyny, as suggested by Brook *et al.* (1994) for the same genus, *G. oregonense.*

Precopulatory mate guarding evolved in many isopods or amphipods. For instance, guarding behaviors have been reported in *Asellus aquaticus* (Manning,1975; Thompson and Manning, 1981) and *Gamarus pulex* (Kusano and Kusano, 1989). *G. chinense,* showing reproductive behavior quite similar to *G. naktongense,* inhabited the same sampling site of the Agano River (Abe and Fukuhara, in preparation). SAM may predict the sex change of these gonochoristic species. It is widespread in plants and animals for taxonomic groups of close relatives or common life to contain both sex changers and non-sex changers (Sadovy and Shapiro, 1987; Wright, 1988). Extensive comparative studies on life cycle and reproductive strategy of sympatric habitants, *G. chinense* and *G. naktongense,* are of interest when considering this question.

Protogynous sex change often occurs in many families of teleost fishes, and proximate hypotheses propose that the social system triggers sex change (Policansky, 1982; Sadovy and Shapiro, 1987; Yogo, 1989). In crustaceans, protogynous sex change has been suggested also to be socially mediated except in the case of *G. oregonense* (Brook *et al.*, 1994). For instance, the presence of males inhibits sex change of females in the tanaid, *Leptochelia dubia* (Highsmith, 1983). In our culture experiments, females of *G. naktongense* changed sex in the presence of males. Also, no observations have suggested any social structure of *G. naktongense* in the field. An alternative hypothesis would be necessary to explain the protogyny in *Gnorimosphaeroma.*

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