Reproductive behavior of three tube-building peracarid crustaceans: the amphipods *Jassa falcata* and *Ampithoe valida* and the tanaid *Tanais cavolinii*

B. Borowsky

Osborn Laboratories of Marine Sciences; Boardwalk at West 8th Street, Brooklyn, New York 11224, USA

Abstract

Laboratory observations indicate that *Jassa falcata*, *Ampithoe valida*, and *Tanais cavolinii* have quite similar patterns of behavior: males attend females until ovulation and copulation occur, then the male and female separate. Females tend to remain inside their own tubes, and males tend to move between the tubes of receptive females. This pattern of behavior (called "cruising males") may be common in crustaceans that exhibit some fidelity to a specific site, especially if the females produce several broods in succession, do not store sperm, and reproduce asynchronously relative to each other. Male *J. falcata* have a terminal molt which is marked by the presence of a specific sexually dimorphic characteristic, the "thumb" on the second gnathopod. Alternating ovulatory and anovulatory molts occur in *T. cavolinii*.

Material and methods

Source of animals

Adult *Ampithoe valida* were taken from laboratory stock cultures, founded by individuals collected from the intertidal zone at Jamaica Bay, Gateway National Park, Brooklyn, New York, USA. Stocks were maintained in 20-cm diameter glass culture dishes, with a glass cover plate to reduce evaporation. They were held at room temperature (20.6 °C ± 2.3 °C) at 15 hL:9 hD, in Instant Ocean Sea Salts (Eastlake, Ohio) diluted with tap water to 24‰ S (the average salinity of the collection site).

Individuals of *Jassa falcata* and *Tanais cavolinii* were taken from the cold-water exhibit tanks at the New York Aquarium, Brooklyn, New York. These tanks are continuously supplied with sea water from a well whose average temperature and salinity is 14.5 °C and 29‰ S, respectively.

Observations of individuals in pairs

Individuals were arranged in single heterosexual or isosexual pairs in individual 10-cm culture dishes in water of the appropriate salinity. Individuals were provided with *Ulva* sp. thalli *ad libitum* and occasional bits of mussel adductor muscle, which they used for food and for tube-building materials. Dishes were kept at room temperature, 15 hL:9 hD, and observed twice daily, at 7.00hrs and 19.00hrs during the light part of the cycle. The presence of casts, the occurrence of tube-sharing, ovulation and hatching, and any other pertinent reproductive activities were noted.

Introduction

The amphipods *Jassa falcata* and *Ampithoe valida*, and the tanaid *Tanais cavolinii*, are benthic, tube-building peracarid crustaceans. Males and females of these three species construct individual residential tubes by gluing debris together with secretions from specialized glands. Females have several broods in succession during the reproductive season but do not store sperm. Thus, for a viable brood, copulation must occur each time the female ovulates. Another common characteristic of these species is that females of a given species reproduce asynchronously relative to each other.

Related species subjected to similar environmental factors often exhibit convergent adaptations. Convergence is most easily recognized in morphology but can occur in behavior patterns as well. The purpose of this study was to test the hypothesis that species having similar reproductive physiologies and subjected to similar ecological factors have similar reproductive behaviors.
latory molts were used in behavioral analyses (21, 42, and 14 d for Ampithoe valida, Tanais cavolinii, and Jassa falcata, respectively). This was done to maximize the probability that the individuals were healthy and their behavior normal. Isosexual pairs of T. cavolinii were only observed once a day.

Observations of isolated male Jassa falcata

Fifty male Jassa falcata were isolated in individual 10-cm glass culture dishes and the occurrence of molts observed daily until the males died. In males of this species, the propodus of the fully formed posterior gnathopod has a nonprehensile posterio-ventral process resembling a thumb. After each individual died, its body, second gnathopod, and “thumb” lengths were measured. Body lengths were measured from the dorso-anterior tip of the rostrum to the dorso-posterior tip of the telson. Both the gnathopod and “thumb” lengths were measured from their dorso-anterior to their dorso-posterior tips.

Observations of Ampithoe valida in mass culture

Mass cultures were established by placing ten males and ten females in a 30 x 20 x 5.5 cm glass dish. The behavior of individuals outside tubes was observed daily for a five-minute period. These individuals were removed from the dish and replaced with an equal number of new individuals of the same sexes. The numbers and behaviors of each sex observed were recorded. This procedure maintained the number and sex ratio of adults in the dishes while guaranteeing that individuals outside tubes would only be scored once. Observations were continued until 50 individuals had been scored.

Results

Molt and reproductive cycles

The average lengths of intermolt periods differed among the species and between the sexes of each species (Table 1). Female Jassa falcata molted regularly, but males stopped molting when the “thumbed” stage appeared. When isolated, 27 males had “thumbs” and 23 did not. “Thumbed” and “thumbless” males survived about 1/4 the length of time (20.4 ± 8.5 d, range 1–36 d; 17.0 ± 10.5 d, range 1–36 d, respectively; \( t = 1.299, P > 0.05 \)).

Eighteen “thumbless” male Jassa falcata molted; fifteen molted one time and three, twice. The former group molted directly into a “thumbed” gnathopod stage, while the latter group’s “thumbed” gnathopod appeared after the second molt. The intervals between the two successive molts of the three individuals were 6, 7, and 7 d. Five of the original 23 “thumbless” males did not molt. Since they only survived from one to four days and the average inter-molt period was 6.7 d, it is possible that these five simply did not survive long enough to molt.

No “thumbed” male Jassa falcata ever molted; neither the 27 males that had “thumbs” at the beginning of the experiment nor the 18 males that molted into “thumbed” stages during the course of the observations. Thus male J. falcata have terminal molts marked by the appearance of a “thumb” on their second gnathopods. In contrast, females have indeterminate growth.

The size distribution for “thumbed” and “thumbless” male Jassa falcata overlapped broadly (Fig. 1). Thus the occurrence of the terminal molt was not triggered by the males’ absolute body length. In addition, the size of the “thumb” increased allometrically with male size even though the “thumb” exhibited no growth per se.

Female Ampithoe valida and Tanais cavolinii molted more frequently than males of the same species when maintained in heterosexual pairs (Table I). No male Jassa falcata molted, because only “thumbed”, terminal molt stage males had been isolated in observations on pairs.

In the amphipods, every female molt was accompanied by ovulation when a male was present. But in Tanais cavolinii, ovulatory molts alternated regularly with anovulatory molts (44 molts observed; only two molts in which two anovulatory molts were observed in succession). Ovulatory intermolt periods were significantly longer than anovulatory intermolt periods in the same female (paired Student’s \( t \)-test: \( t = 2.88, df = 10, P < 0.05 \)).

Anovulatory intermolt periods of Tanais cavolinii were readily distinguishable from ovulatory intermolt periods on the basis of brood sac morphology. In this species there are two brood sacs suspended from the ventral portion of the coxae of the fifth pair of pereaeopods (Lang, 1961). The brood sacs of females in anovulatory intermolt periods were about 1/4 the volume of ovulatory period brood sacs, and also lacked a brood. Ovulatory females cast off their brood sacs, not their entire exoskeletons, toward the end of this intermolt period, leaving either ragged ends, or

Fig. 1. Jassa falcata. The relationship between body length and length of the thumb of the second gnathopod of male J. falcata. Males with thumbs are indicated by dots; males without thumbs are indicated with “X”’s.