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SHORT COMMUNICATION

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Change of external sexual characteristics during consecutive moults in *Crangon crangon* L

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Abstract Adult males of the North Sea shrimp, *Crangon crangon*, were maintained for 8 months in the laboratory under natural temperature and light cycles. Successive moults were analysed for morphological changes. Out of the 70 shrimps, one male performed morphological sex reversal by reducing the male characteristics and developing female characteristics. The morphological changes including the loss of the appendix masculina appeared within a single moult cycle. This observation proves that *C. crangon* males may be capable of changing sex. The low number of sex reversals indicates that *C. crangon* is a facultative rather than an obligate protandric hermaphrodite.

Keywords *Crangon crangon* · Sex reversal · Protandric hermaphroditism · Moulting · Morphology

Introduction

The brown shrimp *Crangon crangon* (Decapoda, Caridea) inhabits shallow waters and estuaries along the north-western coasts of Europe. In the North Sea, it is most abundant in the intertidal zones and forms a key species in the Wadden Sea ecosystem (Lloyd and Yonge 1947; Tiews 1970; Pihl and Rosenberg 1984). Furthermore, it is one of the most important targets in North Sea coastal fisheries (Neudecker and Damm 1992; Del Norte-Campos and Temming 1994).

In shrimp populations, the number of large adult females is higher than that of large adult males (Boddeke 1976; Oh et al. 1999). Large males are almost absent in commercial shrimp catches (Tiews 1954; Martens and Redant 1986; Tiews 1987). Boddeke (1962) suggested that *C. crangon* is a protandric hermaphrodite changing sex after reaching a certain size, while other authors (Meixner 1969; Tiews 1954; Lloyd and Yonge 1947) could not observe sex change. A comprehensive synopsis on the biological data of *C. crangon* by Tiews (1970) did not help to terminate the discussion. In the latest contribution, Boddeke et al. (1991) described *C. crangon* as a partially protandric hermaphrodite.

In order to identify sex reversal, we maintained in a long-term experiment mature male *C. crangon* individually in aquaria. Over a period of 8 months, we collected the moults of each animal and analysed them for external sex-specific morphological features, that is, the endopodites of the first and the second pleopods (Ehrenbaum 1890; Lloyd and Yonge 1947). Mature males have much smaller endopodites on the first pair of pleopods than mature females. Male endopodites are spine-like, round and pointed. They lie close to or behind the exopodites and are bare (Tiews 1954; Dornheim 1969). The endopodites of females are modified to carry eggs. They are distinctly larger than male endopodites, flat and spatula-shaped, slightly twisted along their longitudinal axis, never concealed by the exopods, and bare setae. The second pair of pleopods is of the same size in males and females. However, not visible to the naked eye, the male endopod bears a small protuberance, the appendix masculina which is lacking in females. So the first and second pleopods were used to determine the sex of the individuals in the present work.

Material and methods

Crangon crangon were captured with a beamtrawl in November 2003 off the Helgoland "Dünenhafen," North Sea (54°11′N, 7°54′E). Seventy mature males of 26–39 mm total length were selected and reared individually in the Marine Station on Helgoland (BAH)

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until the end of July 2004. The rearing tanks contained five rows of seven separate small compartments each. Each compartment measured 10×10×15 cm and was filled with 50 ml of sand with a grain size of less than 1,000 µm. The tanks received continuously gravel-filtered seawater. The water flew successively through all of the seven compartments in one row. The water was pumped directly from the sea. The temperature in the tanks corresponded largely with the natural outdoor temperature. The LD cycle in the aquarium-room was regularly adjusted to the natural LD cycle at Helgoland.

The rearing tanks were controlled twice daily. Animals were fed with pieces of frozen *C. crangon* or *Mytilus edulis* every other evening. Food residues were removed next morning. Moults were collected every morning and were preserved in ethanol (70%). The moults were measured and sexed. Photographs of the moults were taken with an Olympus ColorView system mounted on an Olympus SZX12 binocular microscope. Digital processing of the pictures was carried out with the analySIS® 3.1 Camera software (Software Imaging Systems Ltd.).

Results

The duration of the intermoult period decreased when water temperature increased during spring (Fig. 1). Animals which moulted in January had intermoult periods of 41 ± 17 days. The duration of the intermoult phase increased in February towards 46 ± 11 days and thereafter continuously decreased. In July (last month of record), the intermoult period amounted to 22 ± 3 days. Overall mortality during the experiment was 47%.

At the beginning of the experiment, all moults showed male characteristics. In February, the moult of one individual showed for the first time female characteristics. The previous moults of the same individual were clearly identifiable as male, having a small, round and bare endopodite at the first pleopod, which was partially covered by the exopod (Fig. 2a). The endopodite of the second pleopod had an appendix masculina (Fig. 2b). This appendix masculina completely disappeared in a single moult (Fig. 2d). The subsequent moults (Fig. 2f) lacked an appendix masculina on the second pleopod.

In the same moult in which the appendix masculina was lacking for the first time, the endopod of the first pleopod changed its appearance. It was no longer round but spatula-shaped although still small (Fig. 2c). Therefore, the moult showed all characteristics of an immature female. In the following moults, the endopod became larger and gained numerous setae (Fig. 2e), similar to the growth of the endopodites of primary females during maturation (Lloyd and Yonge 1947). There were no intermediate stages when the male moult changed into female.

Discussion

Since Boddeke's (1962) first observations on protandric hermaphroditism of *C. crangon*, this topic has been the subject of controversial discussions. Histological investigations by Boddeke (1962) revealed developing ovaries in male *C. crangon* which led to the conclusion that this species is a fully protandric hermaphrodite with males changing into females at a size of 4.2–4.6 cm. This hypothesis was criticised mainly because of the small number of individuals investigated and the very small ratio of sex changers found.

Meixner (1969), in contrast, reported that none of the 18 male *C. crangon* kept in aquaria for 14–15 months changed sex. The author raised them from the third and

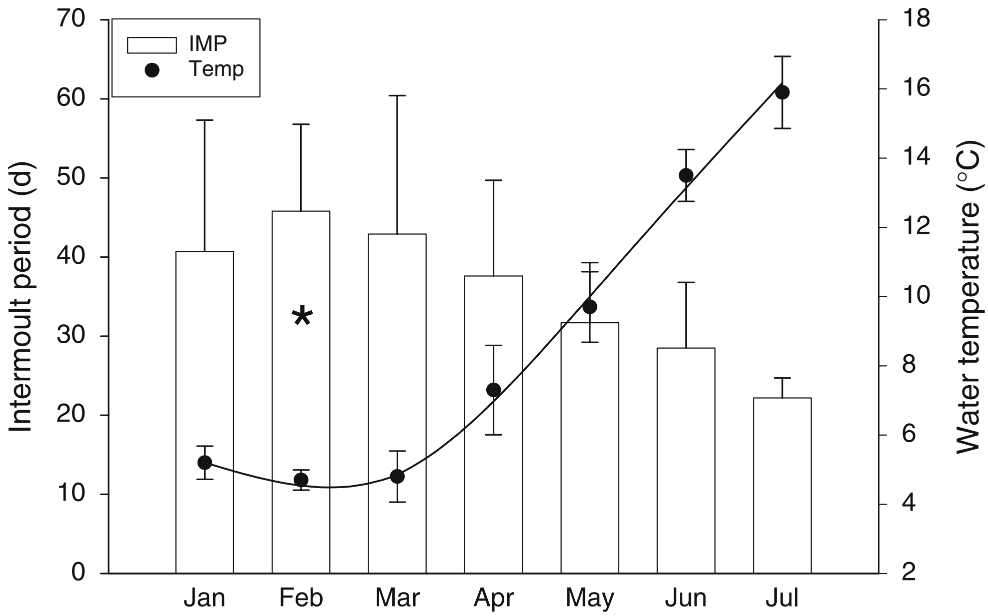

Fig. 1 Duration of the intermoult periods (IMP) of *Crangon crangon* (means ± SD, $n = 17$–41) and the water temperature off Helgoland (monthly means ± SD, $n = 12$–22) in 2004. The change of external sexual characteristics was observed in February (indicated by the *asterisk*)

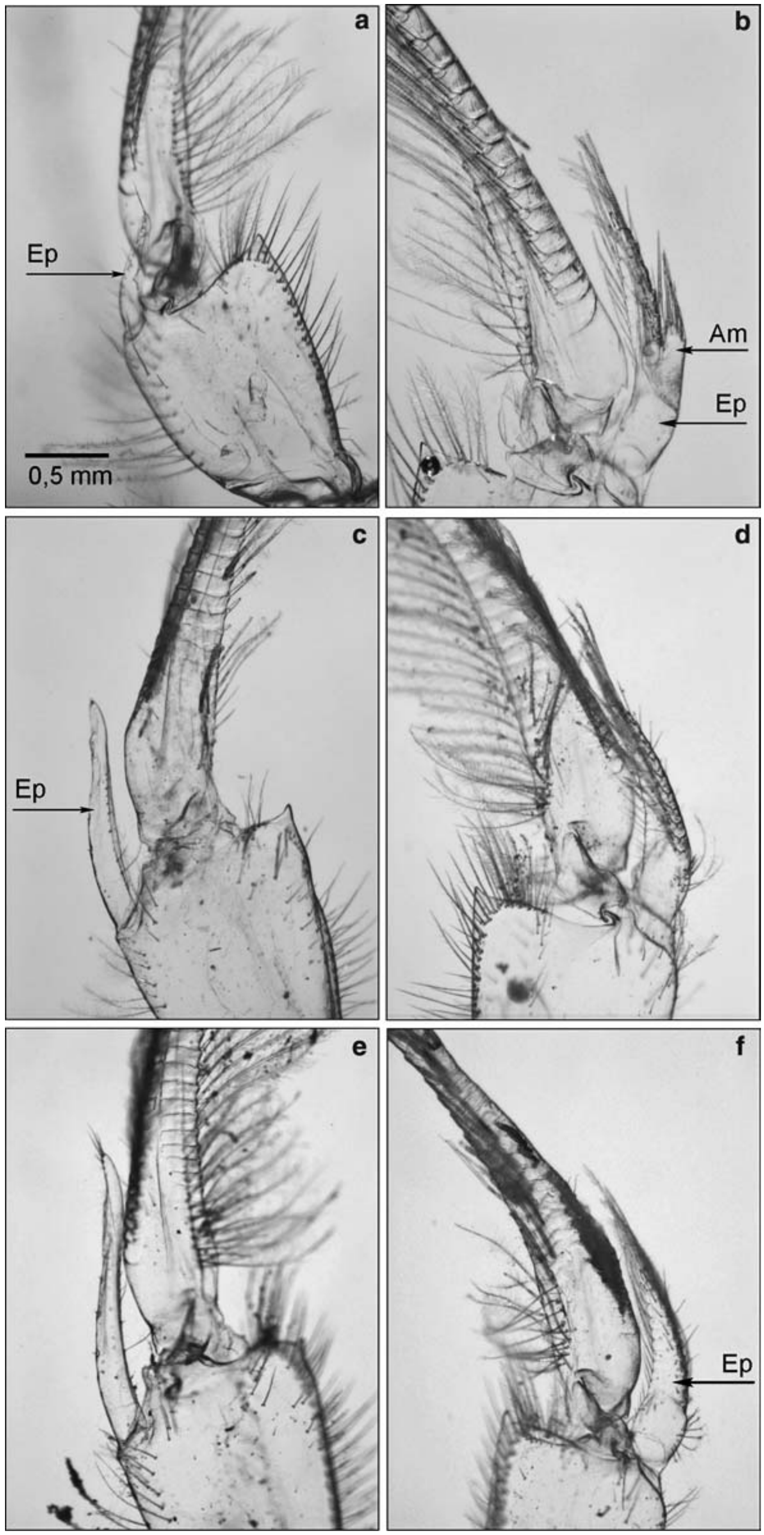

Fig. 2 Changes of morphological sexual characteristics in consecutive moults of *Crangon crangon*: first pleopod (**a**) and second pleopod (**b**) of last moult with male characteristics; first pleopod (**c**) and second pleopod (**d**) of the subsequent moult with now female characteristics; first pleopod (**e**) and second pleopod (**f**) of third moult after the change. The *arrows* indicate the endopodites (Ep) and the appendix masculina (Am)

second larval stages up to a size larger than 5 cm. Accordingly, Meixner (1969) concluded that *C. crangon* may be an optional protandric hermaphrodite. In the same year, Dornheim (1969) reported that female shrimps grow faster and become larger than male shrimps. Although he cited the work of Boddeke (1962) he completely ignored the sex-change hypothesis.

Martens and Redant (1986) investigated 630 specimens of *C. crangon* with a size between 4.1 and 5 cm. Depending on season, the authors found 2–9% of males which developed ovaries. They concluded that only a part of the adult males perform sex reversal. Since males with developing oocytes always contained sperm cells and never had degenerating androgenic glands, they suggested that this partial protandric hermaphroditism may not be functional. Furthermore, Martens and Redant (1986) discussed that the presence of oocytes in male gonads might not necessarily indicate sex reversal but could be due to malfunction of the testes. Sperm development is controlled by the androgenic hormone. Individual germ cells may occasionally receive insufficient hormone and therefore develop into oocytes. Accordingly, oocytes may appear in functional males while sperm cells never occur in functional females (Charniaux-Cotton 1957).

Tiews (1987) reviewed the discussion and concluded that *C. crangon* was not protandric. This conclusion was mainly based on his own observations (Tiews 1954) and those of Meixner (1969). Both authors did not observe a sex change of *C. crangon* in their aquaria. Moreover, Tiews (1954) believed that males with developing ovaries would not change sex because transitional stages could never be identified on the basis of external characteristics.

Histological studies by Boddeke et al. (1991) showed that oocytes developed in the caudal and distal parts of the testes, which then changed into sponge-like structures before completely turning into ovaries. Since then Boddeke et al. (1991) described *C. crangon* as a partially protandric hermaphrodite. The authors adapted their view to that of Martens and Redant (1986), however, still contradicting Tiews (1987) and Meixner (1969).

Our results showed that *C. crangon* can change its sex-specific morphology. However, since only one out of 70 animals changed within the 8 months of rearing, it is likely that *C. crangon* is only partially rather than fully protandric. The reason why Meixner (1969) never observed sex change during his investigations is possibly due to the very low number of individuals in his experiment. He captured larvae in the field and maintained them until they reached maturity after about 1.5 years; only 18 males reached the critical size for sex reversal.

No intermediate stages appeared when the male moult changed into female. Accordingly, transitional stages as they were demanded by Tiews (1954) do not occur with respect to external morphological characteristics. Our results confirm Martens and Redant (1986) who expected a sex change within a single moult cycle. Morphologically, animals were identified as either males or females but not as transitional stages or hermaphrodites. In the study of Martens and Redant (1986), the histologically identifiable intermediate stages always showed male external characteristics.

The reproductive success of female shrimps increases with size and thus with age because larger females are able to lay and carry more eggs than smaller ones. In contrast, male reproductive success is independent of size and age but mainly depends on the number of females present. Accordingly, protandric hermaphroditism may improve the genetic contribution of an individual shrimp to the next generation (Charnov et al. 1978).

The very low number of large males, however, cannot be explained by the small amount of sex changers only. In addition to occasional hermaphroditism, female shrimps may grow faster and become larger than male shrimps (Lloyd and Yonge 1947; Meixner 1969; Oh et al. 1999). Both optional protandric hermaphroditism and high growth rates of females may contribute to the female-dominated sex distribution in *Crangon* populations. However, it is still unknown whether hermaphrodites are actually fertile after sex reversal.

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