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REPRODUCTION AND LARVAL DEVELOPMENT OF THE
MANTIS SHRIMP *GONODACTYLUS BREDINI*
(CRUSTACEA: STOMATOPODA) MAINTAINED IN
THE LABORATORY

Steven G. Morgan and Joseph W. Goy

ABSTRACT

A male and a female of *Gonodactylus bredini* collected off the coast of North Carolina were maintained in the laboratory for 16 months. Five clutches were spawned during a period of one year. Egg masses were pinkish orange, hollow spheres approximately 15 mm in diameter. Each egg mass consisted of 800-900 ovoid eggs ranging from 0.75-0.79 mm in length and 0.64-0.67 mm in width. The periodicity between emergences of pelagic larvae from the burrow ranged from 32-91 days, with a mean of 62 days. At 28°C developmental times were as follows: approximately 29-30 days from mating to the pelagic larval stage when brooding is no longer required, 20-21 days from spawning to the pelagic stage, and six days from the propelagic to the pelagic stage. The female appeared to sculpt a burrow in hard coral and then seal the burrow while larvae remained within. Only one molt was observed, during which time the stomatopod changed color before reverting to its normal hue.

Larvae of *G. bredini* were reared to metamorphosis from the eggs spawned and hatched in the laboratory. Three propelagic, four pelagic, one supernumerary, and the first postlarval stage were described for *G. bredini*. The unequivocal existence of supernumerary instars has not been determined previously for any species of stomatopod. The duration of larval development is approximately 35-40 days at 25°C and 30 days at 30°C when larvae progress through seven stages before metamorphosing, and 40-50 days at 25°C and 36 days at 30°C for larvae metamorphosing after eight stages. Of the 454 larvae reared, only 4% metamorphosed successfully. Differences in color patterns, degree of aggressiveness, developmental times, and postlarval and adult characters between Bermudan and North Carolinian populations of *G. bredini* raise the possibility that the two populations may be distinct species.

Stomatopods are noted for being rapacious predators and for aggressive defense of their burrows (Caldwell and Dingle, 1976; Reaka and Manning, 1981). The coelobitic life-style of mantis shrimps makes it difficult to investigate their reproductive behavior in the field. Stomatopods usually mate, spawn, brood, and hatch their eggs within the burrow (Dingle and Caldwell, 1972; Hamano and Matsuura, 1984). Furthermore, stomatopod larvae remain in the burrow after hatching and pass through one to three propelagic stages before entering the plankton. The difficulty in obtaining eggs (as compared to many other crustaceans which attach them to their bodies), in capturing propelagic larvae, and in rearing larvae once collected has resulted in a paucity of larval descriptions. Of the 350 known species of stomatopods, only 10% can be identified with their larvae (Provenzano and Manning, 1978; Morgan and Provenzano, 1979), and only two have been reared from hatching to metamorphosis, *Gonodactylus oerstedii* (Manning and Provenzano, 1963; Provenzano and Manning, 1978) and *Heterosquilla tricarinata* (Greenwood and Williams, 1984).

Descriptions of courtship, copulation, spawning, or brooding have been provided for a few species of stomatopods (Giesbrecht, 1910; Verrill, 1923; Serène, 1954; Deecaraman and Subramoniam, 1983; Hamano and Matsuura, 1984), including *Gonodactylus bredini* (Dingle and Caldwell, 1972). However, little information exists on the frequency of these reproductive events. Populations of stomatopods apparently breed throughout the year, often with peaks in frequency, in most tropical regions (Kinzie, 1968; Reaka, 1979). They spawn nocturnally

during new and full moons (Reaka, 1976). Stomatopods inhabiting temperate regions breed only during warm months (Senta, 1967; Pyne, 1972; Morgan, 1980; Greenwood and Williams, 1984).

Information on the larval development of *G. bredini* is limited. In Bermuda, Gurney (1946) was able to collect eggs and rear the early larval stages of *G. bredini* (reported by him as *G. oerstedii*; see Manning, 1969). Gurney declined to describe the larval stages because he believed they closely resembled the larvae of *G. falcatus* (reported by him, p. 156, as *G. glabrous*), which he described from the Red Sea. Gurney provided a brief description of a postlarva which molted from the last larval stage in the laboratory, but the account is too incomplete to be of much use.

This paper contributes information on the reproductive periodicity and behavior, as well as the complete larval and postlarval development of the common West Atlantic stomatopod *G. bredini*. *Gonodactylus bredini* ranges from North Carolina to Curaçao, off the coast of Venezuela, and resides in the littoral zone to depths of 55 m (Manning, 1969). It occupies holes in sponges, sabellariid reefs, rock, or coral rubble.

MATERIALS AND METHODS

A male and female *G. bredini* were collected on 12 August 1981 near Frying Pan Shoals, North Carolina (33°31'N, 77°24'W), at a depth of 28 m using a rock dredge. The bivalve *Arca zebra* and rubble predominated in the dredge sample containing the mantis shrimps. Bottom temperature and salinity recorded at the collection site were 22.7°C and 36.37‰. The temperature of surface waters was 27.6°C. Total length (TL) of the adult stomatopods was measured from the anterior margin of the rostrum to the median posterior margin of the telson.

The mantis shrimps were placed in a 10-gal (38-l) aquarium with an undergravel filter. The stomatopods were provided with several pieces of hard coral for cover. The temperature and salinity of the aquarium were maintained at approximately 28°C and 32–36‰.

The stomatopods were allowed to breed, spawn, and hatch in the tank. The larvae then were placed individually in compartmentalized plastic trays. Each tray contained 18 compartments measuring 4.5 × 5 × 4 cm. Two hatches of larvae were reared. Pelagic larvae emerging from the burrow on 19 October 1981 were reared at 36‰ and either 25° or 30°C. Larvae hatched on 15 February 1982 were reared at 32‰ and 25°C through both the propelagic and pelagic stages. A total of 454 larvae were reared: 148 from the first hatch and 306 from the second. All larvae were maintained under a 12 h light:12 h dark photoperiod. Filtered sea water and nauplii of *Artemia* were provided daily. Molting frequency and survival were recorded daily. Larvae and exuviae were preserved in 70% ethyl alcohol for later description. A dissecting microscope with camera lucida attachment was used to illustrate the larvae.

The descriptions were based on 10 specimens per stage. Total length (TL) was measured from the apex of the rostrum to the median posterior margin of the telson. Carapace length (CL) was measured from the tip of the rostrum to the median posterior margin of the carapace. Pleotelson (Kaestner, 1970) length (PL) was measured from the articulation of the fifth pleomere to the median posterior margin of the pleotelson, whereas telson length (tL) was measured from the articulation of the sixth pleomere to the median posterior margin of the telson.

RESULTS

Size, Coloration, and Molting of Adults

The female (35 mm) was pinkish red or rust colored overall, and the male (48 mm) was green. The antennules, antennae, third to fifth maxillipeds, and pereopods of both sexes were yellow distally. The anterior margins of the thoracomeres, pleomeres, and telson of the female were green dorsally, and were red dorsally for the male. Carinae and teeth of the telson and sixth pleomere of both sexes were green. The dactyls of the second maxilliped of both sexes were pink; the propodus was trimmed in green for the female and red for the male; the carpus

Table 1. Time elapsed between mating, spawning, hatching, and emergence of pelagic larvae of the stomatopod *Gonodactylus bredini* from the burrow.

| Reproductive events | Time elapsed (days) | Number of observations |
|-----------------------------------|---------------------|------------------------|
| Mating—spawning | 9–60 | 2 |
| Spawning—hatching | 14–15 | 2 |
| Hatching—larval emergence | 6 | 1 |
| Larval emergence—mating | 16 | 1 |
| Larval emergence—larval emergence | 32–91 | 5 |
| | (\bar{x} = 62) | |

of both sexes was green; and the meral spots of both sexes were white. The uropods of the female were red and the exopods bore pink lateral spines.

The male molted once. Immediately after ecdysis the male changed color from green to red, but slowly reverted to its original greenish color over the following two weeks. However, the male retained a distinctive reddish tinge to its predominantly green coloration.

Reproductive Periodicity and Behavior

The pair of *G. bredini* was maintained in the laboratory from 14 August 1981 until December 1982, a period of 16 months. They mated readily following their collection and introduction to a 19-cm culture dish, even though cover such as coral rubble was not provided.

The female apparently sculpted a burrow approximately 15 mm in diameter and 30 mm deep among branches adjoining the base of a piece of the hard coral *Oculina* sp. by using its second maxillipeds. The male occasionally entered the burrow of the female when eggs or propelagic larvae were not present. Aggressive interactions were not observed, except that occasionally the female chased away the male from the entrance to the burrow without making dramatic displays or physical contact. The male frequented the branches of the same piece of coral occupied by the female, but did not carve a burrow.

Spawning occurred from 9–60 days after the stomatopods were observed copulating, although an episode of hatching and subsequent copulation likely occurred but was not observed during the 60-day period (Table 1). The female was not observed to leave the burrow nor to feed after spawning and prior to the emergence of pelagic larvae from the burrow. Occasionally, the female emerged partially but never exposed the eggs or removed them from the burrow. Egg masses were pinkish orange, hollow spheres about 15 mm in diameter. The number of eggs in two egg masses were counted, and each mass consisted of 800–900 ovoid eggs ranging from 0.75–0.79 mm in length to 0.64–0.67 mm in width. The female brooded the eggs for 14–15 days before eclosion (Table 1).

The female entirely blocked the entrance to the burrow with small pieces of coral and crushed oyster shell upon hatching of the larvae. The entrance to the burrow was opened, and the larvae emerged six days after eclosion. The male was not observed to copulate with the female until 16 days after the pelagic larvae exited from the burrow (Table 1).

The stomatopods were observed for 12 (August–August) of the 16 months they were held in captivity, during which time they produced at least five clutches; more clutches may have been produced and gone undetected due to their coelobitic habits. The presence of a clutch was most noticeable when pelagic larvae emerged from the burrow. Pelagic larvae were observed in October, December, February,

Table 2. Mean percentage survival of larval stages for two hatches of *Gonodactylus bredini* reared at different temperatures and salinities.

| Date of hatching | Temperature (°C) | Salinity (‰) | Larval stages | | | | | | | | Total |
|------------------|------------------|--------------|---------------|------|-------|------|------|------|------|------|-------|
| | | | I | II | III | IV | V | VI | VII | VIII | |
| Oct 1981 | 30 | 35 | — | — | — | 86.8 | 85.3 | 42.3 | 19.0 | 16.7 | 1.7 |
| Oct 1981 | 25 | 35 | — | — | — | 91.5 | 80.9 | 48.3 | 23.8 | 30.0 | 2.5 |
| Feb 1982 | 25 | 32 | 47.5 | 85.7 | 100.0 | 69.7 | 89.1 | 75.6 | 41.9 | 83.3 | 5.6 |

May, and July. The mean periodicity between emergences of pelagic larvae from the burrow was 62 days (Table 1). Of these 62 days, 30 days elapsed between copulation and larval emergence, leaving an average of 32 days from larval emergence to the next observed copulation. However, as few as two days or as many as 61 days may have been required for the pair to copulate again.

In summary, the duration of the reproductive cycle (from one mating to the next) is approximately 45 days at 28°C, assuming 16 days elapsed between larval emergence and copulation. Approximately 29–30 days are required from mating to the pelagic larval stage, 20–21 days from spawning to the pelagic stage, and six days from the propelagic to the pelagic stage.

Larval Development

A total of 454 larvae of *G. bredini* were reared from two hatches; 18, or 4%, metamorphosed to postlarvae. Survival was generally good after the first instar and prior to the sixth; however, mortality increased rapidly thereafter (Table 2). The mean duration of each instar ranged from 1.0–8.2 days with the exception of the seventh instar which lasted from 8.0–13.2 days (Table 3).

The propelagic larval development consisted of three stages. When freshly hatched propelagic larvae were removed from the burrow and placed in a 19-cm culture dish, they clumped together forming a tight ball. The larvae were positively thigmotactic and negatively phototactic until the third stage when the larvae became positively phototactic. However, the larvae did not emerge from the burrow until the fourth instar.

The pelagic developmental phase consisted of four stages, so that usually the entire larval development included seven stages. An eighth supernumerary instar also may occur prior to metamorphosis. Of the 18 larvae that were reared successfully beyond the seventh stage, 10 (55.5%) metamorphosed immediately to postlarva and 8 (44.5%) molted to an eighth larval instar (Table 2). The mean duration of pelagic development for larvae metamorphosing after Stage VII was 28.5–35.6 days at 25°C, and 24.4 days at 30°C (Table 3). Larvae undergoing an eighth larval instar extended the time of larval development by another 5.3–8.2 days, so that their mean pelagic larval duration was 33.8–43.8 days at 25°C, and 30.4 days at 30°C. Assuming that propelagic development of the larvae reared only through the pelagic stages took six days, the entire larval duration after seven instars is approximately 35–40 days at 25°C, and about 30 days at 30°C; whereas with a supernumerary instar larval duration is 40–50 days at 25°C and approximately 36 days at 30°C.

Larvae subsisted on their yolk supply prior to Stage IV, but thereafter began preying on nauplii of *Artemia* following the development of functional mouthparts. Larvae used their second maxillipeds to capture the nauplii and transfer

Table 3. Mean duration (days) of larval stages for two hatches of *Gonodactylus bredini* reared at different temperatures and salinities.

| Date of hatching | Temperature (°C) | Salinity (%) | Larval stages | | | | | | | | Propelagic | | | Pelagic | | | Total | |
|------------------|------------------|--------------|---------------|-----|-----|-----|-----|-----|------|------|------------|--------|---------|---------|--------|-------|-------|--|
| | | | I | II | III | IV | V | VI | VII | VIII | I-III | IV-VII | IV-VIII | I-VII | I-VIII | Total | | |
| Oct 1981 | 30 | 35 | — | — | — | 5.7 | 4.6 | 4.8 | 9.3 | 6.0 | — | — | 24.4 | 30.4 | — | — | — | |
| Oct 1981 | 25 | 35 | — | — | — | 6.1 | 4.1 | 5.1 | 13.2 | 5.3 | — | — | 28.5 | 33.8 | — | — | — | |
| Feb 1982 | 25 | 32 | 2.0 | 2.0 | 1.0 | 7.8 | 7.7 | 7.1 | 8.0 | 8.2 | 5.0 | 5.0 | 35.6 | 43.8 | 40.6 | 48.8 | — | |

them to the mouthparts. Several nauplii were captured by the maxillipeds while one or two nauplii were being masticated simultaneously by the mouthparts.

Stage I (First Propelagic)

Fig. 1

Duration: 2 days at 25°C. Measurements (mm): TL = 2.5–2.65, CL = 1.0–1.3.

Rostrum (Fig. 1A) deflexed, not extending to distal margin of antennal peduncle. Carapace (Fig. 1A, B) bulging dorsally over prominent yolk mass; posterior margin extending to sixth thoracomere, bearing short dorsal spine medially and 2 long posterolateral spines extending to anterior margin of eighth thoracomere; supraorbital spines absent. Eyes (Fig. 1A) sessile.

Antennule (Fig. 1C) with 3-segmented peduncle and 2 terminal flagella; inner flagellum 2-segmented, apical segment armed terminally with 2 strong and 1 weak seta, proximal segment armed terminally with 1 strong and 1 weak seta; outer flagellum 1-segmented, armed terminally with 2 strong and 2 weak setae, armed medially with 5 aesthetascs arranged into 2 groups (2 + 3) along inner margin. Antenna (Fig. 1D) armed with 8–10 plumose setae, endopod absent.

Mandible, maxillule, and maxilla absent.

First maxilliped (Fig. 1E) articulated partially into 5 segments, dactyl not reflexed, epipod absent. Second maxilliped (Fig. 1F) articulated partially into 5 segments, dactyl not reflexed, epipod present. Third, fourth, and fifth maxillipeds present as minute buds.

Pereiopods absent.

Abdomen (Fig. 1A, B) with 5 pleomeres, each bearing small posterolateral spines and 1 pair of functional pleopods (Fig. 1G–I); fifth pleopod shorter than preceding 4, but all bearing appendices internae and plumose setae as summarized in Table 4. Sixth pleomere fused with telson, submedian spines absent, uropods absent. Pleotelson (Fig. 1J) with 3 pairs of articulated lateral spines, 1 pair of fixed posterolateral spines, and 11 or 12 denticles on either side of emarginate midline.

Stage II (Second Propelagic)

Fig. 2

Duration: 2 days at 25°C. Measurements (mm): TL = 2.9–3.1, CL = 1.4–1.7.

Rostrum (Fig. 2A, B) deflexed, extending beyond antennular peduncle. Carapace (Fig. 2A, B) swollen less around reduced yolk sac than in previous stage; posterolateral spines extending to second pleomere, bearing small basal spinule ventrally. Eyes (Fig. 2A) stalked.

Antennule (Fig. 2C) with inner flagellum armed with 2 strong and 2 weak (1 obscured from view) terminal setae, 1 strong and 2 weak distal setae on distal margin of proximal segment; outer flagellum armed with 5 terminal setae and 5 aesthetascs arranged in 2 groups (2 + 3). Antennal scale (Fig. 2D) with 12–15 plumose setae.

Mandible absent; maxillule and maxilla present as buds.

First maxilliped (Fig. 2E) articulated fully into 5 segments; epipod present. Second maxilliped (Fig. 2F) with dactyl reflexed. Third, fourth, and fifth maxillipeds (Fig. 2B) present as buds.

Pereiopods absent.

Pleopod (Fig. 2G–I) setation summarized in Table 4. Pleotelson (Fig. 2J) essentially unchanged.

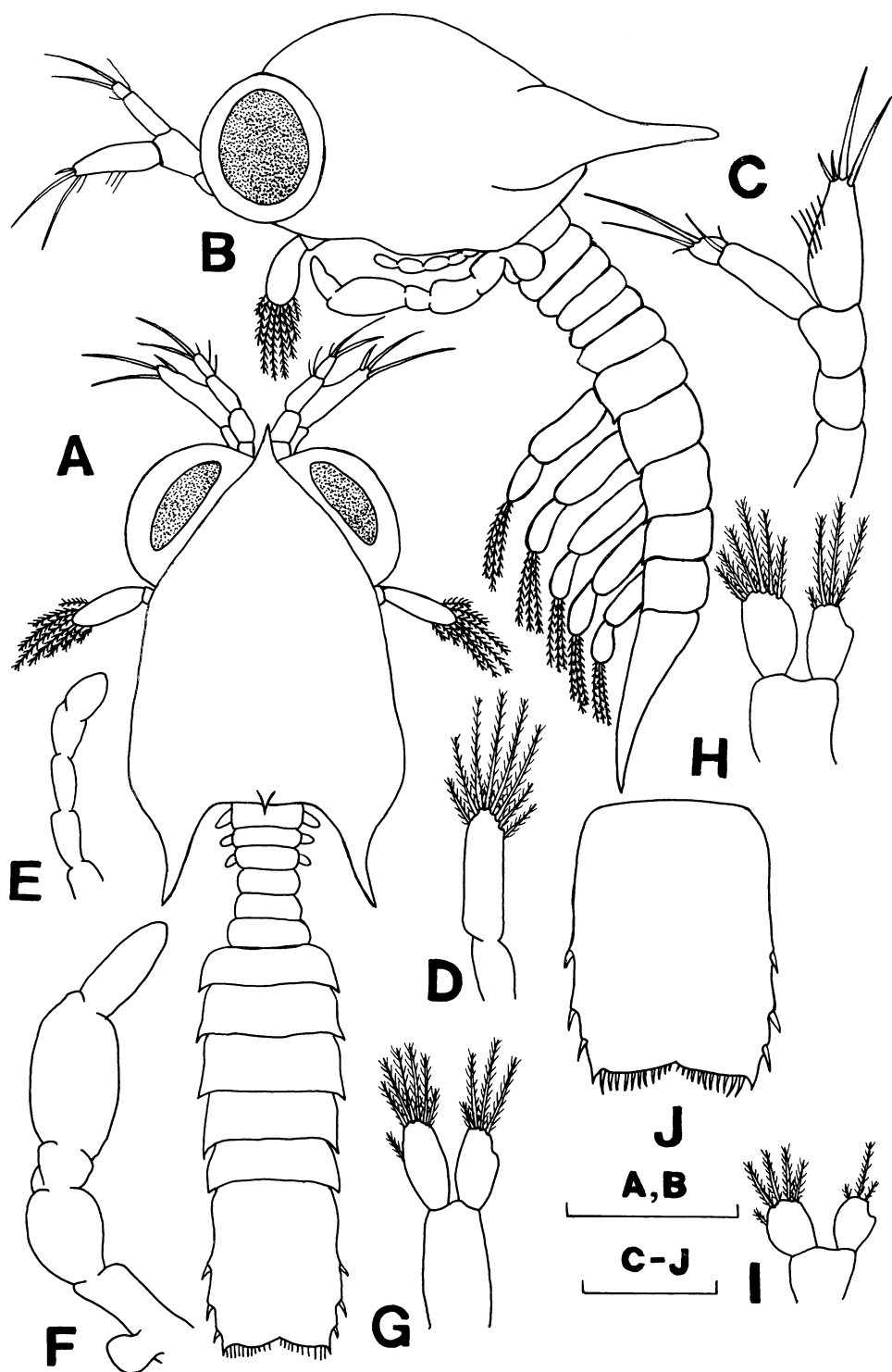


Fig. 1. *Gonodactylus bredini*, Stage I: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, F, first and second maxilliped; G-I, first, third, and fifth pleopods; J, telson. Scales: A, B = 0.5 mm; C-J = 0.25 mm.

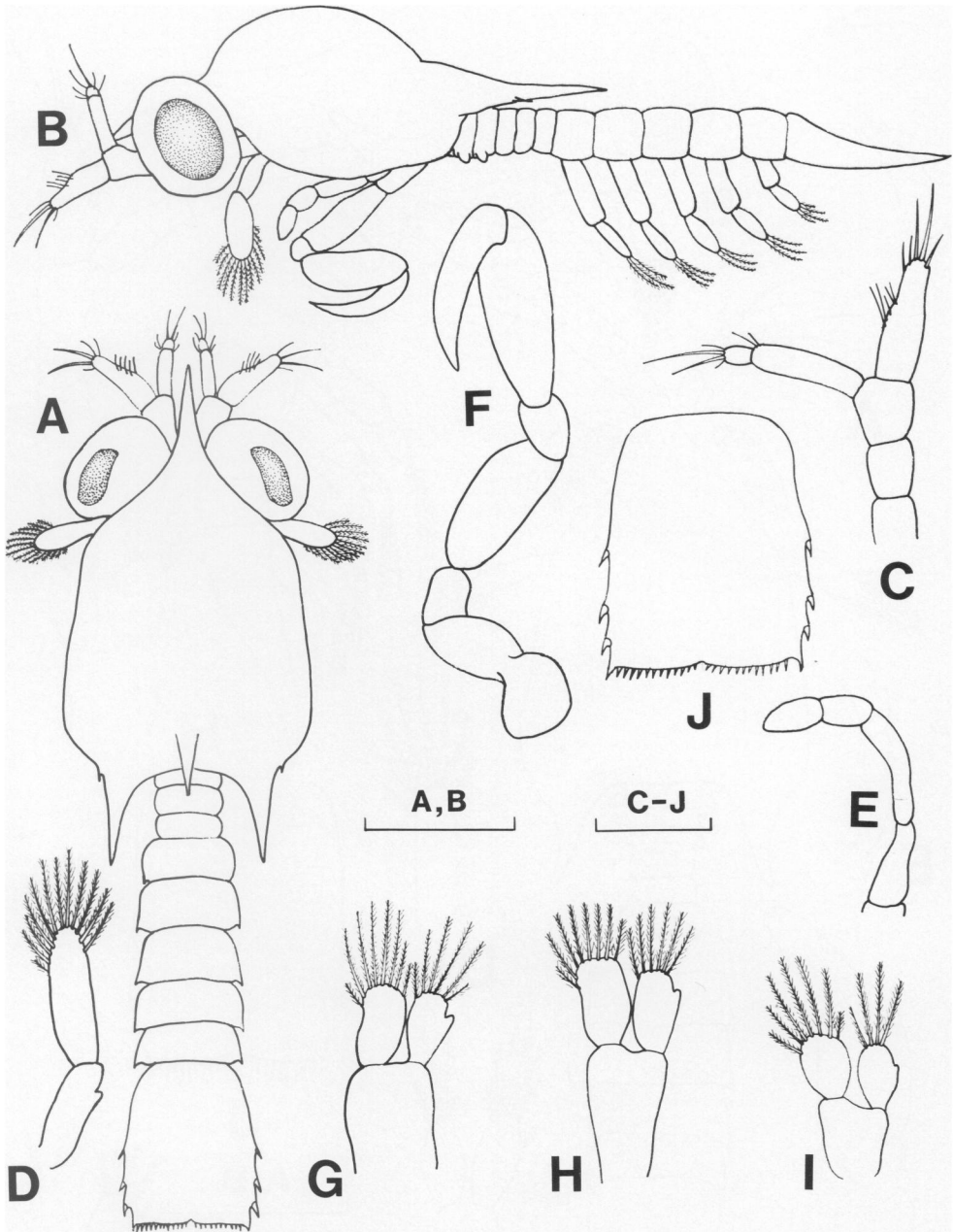


Fig. 2. *Gonodactylus bredini*, Stage II: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, F, first and second maxilliped; G-I, first, third, and fifth pleopods; J, telson. Scales: A, B = 0.5 mm; C-J = 0.25 mm.

Table 4. Pleopod setation of endopodites (Endo-) and exopodites (Exo-) of the larvae (I-VIII) and postlarva (PL) of *Gonodactylus bredini*; N + 1 or 2 indicates number of setae and one or two rudimentary setae.

| Stage | Pleomere | | | | | | | | | |
|-------|------------|----------|------------|------------|----------|----------|------------|------------|----------|------------|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| | Endo- | Exo- | Endo- | Exo- | Endo- | Exo- | Endo- | Exo- | Endo- | Exo- |
| I | 3 or 4 + 1 | 6 + 1 | 3 or 4 + 1 | 6 or 7 + 1 | 3 + 1 | 6 + 1 | 3 + 0 or 1 | 6 + 0 or 1 | 1 + 2 | 3 or 4 + 1 |
| II | 6 | 8 | 6 | 8 or 9 | 6 or 7 | 8 | 5 or 6 + 1 | 8 | 4 | 7 |
| III | 7 | 9 | 8 | 10 | 8 | 9 or 10 | 8 | 9 | 7 | 8 |
| IV | 10 or 11 | 10 or 11 | 10 | 11 or 13 | 10 or 11 | 11 or 13 | 10 | 10 or 11 | 8 or 9 | 9 or 10 |
| V | 11 or 12 | 14 or 15 | 12 | 15 or 16 | 12 | 15-17 | 12 | 14 or 16 | 10 or 11 | 9 or 10 |
| VI | 12 or 13 | 16 or 17 | 13 | 17 or 18 | 13 or 14 | 17-19 | 13 or 14 | 16-18 | 11 or 12 | 14-16 |
| VII | 12 or 13 | 17 or 18 | 14 or 15 | 19 or 20 | 14 or 15 | 20-22 | 15 | 23 | 12 | 18 |
| VIII | 14-16 | 19 or 20 | 14 or 15 | 20 or 21 | 15 | 20-22 | 14 or 15 | 21 or 22 | 13 or 14 | 18 or 19 |
| PL | 14 or 15 | 21 or 22 | 15 or 16 | 21-23 | 15 or 16 | 21-23 | 14 or 15 | 21 or 22 | 12 or 13 | 17 or 18 |

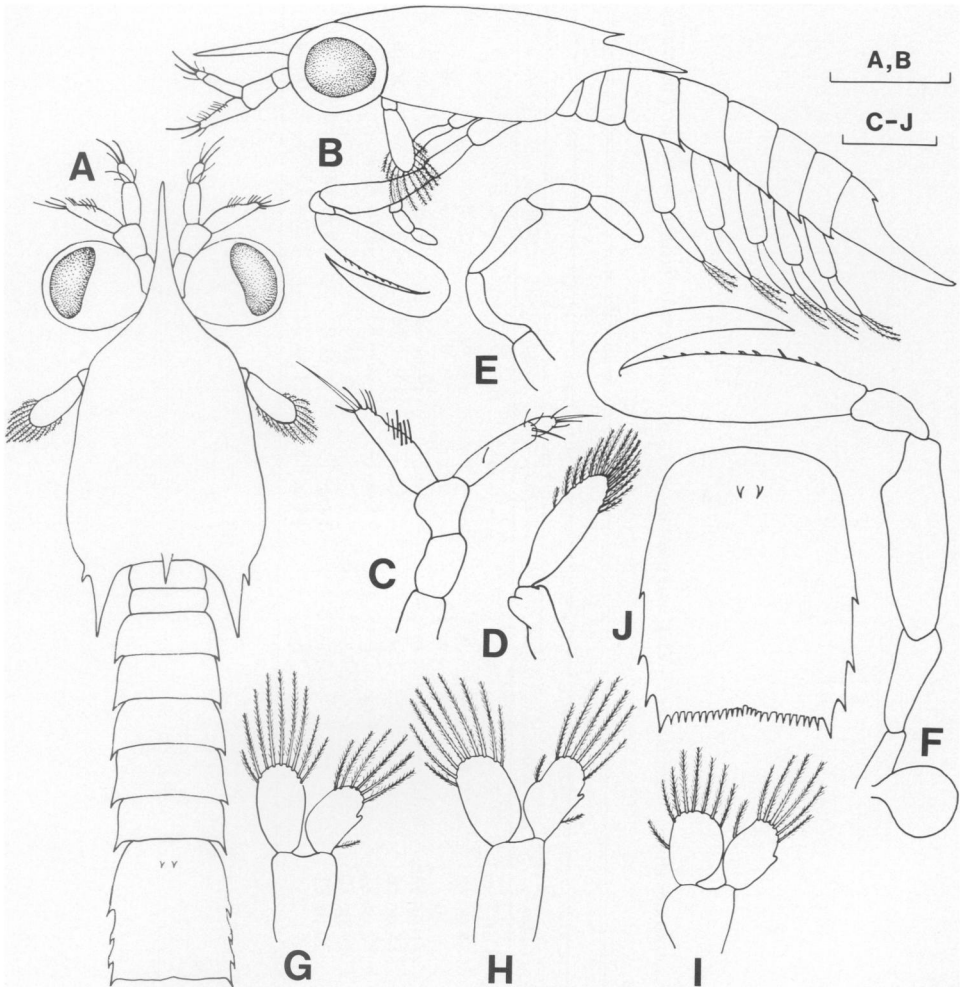


Fig. 3. *Gonodactylus bredini*, Stage III: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, F, first and second maxilliped; G-I, first, third, and fifth pleopods; J, telson. Scales: A, B = 0.5 mm; C-J = 0.25 mm.

Stage III (Third Propelagic)
Fig. 3

Duration: 1-2 days at 25°C. Measurements (mm): TL = 3.1-3.4, CL = 1.4-1.8.

Rostrum (Fig. 3A, B) extending to apical segment of antennular inner flagellum. Carapace (Fig. 3A, B) swollen much less around reduced yolk supply than in previous stage, posterior margin extending to seventh thoracomere, posterolateral spines extending to first pleomere.

Antennular inner flagellum (Fig. 3C) with 4 terminal setae on apical segment, 4 distal and 1 mesial setae on proximal segment; outer flagellum with 2 or 3 terminal setae, 1-3 distal setae, and 5 or 6 aesthetascs arranged in 2 or 3 groups [(1) + 2 + 3]. Antennal scale (Fig. 3D) with 15 or 16 plumose setae.

Mandible absent; maxillule and maxilla present as buds.

First maxilliped (Fig. 3E) longer than in previous stage. Second maxilliped (Fig. 3F) armed with 8–10 denticles on flexor margin of propodus. Third, fourth, and fifth maxillipeds present as elongate buds.

Pereiopods absent.

Pleopods (Fig. 3G–I) each with seta prior to appendix interna of exopodite, but sometimes absent on fifth pleopods; setation summarized in Table 4. Pleotelson (Fig. 3J) with 3 fixed pairs of lateral spines and 3 minute spinules (not shown) between each pair of denticles.

Stage IV (First Pelagic)

Fig. 4

Duration: 6–8 days at 25–30°C. Measurements (mm): TL = 3.9–4.0, CL = 2.2–2.5.

Rostrum (Fig. 4A, B) extending well beyond antennular flagella, armed with 6 ventral spinules. Carapace (Fig. 4A, B) armed with anterolateral spines, lateral margin lined ventrally with 24–27 minute spinules (not shown); posterior margin of carapace extending to first pleomere, posterolateral spines extending to third pleomere. Eyes pigmented green rather than black as in prior instars.

Antennule (Fig. 4C) with apical segment of inner flagellum bearing 4 setae, proximal segment bearing 4 distal and 1 mesial setae; outer segment bearing 3 distal setae and 6 aesthetascs arranged in 3 groups (1 + 2 + 3). Antenna (Fig. 4D) bearing bud of endopodite, scale with 16 or 17 plumose setae.

Mandible (Fig. 4E) with 9 denticles. Maxillule (Fig. 4F) with proximal endite bearing 7 denticles; distal endite with 1 strong and 2 weaker spines on distal margin; distal margin also bearing 1 long proximal seta. Maxilla (Fig. 4G) with 3 pairs of setae.

First maxilliped (Fig. 4H) with small dactyl present; propodus bearing 1 pair of strong and 1 pair of weak setae distally, and 3 pairs of hooked setae; carpus with 2 or 3 plumose distal setae; merus with 1 distal plumose seta. Second maxilliped (Fig. 4I) with dactyl bearing minute serrations on distal portion of cutting margin and 6 setae; propodus with 1 large proximal spine, 3–5 small spines, and 19–21 denticles on cutting margin; carpus with or without 1 distal seta; blue chromatophore at articulation of propodus and dactyl. Third, fourth, and fifth maxillipeds present as elongate buds.

Pereiopods present as buds.

Sixth pleomere (Fig. 4A, B) articulated partially from telson (Fig. 4J–L); pleopods with exopodite bearing 1 seta proximal to appendix interna, but sometimes absent on first pleopods; setation summarized in Table 4. Pleotelson (Fig. 4M) with 4 minute spinules between each pair of denticles.

Stage V (Second Pelagic)

Fig. 5

Duration: 4–8 days at 25–30°C. Measurements (mm): TL = 5.1–5.2, CL = 2.7–3.1.

Rostrum (Fig. 5A, B) as in previous stage. Carapace (Fig. 5A, B) with 16–22 minute spinules (not shown) ventrally on posterior portion of lateral margin.

Antennular inner flagellum (Fig. 5C) with 5 (2 strong and 3 weak) terminal setae, 4–6 distal and 2 mesial setae on proximal segment; outer flagellum divided

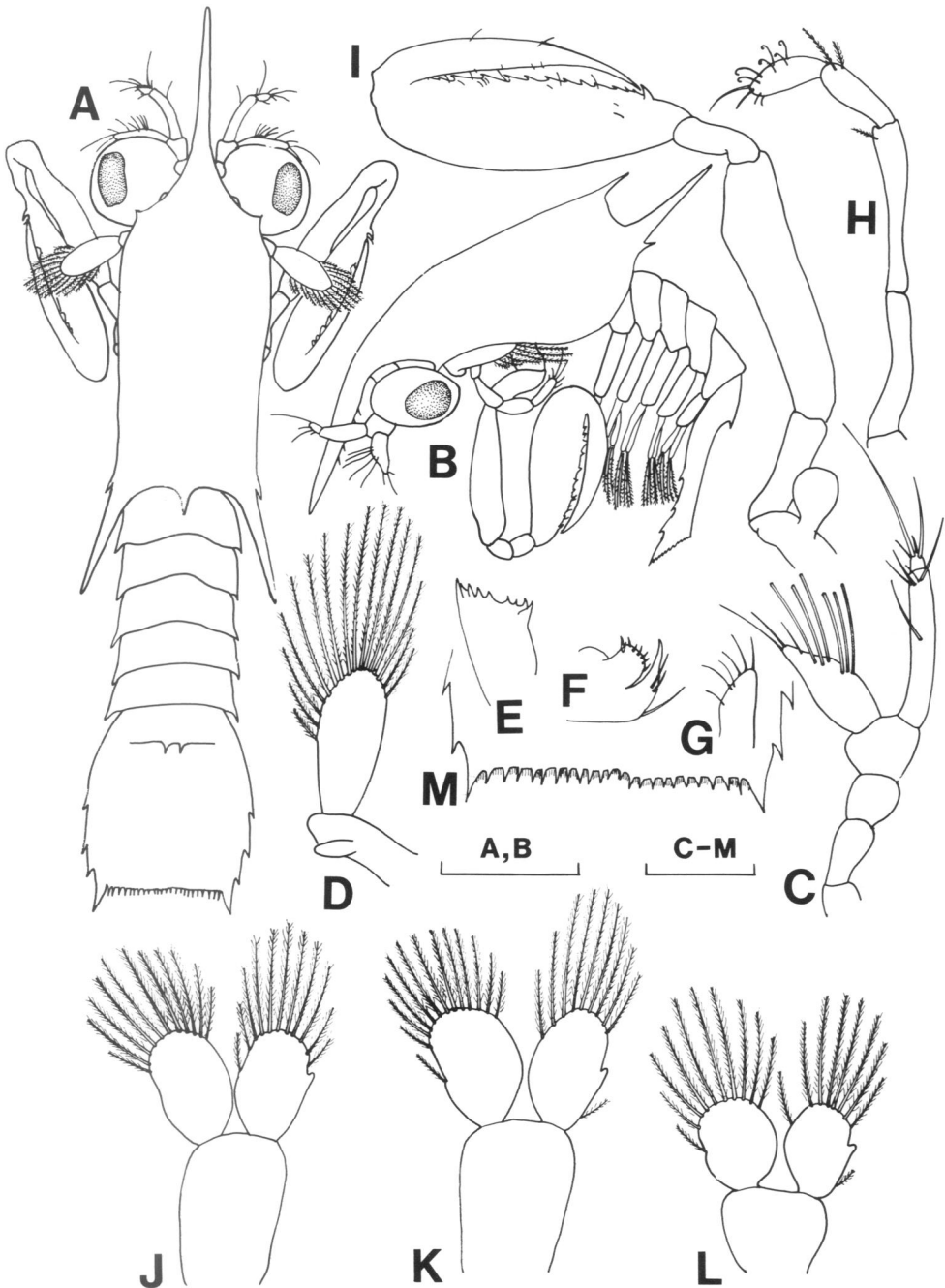


Fig. 4. *Gonodactylus bredini*, Stage IV: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, I, first and second maxilliped; J-L, first, third, and fifth pleopods; M, telson. Scales: A, B = 0.5 mm; C-M = 0.25 mm.

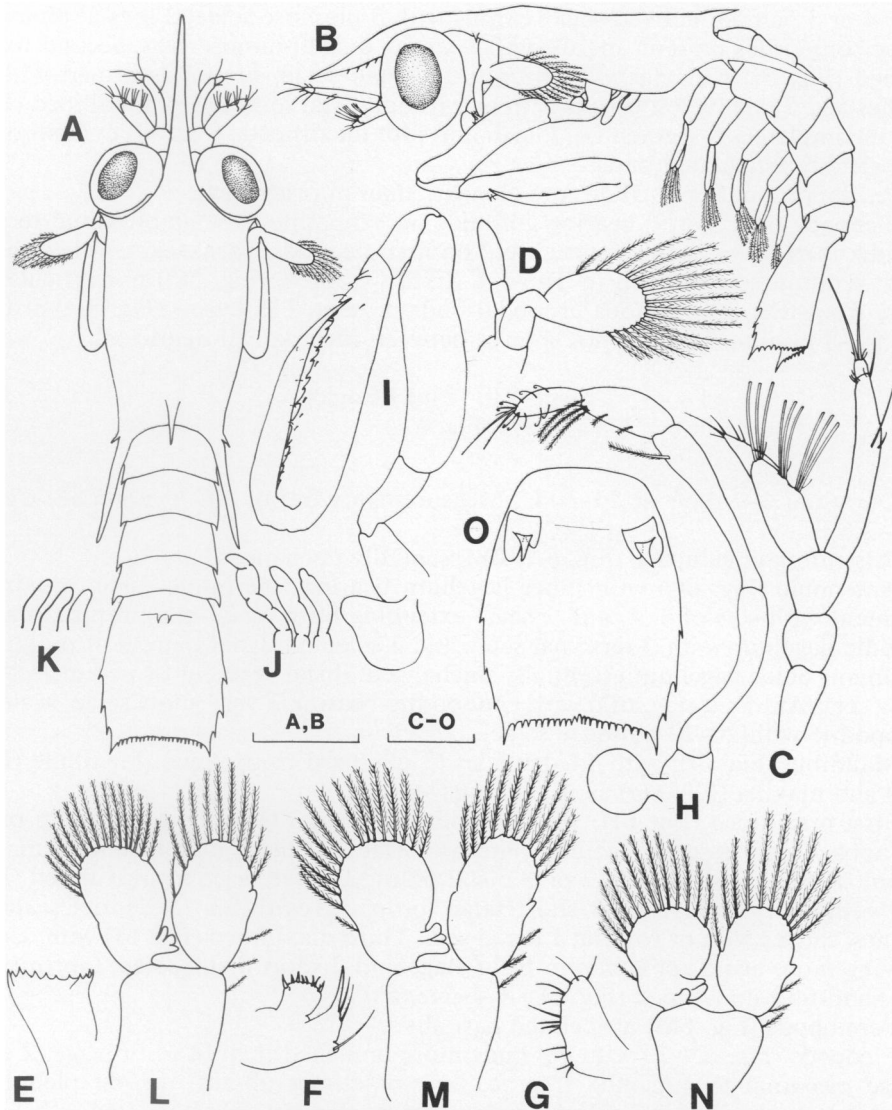


Fig. 5. *Gonodactylus bredini*, Stage V: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, I, first and second maxillipeds; J, third-fifth maxillipeds; K, first-third pereopods; L-N, first, third, and fifth pleopods; O, telson, ventral view. Scales: A, B = 0.5 mm; C-O = 0.25 mm.

into 2-segmented middle flagellum and broader outer flagellum, middle flagellum bearing 4 or 5 distal setae, outer flagellum bearing 8 or 9 aesthetascs arranged in 3 groups of 2 or 3, each row of aesthetascs accompanied by single seta. Antenna (Fig. 5D) with 3-segmented endopodite, scale with 16-18 plumose setae.

Mandible (Fig. 5E) with 13 denticles (1 obscured from view). Maxillule (Fig. 5F) with proximal endite bearing 9 stout marginal spines and 1 or 2 small mesial spines; distal endite unchanged. Maxilla (Fig. 5G) with 12-15 marginal setae.

First maxilliped (Fig. 5H) with propodus bearing 1 terminal pair of strong setae

and 4 or 5 pairs of hooked setae; carpus with 3 plumose setae, 2 mesial plumose setae sometimes present; merus with 1 strong distal plumose seta. Second maxilliped (Fig. 5I) with dactyl bearing 6–11 small setae; propodus armed with 3 spines and 22 denticles; carpus with or without distal seta. Third maxilliped (Fig. 5J) incompletely 5-segmented, fourth and fifth maxillipeds (Fig. 5J) evident only as partially articulated buds.

Pereiopod buds (Fig. 5K) more elongate than in prior stage.

Pleopods (Fig. 5L–N) bearing gill buds on exopodite; 2 setae proximal to appendix interna, but sometimes absent on first pleopods; basal segment bearing 1 seta; setation summarized in Table 4. Sixth pleomere (Fig. 5O) not articulated fully from telson, triramous uropodal buds present. Pleotelson (Fig. 5O) armed with 4–8 minute spinules (not shown) between each pair of denticles.

Stage VI (Third Pelagic)

Fig. 6

Duration: 5–7 days at 25–30°C. Measurements (mm): TL = 5.8–6.36, CL = 3.3–3.6.

Rostrum and carapace (Fig. 6A, B) essentially unchanged.

Antennule (Fig. 6C) with inner flagellum bearing 5 terminal setae, proximal segment with sets of 4, 4, and 2 setae extending from distal margin proximally; middle flagellum with 3 terminal setae and 3 setae on distal margin of proximal segment; outer flagellum essentially unchanged; distal segment of peduncle with long seta. Antenna (Fig. 6D) with endopodite bearing 2 very short setae, scale of exopodite with 20–22 plumose setae.

Mandible (Fig. 6E) with 14 denticles (3 obscured from view). Maxillule (Fig. 6F) and maxilla (Fig. 6G) as in previous stage.

First maxilliped (Fig. 6H) with propodus bearing 3 terminal setae and 5 pairs of hooked setae; carpus with 4 plumose setae on distal margin and 3 mesial plumose setae; merus with 2 or 3 distal plumose setae. Second maxilliped (Fig. 6I) with dactyl bearing 6–8 short setae; propodus with 23–25 denticles and 3 spines; carpus with or without 1 distal seta. Third maxilliped (Fig. 6J) with dactyl having more acute apex than in prior stage and 2 short distal setae; fourth (Fig. 6K) and fifth maxilliped (Fig. 6L) 4-segmented.

Pereiopods (Fig. 6M) articulated partially.

Pleopods (Fig. 6N–P) with gill buds more branched than in prior stage; 2 or 3 setae proximal to appendix interna, but sometimes absent on first pleopods; setation summarized in Table 4. Sixth pleomere (Fig. 6A, B) articulated fully from telson; uropods bearing 1 spine and 3 setae on exopod, 2 or 3 setae on endopod, basal prolongation nearly extending to second lateral spine of telson and bearing medial spinule. Telson (Fig. 6Q) essentially unchanged.

Stage VII (Fourth Pelagic)

Fig. 7

Duration: 8–13 days at 25–30°C. Measurements (mm): TL = 6.5–7.2, CL = 3.3–3.6.

Rostrum and carapace (Fig. 7A, B) essentially unchanged.

Antennule (Fig. 7C) with 3-segmented inner flagellum bearing 5 terminal setae, 4–6 setae on distal margin of penultimate segment, and groups of 3 or 4, 0–4, 2–4, and 0–3 setae extending from distal margin proximally on antepenultimate

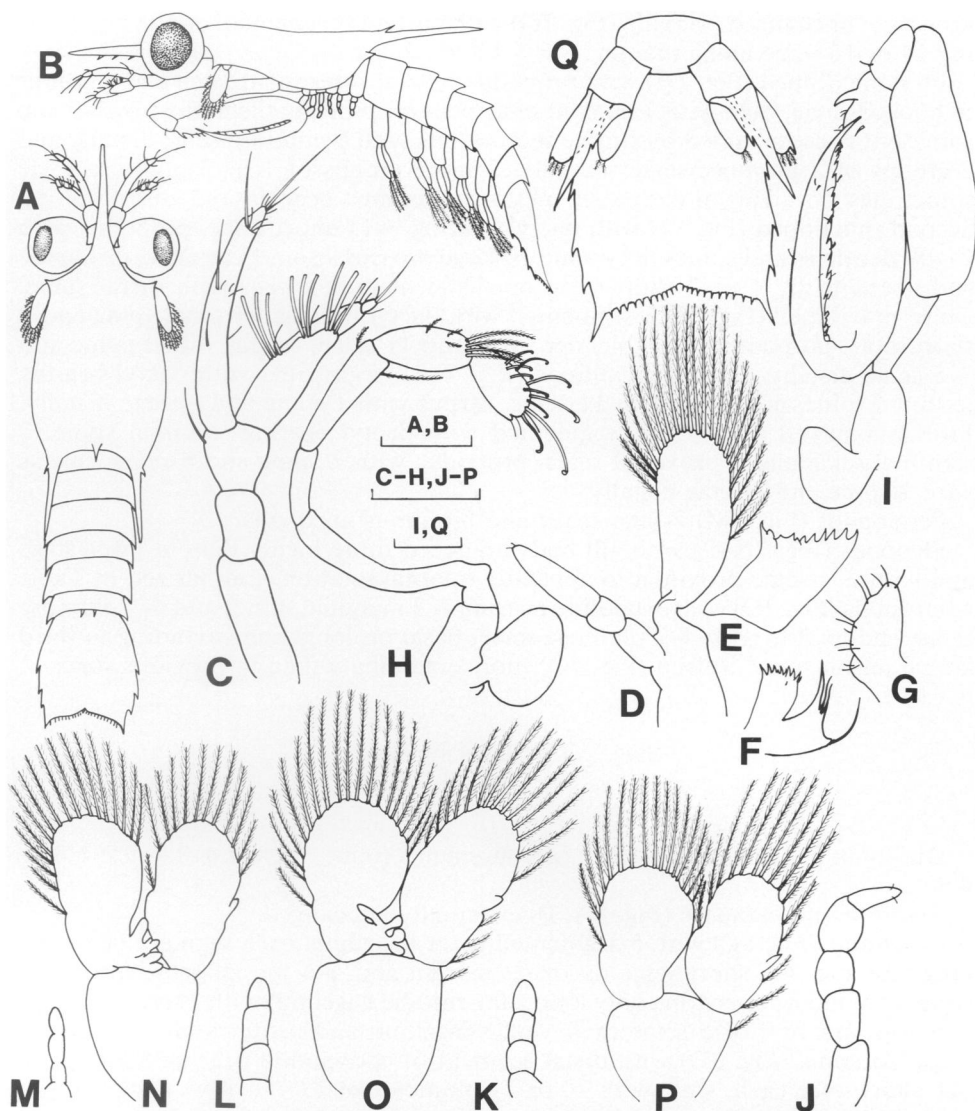


Fig. 6. *Gonodactylus bredini*, Stage VI: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-L, first-fifth maxillipeds; M, first pereopod; N-P, first, third, and fifth pleopods; Q, telson, ventral view. Scales: A, B = 1.0 mm; C-Q = 0.5 mm.

segment; middle flagellum with 3 terminal setae, proximal segment with groups of 3 or 4, 2 or 3, 2 or 3, 2-5, 2-5, and 0-3 setae extending from distal margin proximally; outer flagellum essentially unchanged; each peduncular segment sometimes bearing up to 6 setae. Antenna (Fig. 7D) with endopodite bearing 2 or 3 short terminal setae and as many as 4 groups of 1-3 setae present; scale with 20 or 21 plumose setae.

Mandible (Fig. 7E) essentially unchanged. Maxillule (Fig. 7F) with proximal endite bearing 10 or 11 stout marginal spines and 1 or 2 small mesial spines,

otherwise unchanged. Maxilla (Fig. 7G) with partially segmented endite and bearing 15 or 16 setae along margin.

First maxilliped (Fig. 7H) with propodus bearing 4 terminal setae and 5 groups of hooked setae, each with 3 hooked setae per group except distalmost with 2 and sometimes accompanied by simple seta; carpus with 6 plumose setae distally and 2 groups of 2 plumose setae mesially, 2 more groups of 1 or 2 plumose setae sometimes occurring proximally; merus sometimes bearing 1–3 distal spines. Second maxilliped (Fig. 7I) with dactyl bearing 9–11 short setae; propodus with 27–30 denticles and spines not including large proximal spine; carpus with 1 spine and occasionally 1 or 2 short setae on distal margin; merus with distal spine. Third maxilliped (Fig. 7J) 6-segmented with dactyl bearing terminal spine and 2 short setae, propodus with 1 slender spine and 11 setae, carpus with 1 spine and 3–5 setae distally. Fourth maxilliped (Fig. 7L) 6-segmented with dactyl bearing terminal spine, propodus with 11 setae, carpus with 1 spine and 2 setae distally. Fifth maxilliped (Fig. 7K) 6-segmented with dactyl bearing terminal spine, 2 terminal setae and 2 proximal setae, propodus with 1 spine and 6 setae, carpus with 1 spine and 2 setae distally.

Pereiopods (Fig. 7M) 2-segmented and biramous unequally.

Pleopods (Fig. 7N–P) with gill buds branched more highly than in prior stage and with 2–4 setae proximal to appendix interna; setation summarized in Table 4. Uropods (Fig. 7Q) with exopodite bearing 1–3 marginal spines and 4–7 plumose setae, endopodite with 4–7 plumose setae, basal prolongation extending to third lateral telson spine. Telson (Fig. 7Q) more emarginate than in previous stage.

Stage VIII (Supernumerary)

Fig. 8

Duration: 5–8 days at 25–30°C. Measurements (mm): TL = 7.4–7.9, CL = 4.1–4.5.

Rostrum and carapace (Fig. 8A, B) essentially unchanged.

Antennule (Fig. 8C) with 5-segmented inner flagellum, each segment bearing 1 long seta and 4–6 short setae on distal margin and 4–6 mesial setae (proximal segment sometimes bearing only long seta); middle flagellum with 3 terminal setae and 7 groups of 4 or 5 setae each; outer flagellum and peduncle as in previous stage. Antenna (Fig. 8D) with distal segment of endopodite bearing 5 groups of 4–6 short setae each, scale with 20 or 21 plumose setae.

Mandible (Fig. 8E) essentially unchanged.

Maxillule (Fig. 8F) with proximal endite bearing 12 or 13 stout marginal spines and 2 or 3 small mesial spines, otherwise unchanged. Maxilla (Fig. 8G) articulated better than in previous stage and with 27 marginal setae.

First maxilliped (Fig. 8H) essentially unchanged except carpus sometimes bearing as many as 8 plumose distal setae followed by 4 groups of 4 plumose setae proximally. Second maxilliped (Fig. 8I) essentially unchanged. Third maxilliped (Fig. 8J) subchelate, dactyl with 5 or 6 short setae, propodus with 1 or 2 stout spines and 20 smaller spines, carpus with 1 stout spine and 4 smaller spines (2 obscured from view). Fourth maxilliped (Fig. 8K) subchelate, 4 short setae on dactyl, 1 stout spine and 13 smaller spines on propodus, and 1 stout spine and 4 smaller spines on carpus. Fifth maxilliped (Fig. 8L) subchelate, dactyl with 5 or 6 short setae, propodus with 1 stout spine and 9 smaller spines, carpus with 1 stout spine and 3 smaller spines.

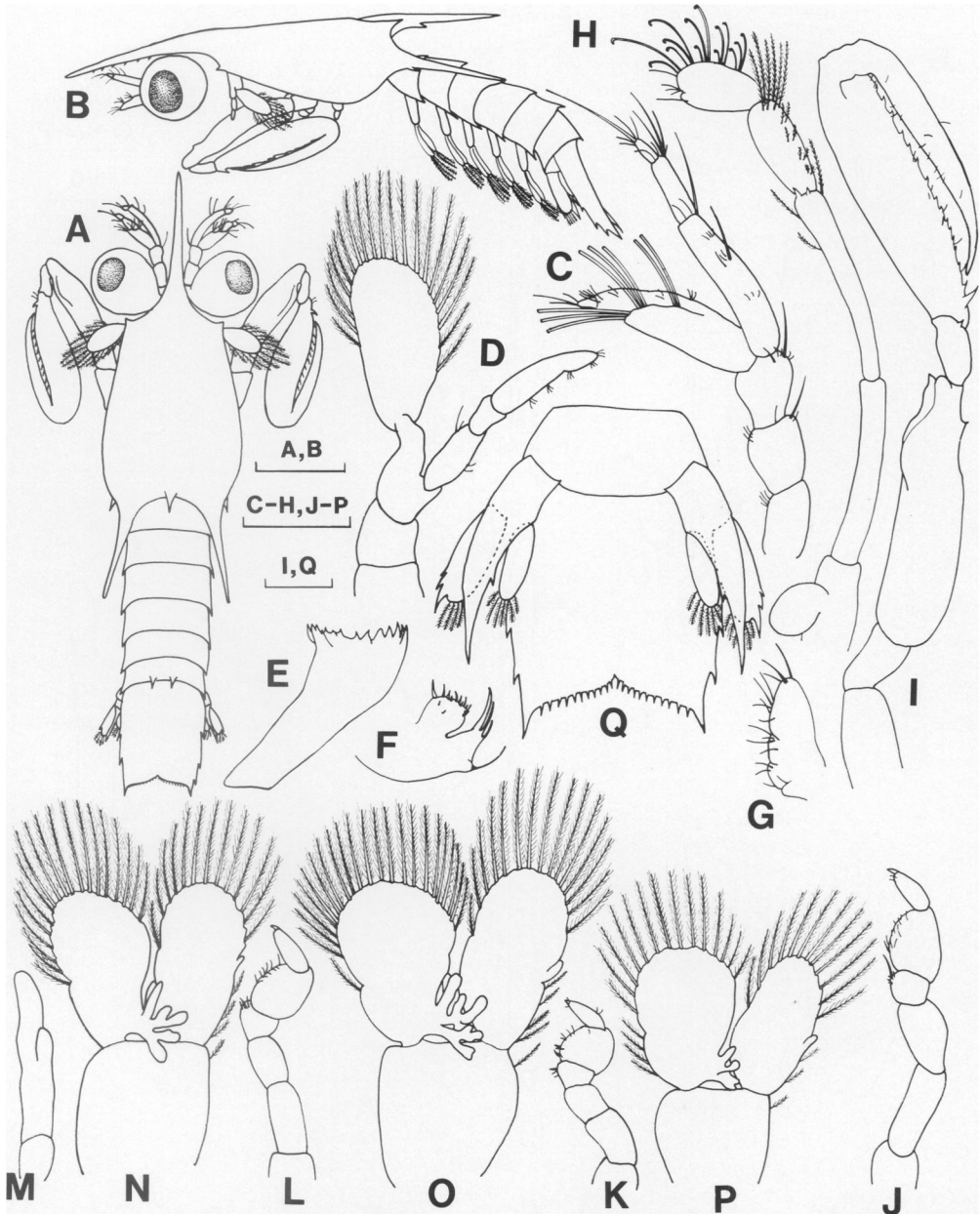


Fig. 7. *Gonodactylus bredini*, Stage VII: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-L, first-fifth maxillipeds; M, first pereiopod; N-P, first, third, and fifth pleopods; Q, telson, ventral view. Scales: A, B = 1.0 mm; C-Q = 0.5 mm.

Pereiopods (Fig. 8M) with 2-segmented endopodite and slender exopodite.

Pleopods (Fig. 8N-P) with gill buds more branched than in previous stage; 2-4 setae proximal to appendix interna, setation summarized in Table 4. Uropods and telson (Fig. 8Q) essentially unchanged.

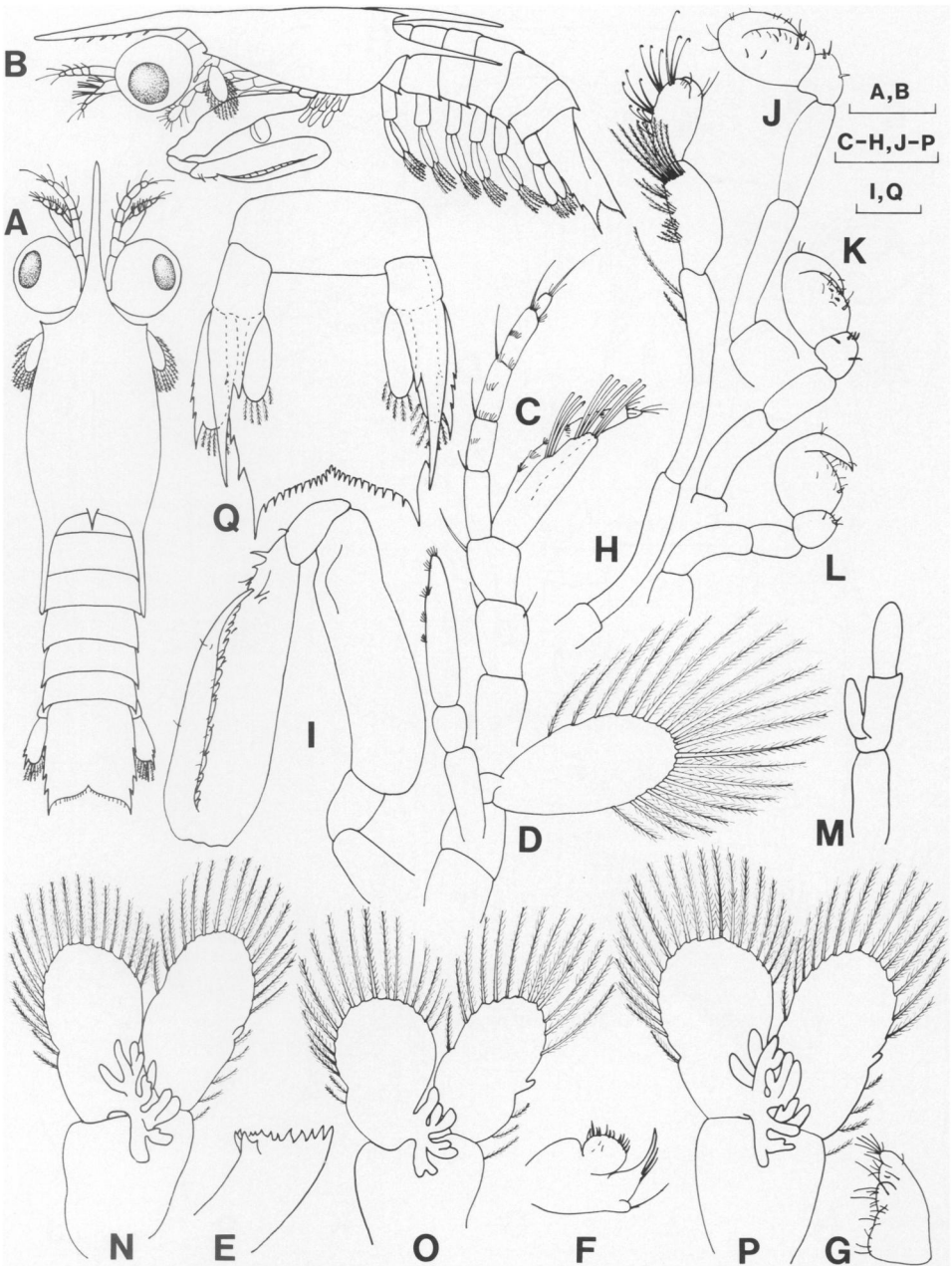


Fig. 8. *Gonodactylus bredini*, Stage VIII: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-L, first-fifth maxillipeds; M, first pereopod; N-P, first, fifth, and third pleopods; Q, telson, ventral view. Scales: A, B = 1.0 mm; C-Q = 0.5 mm.

Postlarva Fig. 9

Duration: 9–14 days at 25–30°C. Measurements (mm): TL = 6.5–7.4, CL = 2.0–2.5.

Rostrum (Fig. 9A–C) movable, triangular, concave laterally, rounded at proximal corners, apex acute. Carapace (Fig. 9A–C) lacking spines, extending to sixth thoracomere, gastric grooves distinct.

Antennule (Fig. 9D) with inner flagellum 8-segmented, each segment bearing 4–7 setae on distal margin; middle flagellum 7-segmented, each segment bearing 5–9 setae on distal margin, proximal segment sometimes with mesial seta; outer flagellum essentially unchanged; basal segment of peduncle with 10–17 short proximal setae. Antenna (Fig. 9E) with 9-segmented endopodite, each segment bearing from 2–12 short setae on distal margin, proximal segment bearing 4–8 mesial setae; scale bearing 21 plumose setae.

Mandible (Fig. 9F) and maxillule (Fig. 9G) essentially unchanged. Maxilla (Fig. 9H) with 5-segmented endopodite bearing 38–44 setae.

First maxilliped (Fig. 9I) with 1 pair of brushlike terminal setae, otherwise essentially unchanged except carpus sometimes bearing as many as 10 distal plumose setae. Second maxilliped (Fig. 9J) with propodus bearing stout articulated spine proximally, 16–18 denticles, and 4 smaller spines. Third, fourth, and fifth maxillipeds (Fig. 9K–M) with dactyl bearing 2 or 3 setae; propodus with 11–13 denticles, 8–10 slender spines, and 1 stout spine; carpus with 7–10 slender spines; merus with 5–9 setae.

Pereiopods (Fig. 9N) with distal segment of endopodite bearing 9–12 slender spines and 1–3 setae, proximal segment with 2 or 3 slender spines and 1 or 2 setae; exopodite with 8–11 distal setae and 1 proximal seta.

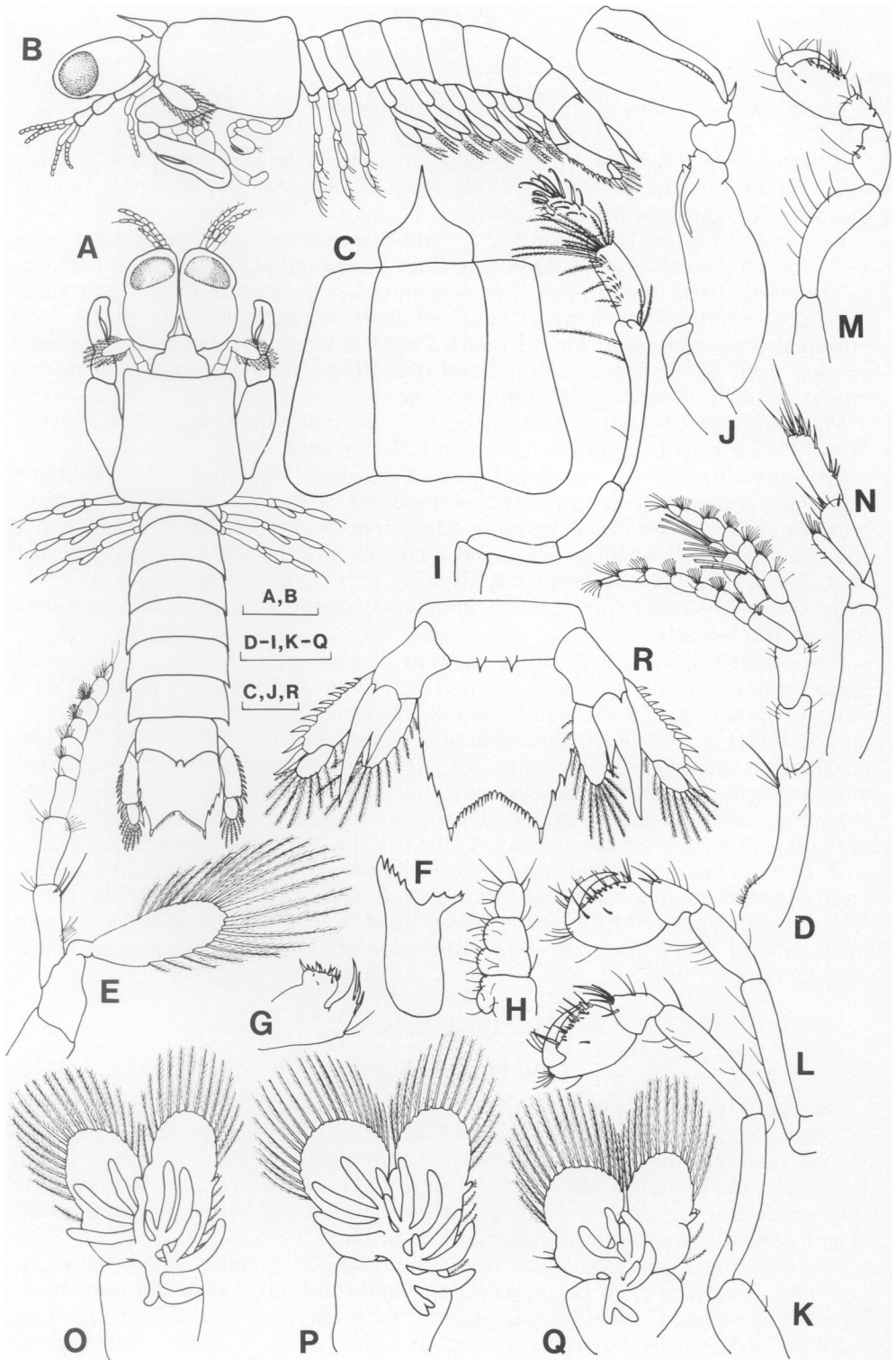
Pleopods (Fig. 9O–Q) with gill buds of increased size and complexity; 2–5 setae proximal to appendix interna, appendix interna bearing 2 or 3 short hooked setae, basal segment with short seta, setation summarized in Table 4. Uropods (Fig. 9R) extending nearly to posterolateral spines of telson; exopodite with 10 articulated marginal spines and articulated distal lobe bearing 10 plumose setae; endopodite with 11 or 12 plumose setae and 10 or 13 rudimentary setae along outer margin; basal segment bearing bifurcated spine and short spine on distal margin. Telson (Fig. 9R) with posterior margin concave, much narrower than anterior margin, lined with 11 or 12 denticles along either side of midline, posterolateral spines articulated.

DISCUSSION

Adult Reproduction

The reproductive and maternal behavior of *Gonodactylus bredini* was generally as described by Dingle and Caldwell (1972) for *G. bredini* in Bermuda, although the interactions appeared to be somewhat less aggressive than described for the Bermudan population. Caldwell and Dingle (1976) observed that *Gonodactylus* spp. with white meral spots, like *G. bredini*, are less aggressive than those with brightly colored spots or white spots edged in black.

The duration from copulation to larval emergence is about 39–44 days (24–26°C) for *G. bredini* from Bermuda (Dingle and Caldwell, 1972), but only 30–31 days for those from North Carolina (28°C). *Gonodactylus bredini* from Bermuda required 10 days between copulation and spawning, which is similar to the findings



reported here (9 days). However, 30–35 days were required from spawning to larval emergence for *G. bredini* from Bermuda, whereas only 20–21 days were necessary for those from North Carolina. Other gonodactylids also brood their eggs (from spawning to the emergence of pelagic larvae from the burrow) for about three weeks at 19–26°C (Reaka, 1979). Embryonic development of the squillid *Oratosquilla oratoria* requires two weeks at 26°C (Hamano and Matsuura, 1984). Reports on the time elapsing between consecutive spawnings of other gonodactylids were not found. However, *O. oratoria* spawns about 40 days apart (Hamano and Matsuura, 1984), which falls within the range (32–91 days) for *G. bredini* from North Carolina.

Larval Development

As with other members of the genus *Gonodactylus*, the larval development of *G. bredini* is composed of three propelagic and four pelagic stages. The only congener of *G. bredini* in the Western Atlantic for which larvae have been described is *G. oerstedii* (Manning and Provenzano, 1963; Provenzano and Manning, 1978). The larvae of the two species are very similar, but can be distinguished by slight differences in setation of the antennules, antennae, first maxillipeds, and pleopods. Pleopod setation in propelagic stages of *G. oerstedii* was generally greater than in *G. bredini*, but after setae proximal to the appendix interna began occurring in stage IV, the setal counts were equal or greater for *G. bredini* than for *G. oerstedii*. Differences in pleopod setation of pelagic larvae could have resulted if Provenzano and Manning (1978) did not include setae proximal to the appendix interna in their counts.

Rearing stomatopod larvae by conventional methods results in poor survival. Because bacterial, fungal, or protistan infestations were not observed to afflict the larvae, it is probable that dietary insufficiencies are responsible for the poor larval survival obtained for both species of stomatopods. The larvae survived well for two molts after the yolk supply was depleted.

The entire larval development takes approximately 35–40 days after seven instars when reared at 25°C, and is comparable to that determined by Provenzano and Manning (1978) for *G. oerstedii* (35 days at 25°C). The pelagic larval duration of both gonodactylids is much shorter than that of squillids or lysiosquillids, which usually undergo nine pelagic stages (Alikunhi, 1950; Gohar and Al-Kholy, 1957; Pyne, 1972; Morgan and Provenzano, 1979) and take approximately six weeks to develop at comparable temperatures (Morgan, 1980). The lysiosquillid *Heterosquilla tricarinata* has an abbreviated larval development and has only one propelagic and two pelagic stages, but the larval duration is still approximately 60–70 days at 15°C (Greenwood and Williams, 1984).

The propelagic stages remained within the burrow and were positively thigmotactic and negatively phototactic as found by Dingle (1969) for *G. bredini* from Bermuda, with the exception that the third propelagic stage was positively phototactic. Dingle (1969) noted that the thigmotactic response took precedence over the phototactic, which would keep the photopositive third stage larvae in the burrow. Propelagic development lasted 5–6 days at 25–30°C for *G. bredini*, and

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Fig. 9. *Gonodactylus bredini*. Postlarva: A, dorsal view; B, lateral view; C, carapace; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I–M, first–fifth maxillipeds; N, first pereopod; O–Q, first, third, and fifth pleopods; R, telson, ventral view. Scales: A, B = 1.0 mm; C–R = 0.5 mm.

7–8 days at 26–29°C for *G. oerstedii* (Manning and Provenzano, 1963). The abbreviated propelagic larval development of the lysiosquillid *H. tricarinata* was 30 days at 15°C (Greenwood and Williams, 1984).

This study provides the first unequivocal evidence of flexibility in the number of larval stages for the Stomatopoda. The high degree of variability in the last larval instars of *Squilla empusa* and *Chorisquilla tuberculata* suggested the occurrence of supernumerary instars; however, because the larval developments were reconstructed from the plankton, supernumerary instars could not be described (Michel and Manning, 1972; Morgan and Provenzano, 1979). Flexibility in the timing of metamorphosis probably permits a greater degree of habitat selection, because larvae may not settle unless the appropriate substrate cue is present (Chia and Bickell, 1978; Sandifer and Smith, 1979; Hudon *et al.*, 1983). Alikunhi (1950) and Morgan (1977) have described the last instars of squillids digging pits in the substrate with their second maxillipeds, apparently testing the suitability of the substrate for burrowing.

Differences Among Populations

Sexual color dimorphism possibly may occur in populations of *G. bredini* from Bermuda (Dingle, 1964) and North Carolina, but not from Caribbean populations (Manning, 1969). Five color morphs were described by Dingle (1964) for *G. bredini* collected from Bermuda. However, only the green color pattern from the Bermudan population was remotely similar to that of individuals collected from North Carolina, and the red color pattern was not observed in Bermuda. Color patterns of *G. bredini* from Caribbean populations are distinctive from both northern populations (Manning, 1969). Other morphological characters distinguish five distinct populations of *G. bredini* in the Western Atlantic (Manning, 1969). Furthermore, Gurney (1946) described the posterior margin of the telson as having 28 spinules, whereas the postlarvae from North Carolina usually had a total of 22 but not more than 24. Gurney also described the carapace as being without longitudinal grooves which were present in the specimens from North Carolina. Lastly, the terminal notch in the maxilla of Gurney's specimen was not present in those described here.

Gonodactylids generally possess limited dispersal ability, small geographic ranges, and high evolutionary rates compared to other stomatopods (Reaka, 1980). Differences in the color patterns, degree of aggressiveness, development times, and postlarval and adult morphological traits between Bermudan and North Carolinian populations of *G. bredini* may indicate that two species exist.

ACKNOWLEDGEMENTS

We thank Kirsti Sandoy and William Kirby-Smith who collected the stomatopods while conducting a faunal survey for the Bureau of Land Management (contract number AA551-CT1-18), and made them available to us. We are grateful to John Costlow for use of the facilities at the Duke University Marine Laboratory. We are also grateful to Raymond Manning and Marjorie Reaka for commenting on the manuscript.

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ANNOUNCEMENT

Call for nominations for new members of the International Commission on Zoological Nomenclature

The following members of the Commission reach the end of their terms of service at the close of the XXIII General Assembly of the International Union of Biological Sciences to be held in Canberra in October 1988: Prof. Dr. R. Alvarado (Spain; specialist field Echinodermata); Dr. G. Bernardi (France; Lepidoptera); Prof. C. Dupuis (France; Heteroptera), and Dr. L. B. Holthuis (The Netherlands; Crustacea). A further vacancy arises from the death of Prof. B. S. Zheng (People's Republic of China; Ichthyology).

The addresses and specialist fields of the present members of the Commission may be found in the *Bulletin of Zoological Nomenclature* 44(1):2–3 (March 1987). Under Article 3*b* of the Commission's Constitution a member whose term of service has terminated is not eligible for immediate reelection unless the Council of the Commission has decided to the contrary.

The Commission now invites nominations, by any person or institution of candidates for membership. Article 2*b* of the Constitution prescribes that:

“The members of the Commission shall be eminent scientists, irrespective of nationality, with a distinguished record in any branch of zoology, who are known to have an interest in zoological nomenclature.”

(It should be noted that “zoology” here includes the applied biological sciences (medicine, agriculture, etc.) which use zoological names.)

Nominations, giving the dates of birth, nationality, and qualifications (by the criteria mentioned above) of each candidate should be sent by 31 March 1988 to: The Executive Secretary, International Commission on Zoological Nomenclature, % British Museum (Natural History), Cromwell Road, London, SW7 5BD, United Kingdom.