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Nocturnal release of parthenogenetic neonates of the marine cladocerans, *Pseudevadne tergestina* and *Evadne nordmanni* (Branchiopoda: Onychopoda), in the Inland Sea of Japan with observations by infrared-light video microscopy

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Abstract: The marine cladoceran *Pseudevadne tergestina* Claus (Branchiopoda: Onychopoda: Podonidae) was once again confirmed to release its neonates during the hours of total darkness almost exclusively between 10 p.m. and 4 a.m. based on specimens collected in July 1973 and 1985 in the central part of the Inland Sea of Japan. The behavior of nocturnal release of neonates of this species, together with another podonid *Evadne nordmanni* Lovén, collected respectively in September 1992 and May 1993, was successfully observed and recorded in the laboratory for the first time by means of infrared-light video microscopy. Molting of a mother animal in both species begins at the basal part of the carapace, either posterior to the neck or posterior to the postabdomen, which opens the carapace wide and enables neonates quickly to be freed from the mother into the water. Further molting of the mother is delayed until all the neonates are released. Subsequent molting is centered in the cephalothoracic regions, ending with shedding of the casts of thoracic appendages, and the newly molted individual immediately swims away. Some mother animals were recorded to have died after completing the release of their neonates successfully but without executing their final molt.

Key words: *Pseudevadne*, *Evadne*, nocturnal neonate release, infrared-light video microscopy, the Inland Sea of Japan

Introduction

Marine cladocerans of the family Podonidae (Branchiopoda: Onychopoda) are reported to release their parthenogenetic neonates only during the nighttime in complete darkness (Rivier 1969, 1998; Mordukhai-Boltovskoi & Rivier 1971; Onbé 1974; Bryan 1979; Mullin & Onbé 1992). In the Anomopoda, such as *Daphnia* and most other freshwater forms having a bivalved carapace, their neonates are released through the opening between the trunk and carapace created as a result of an abrupt bend of the postabdomen in the forward direction, without molting by the mother. In contrast, most onychopods, the carapaces of which are completely closed, are believed to liberate their neonates concurrent with molting of the mother, as already described and illustrated in *Evadne anonyx* G. O. Sars (Mordukhai-Boltovskoi & Rivier 1971) and *Pseudevadne tergestina* Claus (Onbé 1974). With regard to this problem, it has only recently become evident that Sars (1861, English translation 1993) had already stated clearly for species of the family Polyphemidae (in which all podonid species were included at that time): "The way the offspring come out is therefore that, through their continued growth, the enveloping cuticle becomes so distended that it finally ruptures; they may also be born through the shedding of the carapace of the mother, as Lovén has observed in *Evadne*." It is surprising that Lovén's observation must have been made as early as 150 years ago, although we have not yet been able to have access to his original literature. So far as I am aware, however, there have been no detailed observa-

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tions and illustrations on the behaviors of molting and neonate release of living specimens, in particular, of onychopods, except for *Polyphemus pediculus* (Linnaeus) (Polyphemidae) whose reproductive behavior has quite recently been reported in detail (Butorina 2000).

In the course of studies on the diel periodicity of the reproductive and feeding behaviors of marine cladocerans (Ctenopoda and Onychopoda) in the Inland Sea of Japan (Mullin & Onbé 1992; Uye & Onbé 1993), I have reconfirmed the nocturnal release of parthenogenetic neonates and succeeded in observing and recording the molting behavior of two species of podonid onychopods, *Pseudevadne tergestina* Claus [formerly *Evadne tergestina* (Claus); for taxonomy see Mordukhai-Boltovskoi & Rivier 1987; Egloff et al. 1997; Onbé 1999] and *Evadne nordmanni* Lovén in complete darkness using an infrared-light microscopic video-recorder. This paper describes their nocturnal neonate release in field populations, and the first record of observations on their reproductive processes in the laboratory.

Materials and Methods

Field observations

Two series of zooplankton samples were used to analyze the diel variation in the reproductive performance of *Pseudevadne tergestina*. From 11:00, July 3 to 10:00, July 4, 1973, hourly samples of zooplankton were collected by a vertical tow of a plankton net (mesh size: NXX13, 0.1 mm) at a shallow station (Stn T: depth 5–6 m; 34°24.6′N, 133°24.8′E) in Fukuyama Harbor in the central part of the Inland Sea of Japan (see Onbé 1974, fig. 3: stn 15). Another series of samples was collected every 2 h between 12:00, July 29 and 12:00, July 30, 1985, at a deeper station (Stn BG-1, depth 22–24 m; 34°18.5′N, 133°26.3′E) near Fukuyama Harbor (See Checkley et al. 1992, fig. 1A), by filtering through a 0.1 mm-mesh (NXX13) net 20-l seawater pumped up with a submersible pump from discrete depths between the surface and the bottom at an interval of 2 m. All these samples were preserved in 5% neutral formalin-seawater.

Pseudevadne tergestina found in the samples were sorted to determine the time of neonate release. Each parthenogenetic female was classified into one of four stages based on the degree of development of embryos contained in its brood pouch according to Rivier (1969), Mordukhai-Boltovskoi & Rivier (1971) and Onbé (1974, 1977, 1978), although Platt & Yamamura (1986) later staged the developmental processes of embryos of *Evadne nordmanni* into six categories.

Of these four stages, Stage I is defined as females having early stage embryos, including both neonate females with parthenogenetic embryos, and primiparous or multiparous females shortly after release of their advanced embryos (neonates). Stage II is indicated by females with developing embryos, and Stage III by females with advanced embryos in which appendages are already formed and the compound eye is completed but without pigmentation. At this stage, the embryos are still retained within the brood pouch. Stage IV denotes females with embryos at their most advanced stage of development (equivalent to "Stage 6" after Platt & Yamamura 1986), in which the compound eye now becomes fully developed with distinct dark pigmentation, the development of thoracic appendages is completed, and pedogenetic eggs are already deposited in their own embryonic brood space (Kuttner 1911; Onbé 1974; Platt & Yamamura 1986). The embryos of this stage are now extruded from the brood pouch into the space between its hypodermis and the carapace.

Laboratory observations

During two seasons from May to September 1992 and from February to July 1993, zooplankton samples were collected near Kure Marine Station (34°14.5′N, 132°33.1′E), Hiroshima University, located in Kure Harbor in the western part of the Inland Sea of Japan, by a vertical tow of a 45cm-diameter net made of 0.33 mm mesh (NGG54) fitted with a 1-l cod-end bucket. Live samples were transported back to the laboratory in insulated containers within an hour, and were acclimatized in an air-conditioned room for several hours. Under dim incandescent light, parthenogenetic females of both species carrying embryos at an advanced stage of development (Stage III or IV) were sorted for experimental observations, which usually started after 8 p.m. and continued overnight under completely dark conditions.

Laboratory observations were made by means of infrared-light video microscopy, as suggested by Price et al. (1988). Devices (Fig. 1) were installed in a walk-in, air-conditioned, light-controlled room to keep temperature and photoperiod close to the field conditions throughout the experiments. A binocular stereoscopic microscope (Wild M8) (Fig. 1F) was connected to a CCD video camera (Victor TK-S200) (Fig. 1G) with an infrared-light source (Fig. 1B) through a power supply unit (Victor TK-A241) (Fig. 1A). Video recordings were achieved using a S-VHS video cassette recorder (Victor BR-S610) (Fig. 1H) at a normal speed of 30 fields s^{-1}. A color monitor (Victor VM-R150S, screen size 29×22 cm) (Fig. 1I) was used for visual observations. High-resolution S-VHS video tapes (Toshiba ST-120SX) were employed for recording and dubbing.

A specially designed plexiglass (1-mm thickness) chamber (35 mm long×16 mm wide×80 mm high) (Fig. 1D) was filled with Millipore-filtered seawater, and into it was placed an experimental female glued with cyanoacrylate glue ("Crazy Glue", Alcaraz et al. 1980) to the tip of a fine glass capillary held in place by a supporting stand (Fig. 1C) for microscopic observations and subsequent video recordings by way of a mirror reflector (Fig. 1E). A mixture of naturally occurring particles filtered through a 0.1 mm-

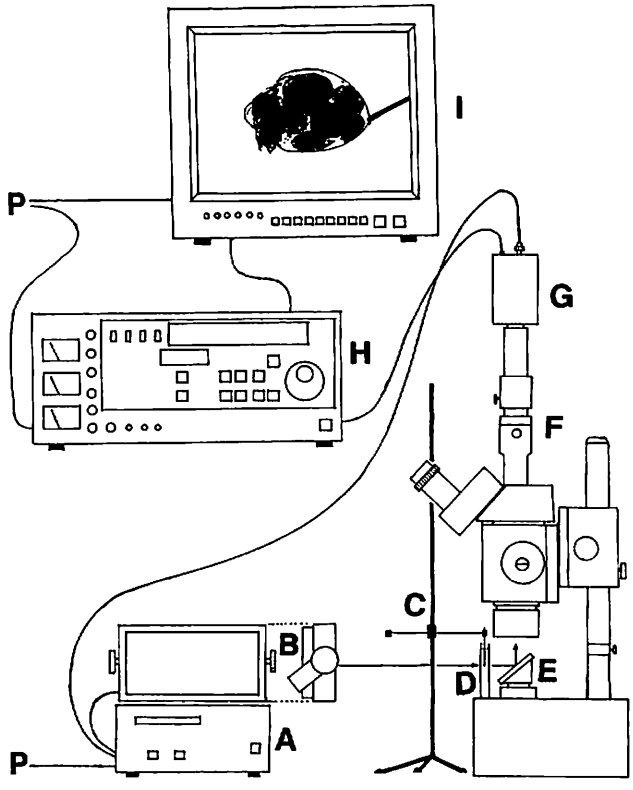

Fig. 1. Devices used for infrared-light video microscopic observations and recordings of molting and neonate-release behaviors in *Pseudevadne* and *Evadne* during hours of complete darkness. A: power supply unit (Victor TK-A241); B: infrared-light source; C: supporting stand; D: plexiglass vessel (35×16×80 mm) for a living tethered animal in seawater; E: mirror reflector; F: stereoscopic microscope (Wild M8); G: CCD video camera (Victor TK-S200); H: S-VHS video cassette recorder (Victor BR-S610); I: color video monitor (Victor VM-R 150-S); P: power.

mesh screen and cultured *Thalassiosira weissflogii* (Grunow) Fryxell & Hasle was added for its diet.

During the course of the experiments, a total of 67 hours of recordings were taken for a total of 18 individual females, of which 9 individuals were observed to have molted and the behavior of their release of neonates was recorded successfully. To help trace and illustrate the processes of molting and behavior of neonate release, a successive series of video images was photographed for two species with Toshiba Digital Video Copy (HC-1000).

Results

Diel changes in the parthenogenetic reproduction of *Pseudevadne tergestina*

We have already demonstrated that both *Evadne nordmanni* and *Pseudevadne tergestina* showed a distinct pattern of nocturnal release of neonates (Onbé 1974, figs. 61–63; Onbé 1978, fig. 3; Mullin & Onbé 1992, figs. 4, 5). Essentially similar patterns were once again observed for *P. tergestina* collected at different places and times, respectively at Stn T in early July, 1973 (Fig. 2A) and Stn BG-1 in late July, 1985 (Fig. 2B). In both cases, Stage IV females appeared in the population only during the period of complete darkness from around midnight to just before dawn, except for one case at Stn BG-1, in which a few Stage IV individuals were caught at dusk (6 p.m.) (Fig. 2B). Conversely, Stage I females, consisting of neonate females and newly-molted primiparous and multiparous females, increased exclusively from dawn to early morning to form the majority of the population resulting from the preceding neonate production before dawn. Stage II females comprised the major portion of the population throughout the

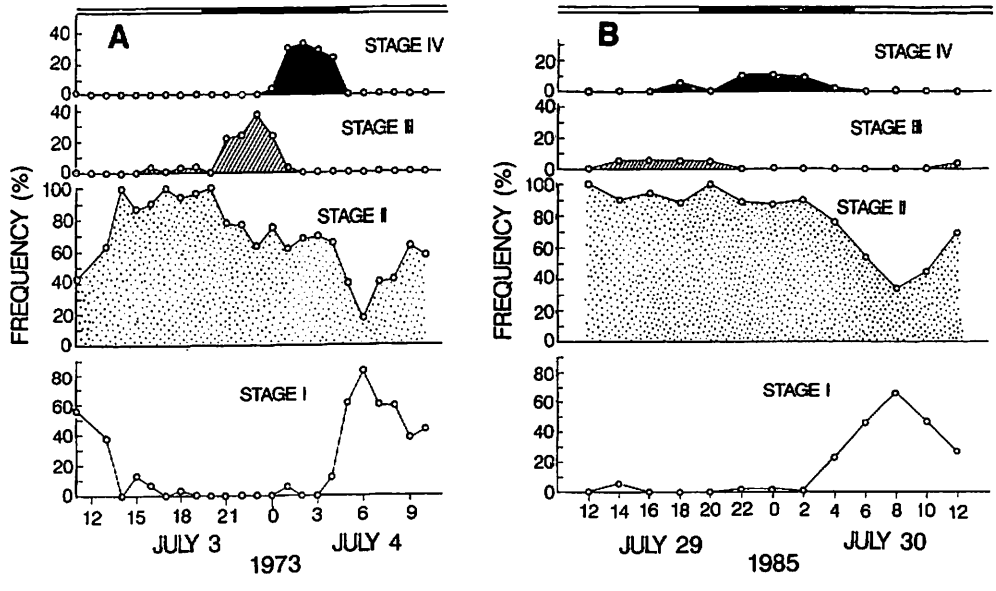

Fig. 2. Diel rhythmicity in the reproductive performance of parthenogenetic females of *Pseudevadne tergestina* of the Inland Sea of Japan, showing nocturnal release of neonates. For stage classification, see text. Bars at the top show day and night. A: July 3–4, 1973 at Stn T; B: July 29–30, 1985 at Stn BG-1.

whole day except for early morning, out of which some individuals began to proceed to Stage III from dusk to midnight, and quickly shifted to Stage IV. As typically shown in Fig. 2A, the shift appears to be complete within approximately 3–4 hrs.

Together with the data previously published, the results presented in Fig. 2 confirmed once again the consistency of a strikingly similar pattern in the diel rhythmicity in the reproductive performance of parthenogenetic females of these species.

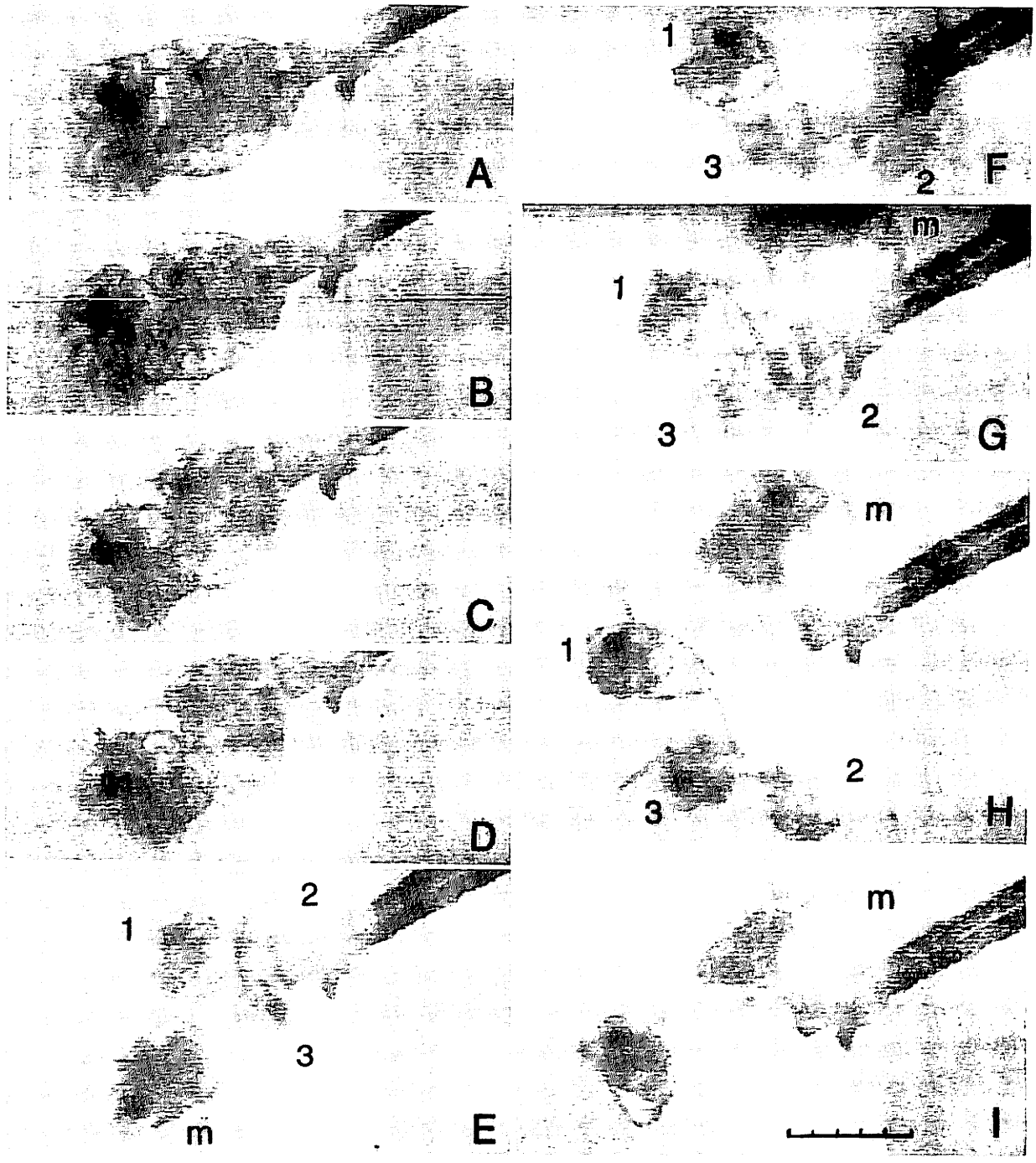

Fig. 3. Successive processes of molting and neonate-release of a tethered parthenogenetic female of *Pseudevadne tergestina*, recorded by infrared-light video microscopy under complete darkness, September 12, 1992. A: female (Stage IV) just before molting with 3 advanced embryos in the carapace; B: molting begins at the neck region; C, D: molting quickly proceeds further; E: neonates (1–3) emerging from the carapace of mother (m), F: mother becomes out of focus behind the glass capillary, while neonates separate from one another; G: mother (m) rotating to coming back to the original position; H: mother coming back with 3 neonates swimming away; I: 2 neonates swimming out of field, mother coming back to near the point of origin with tip of its new carapace sticking to the old cast. (Scale: 0.5 mm).

Behaviors of molting and neonate release observed in the laboratory

As mentioned earlier, complete closure of the carapace of podonid onychopods necessitates molting of the mother immediately preceding its release of neonates. However, no actual observations have ever been made in detail on the molting behavior of living individuals of podonid species, except for Lovén's reported observation in *Evadne* (Sars 1861).

Infrared-light video microscopy was successfully used for recording the behavior of *Pseudevadne* and *Evadne* in

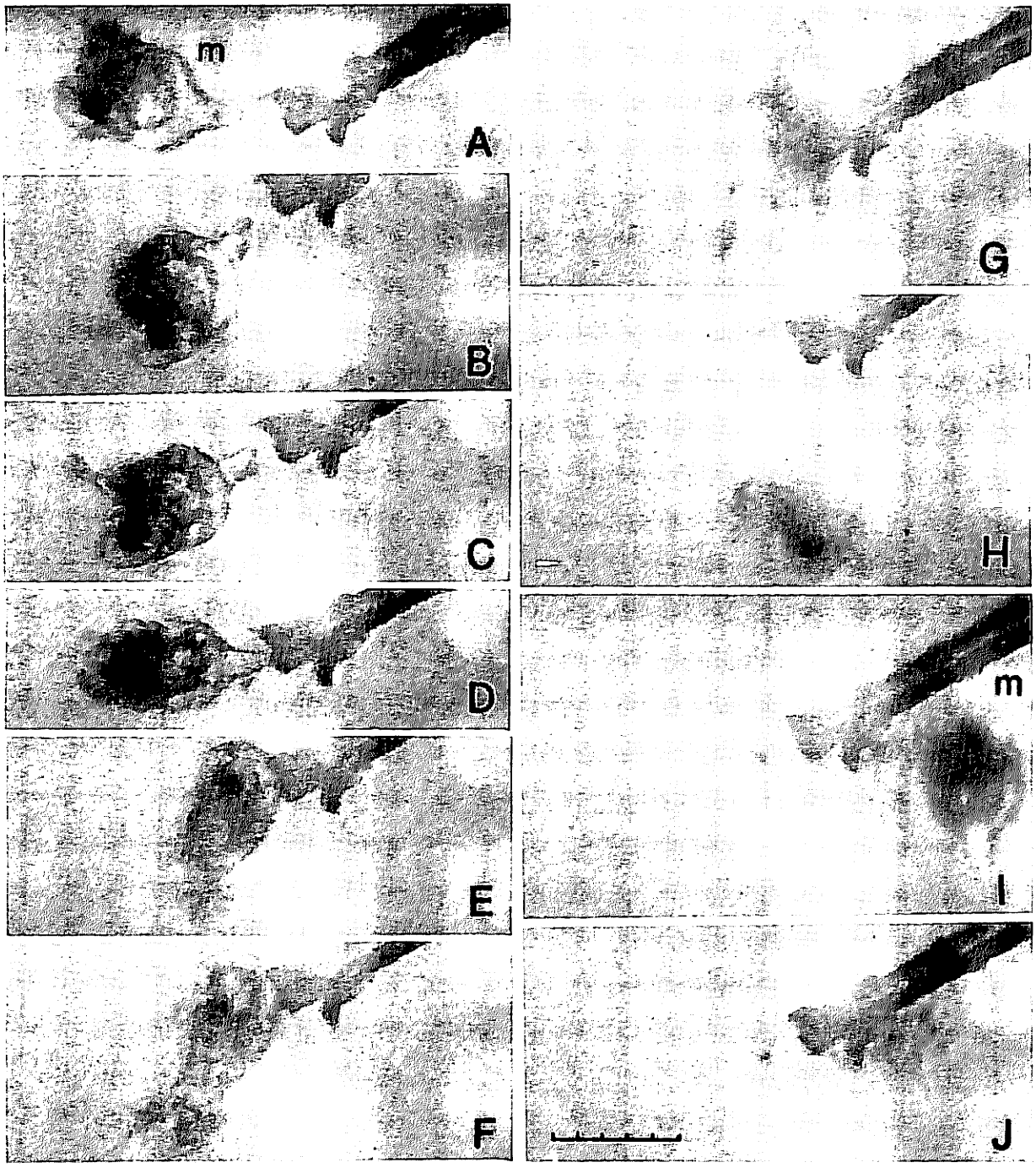

Fig. 4. Successive processes of molting and neonate-release of a tethered parthenogenetic female of *Pseudevadne tergestina*, recorded by infrared-light video microscopy under complete darkness, September 12, 1992. (Continued from Fig. 3). A: mother (m) coming back to the point of origin with tip of its carapace sticking to the cast of old carapace; B, C: the same process; D: molting resumes at the cephalothoracic region; E: shedding the casts of appendages; F: the same process proceeding further; G: shedding the cast almost completed; H: mother just escaping from the cast; I: mother (m) swimming away; J: old cast remaining attached to glass capillary. (Scale: 0.5 mm).

total darkness. An example recorded for *Pseudevadne tergestina* on September 12, 1992 is illustrated in Figs. 3 and 4. A tethered female usually moves its second antennae frequently, albeit intermittently, and thoracic legs less frequently. Late Stage embryos (Stage III) within the brood pouch increased rapidly in size within several hours to become Stage IV embryos (see also Fig. 2). At this last stage of development before being liberated, each embryo was observed to move its body, eye and thoracic appendages frequently within the carapace (Fig. 3A).

Initiation of molting of the mother occurred at the basal region of the carapace, either near the insertion of the elevator muscles of the second antennae positioned posterior to the dorsal organ (neck organ) (Fig. 3B), or near the caudal setae posterior to the postabdomen. This caused an instant opening of the carapace (Fig. 3C), which enabled neonates to be freed from it and released into the water immediately (Fig. 3D–I). After all three neonates were freed from the mother (Fig. 4A–D), she resumed her further molting of the cephalothoracic parts, which ended with shedding of the casts of the thoracic legs (Fig. 4E–H), and swam away (Fig. 4I, J). In the observation shown in Figs. 3 and 4, altogether 57 seconds were required from the initiation of the mother's first molt to the termination of the final

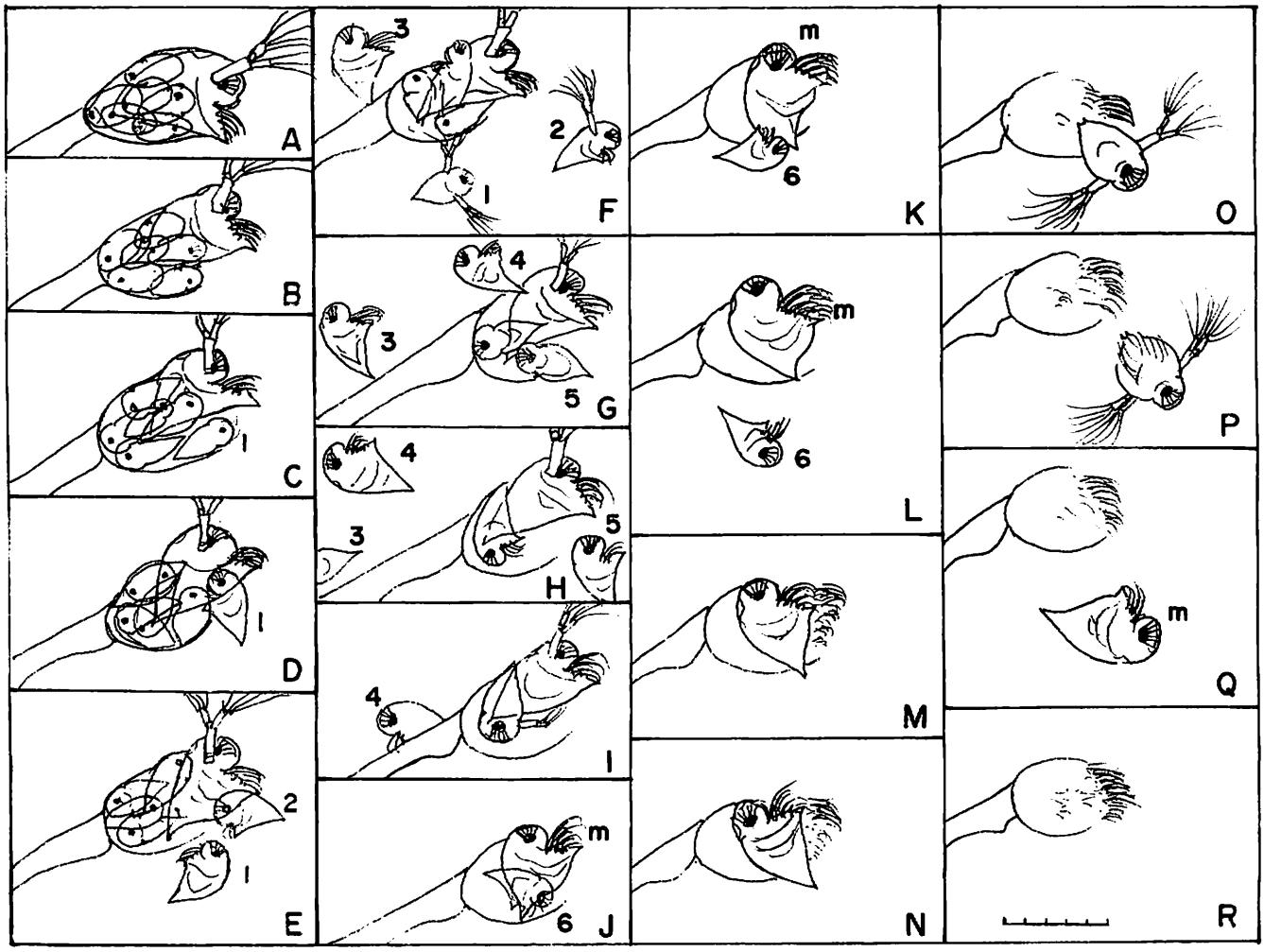

Fig. 5. Successive processes of molting and neonate-release of a tethered parthenogenetic female of *Evadne nordmanni*, recorded by infrared-light video microscopy under complete darkness, May 26, 1993. Line drawings made by tracing photomicrographs from video-images. A: female (Stage IV) with 6 advanced embryos at the beginning of molting, which occurred at the posterodorsal part of postabdomen; B: opening of carapace, 0.67 s. after beginning of molting; C: 1st neonate (1) emerging, 6.63 s.; D: 1st neonate (1) emerged, 10.33 s.; E: 2nd neonate (2) emerging, 40.43 s.; F: 3rd neonate (3) emerged, 50.00 s.; G: 4th neonate (4) emerged, and 5th neonate (5) emerging, 56.73 s.; H: 6th neonate rotating and struggling to emerge from within the hardened enclosure of the carapace, 1 m. 1.23 s.; I: same, 1 m. 5.03 s.; J: 6th neonate (6) emerging from the mother (m), 1 m. 29.83 s.; K: last 6th neonate (6) emerged, and mother (m) just started to molt at cephalothoracic parts, 1 m. 37.90 s.;L: mother (m) shedding casts of thoracic legs, 1 m. 40.92 s.; M: mother half finished shedding casts of thoracic legs, 1 m. 47.00 s.; N: mother finished molting, 1 m. 49.40 s.; O: mother emerging from her own cast, 1 m. 57.40 s.; P: mother emerged, 1 m. 57.79 s.; Q: same, 1 m. 58.67 s.; R: old cast sticking to glass capillary, 2 m. 1.59 s. See posterior part of old carapace hardened to form an enclosure with thin cover of glue, which made it difficult for neonates to emerge quickly. (Scale: 0.5 mm).

molt, with the release of three neonates in between.

Another observation recorded for *Evadne nordmanni* on May 28, 1993 is shown in Fig. 5. To facilitate readers' clearer understandings, this time the sequence of events was expressed in a series of line drawings, which were made by tracing the photomicrographs taken from videotape images, although the outline of each drawing is by no means accurate in detail. In this case, the actual time required for molting and neonate release was recorded on the tape as "1 min. 56 sec.," taking almost twice as long as in the former case. Molting began at the base of the carapace near the caudal setae posterior to the postabdomen (Fig. 5A, B), and gave rise to the successive release of 6 neonates.

The whole process took so long because the posterior half of the carapace was hardened to form an enclosure due to spreading of the glue used, which in turn made it difficult for some neonates positioned within the envelope to emerge. Almost 1.5 min. were needed to complete the release of all neonates (Fig. 5A–J). However, as in the former case, the mother did not start her subsequent molting until the last neonate was liberated (Fig. 5K). The final molting finished within 20 seconds (Fig. 5L–O).

Out of the 9 females for which behaviors were successfully recorded, 8 molted during the hours of total darkness between 9:30 p.m. and 4 a.m., mostly from 2 a.m. to 4 a.m. The stimulus for nocturnal molting is still to be queried. Whether or not females molt under artificial light during the nighttime has not been tested in the present study. However, a Stage IV female trapped at the surface of the water, was apparently unable to molt until the next morning and was tested under normal light from 9 a.m.; this particular individual eventually molted at 4 p.m. of the same day.

Some females died after successfully giving birth to their neonates, but without executing their final molting. They are probably older, multiparous females at the end of their natural life span, because such animals were usually larger females.

Discussion

Diel periodicity in the parthenogenetic reproduction of podonid onychopods has been known since Rivier (1969) and Mordukhai-Boltovskoi & Rivier (1971) first reported the phenomenon in some Caspian species, *Podonevadne camptonyx* (G. O. Sars), *P. angusta* (G. O. Sars), and *Evadne anonyx*, in which liberation of neonates always takes place during the nighttime. Subsequent studies revealed that this is also the case in two of the truly marine podonid species, *Evadne nordmanni* from the Inland Sea of Japan (Onbé 1974; this study) and *Pseudevadne tergestina* from the Inland Sea of Japan (Onbé 1974, Mullin & Onbé 1992; this study), from the Chesapeake Bay (Bryan 1979), and from the Gulf of Mexico (Mullin & Onbé 1992).

From these results, Mordukhai-Boltovskoi & Rivier's (1971, p. 164, fig. 4b) previous description and illustration on the neonate release of Caspian *Evadne anonyx* in connection with molting are assumed to be derived from preserved specimens. A similar observation of my own on *Pseudevadne tergestina* (Onbé 1974, p. 131, fig. 61D, E) was also based on specimens collected during the nighttime.

In the present study, the actual processes of molting and subsequent neonate-release of the two podonid species have been observed under the microscope and recorded on videotapes for the first time. Liberation of neonates always occurs after initiation of molting of the mother animal. Interestingly, it is, without exception, only after all the neonates are freed from the maternal carapace into the water that the mother completes her molt. It can now be concluded that the release of neonates in these species is not a result of mere rupture of the wall of the distended carapace as suggested earlier by Sars (1861) but a part of the process always associated with maternal molting as reportedly observed by Lovén (see Sars 1861).

A defense mechanism has been postulated for this striking behavior. For a female animal, carrying many advanced embryos with remarkably distinct black eyes, in an otherwise transparent body with only a single eye, spending this period under cover of total darkness undoubtedly facilitates her avoidance of selective predation by visual predators such as larval fish (Zaret 1972a, b; Bryan 1979; Mullin & Onbé 1992). Some pond insect larvae are known to feed at their highest rates on the largest available cladoceran prey (Cooper 1983). Larger females full of advanced embryos would also be vulnerable to predators if present in the well-lighted surface layers during the daytime. Molting animals may possibly be attacked easily by predators because of their reduced swimming ability. This might also explain the advantage of molting at night.

While *Pseudevadne tergestina* is found in warm waters from temperate to tropical seas (Onbé 1999), *Evadne nordmanni* is known to be distributed from temperate seas to as far north as the Arctic Ocean including the Barents, Kara, eastern Siberian Seas (Della Croce 1974), and the Chukchi Sea (Onbé et al. 1996). In view of the fact that all the previous records of nocturnal release of neonates in *Evadne* are based solely on specimens taken in mid-latitudinal regions under normal light regimes, it would be interesting to know how the Arctic *Evadne* should behave under circumstances of quite different photoperiods.

In striking contrast, another onychopod species *Polyphemus pediculus* (Polyphemidae) from a shallow freshwater reservoir has been quite recently reported to liberate its neonates one after another through an opening located posterior to the base of its characteristically elongated caudal stem (Butorina 2000). Neonate release of this species is also observed to occur predominantly (80%) at dawn between 4 and 6 a.m., but extends further for some individuals from 9 a.m. to noon and even around 3 p.m.

The release of neonates in Cercopagidae, the remaining family of the Onychopoda, is reported to take place accord-

ing to a different pattern, which involves "liberation to the outer environment, accompanied either by a rupture of the chitinous chamber (often the case in *Bythotrephes*), or by a separation (of the chamber) together with embryos from the maternal body (common in *Cercopagis*) (Rivier 1998)." The latter case (*Cercopagis*) is unique in that "the young individuals jump out, one after another, of the oval opening formed at the site of detachment of the chamber (Rivier 1998)." In *Bythotrephes*, no clear diel reproduction occurred in a shallow pond, but in a larger reservoir, birth of juveniles started at 9 p.m. in July and at 7 p.m. in August, reached a maximum at 11 p.m., and terminated before dawn between 1 and 3 a.m. (Rivier 1998).

Such discrepancy found in the behaviors of parthenogenetic reproduction among species of the three families comprising the Onychopoda may reflect possible differences in the adaptive and evolutionary history within this Order. More explicit observations on living animals are needed for other species, in particular, those occurring at different latitudes under different regimes of temperatures and photoperiods. Whether or not such reproductive behaviors are associated with the presence of predators poses another intriguing problem to be explored, since fish-mediated kairomones are known to induce diel vertical migration (DVM) in freshwater daphniids (Ringelberg 1997).

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