

LARVAL DEVELOPMENT OF *GALATHEA ROSTRATA* UNDER LABORATORY CONDITIONS, WITH A DISCUSSION OF LARVAL DEVELOPMENT IN THE GALATHEIDAE (CRUSTACEA ANOMURA)¹

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ABSTRACT

The complete larval development of the western Atlantic anomuran crab, *Galathea rostrata*, consists of four or five zoeal stages, and a single megalopal stage, based on larvae cultured under laboratory conditions. Variation in the duration and number of zoeal stages appears to be temperature-dependent, with larvae reared at 15°C developing through five zoeal stages and attaining megalopa in 52 days, whereas larvae cultured at 20°C passed through four or five zoeal stages, reaching megalopa in 18 or 23 days, respectively. At 20°C some third stage zoeae molted to a "regular" fourth zoeal stage, without pleopods, which was followed by a subsequent fifth stage before reaching megalopa. Other zoeae molted to an "advanced" fourth stage, possessing pleopods, which subsequently molted directly to megalopa, bypassing stage V completely. The variation noted in larval development in other galatheid genera is briefly discussed, and a provisional synopsis of morphological characters of systematic value is provided for their identification.

The anomuran crab genus *Galathea* is presently represented in the western North Atlantic by two species, *G. agassizii* and *G. rostrata* (A. Milne Edwards 1880). *Galathea agassizii*, primarily tropical and insular in distribution, is a deepwater species known from 166 to 490 fm (304-897 m) off St. Augustine, Fla., and from Cuba, St. Vincent, St. Lucia, and Barbados in the Caribbean Sea. In the eastern Atlantic the species is found from 82 to 898 fm (150-1,643 m) in the vicinity of both the Cape Verde and Canary Islands, and off northwestern Africa (Chace 1942; Miyake and Baba 1970). Contrarily, *G. rostrata* appears to be a warm-temperate or tropical/subtropical species, primarily continental in distribution. The species is recorded from the North American continental shelf at Cape Hatteras, N.C., to southeastern Florida, and in the Gulf of Mexico from western Florida, the Mississippi Delta, and southward to Islas Jolbos, north of the Yucatan Peninsula. There is a questionable record from off Rhode Island (Williams 1965). *Galathea rostrata* is also found in shallower water than *G. agassizii* and has been collected from 10 to 50 fm (18-92 m), with the exception of the possible depth record of 1,178 fm

(2,156 m) from off Rhode Island. The only distributional record of the species for the entire eastern Florida coast was that of Haig (1956) who reported a single specimen collected from 21 fm (38 m) off Hillsboro Lighthouse (Broward County) in southeastern Florida. However, recent collections show that the species is not uncommon in the Indian River region of the central eastern Florida coast, especially on deeper water (60+ m) coquinoid limestone ledges and reefs of the ivory tree coral, *Oculina varicosa* Lesueur.

The few studies made on the larval development of new world galatheid crabs (e.g., Rayner 1935; Boyd 1960; Fagetti 1960; Boyd and Johnson 1963; Fagetti and Campodonico 1971) have all been made on eastern Pacific species, and the larvae of Atlantic American galatheids, including the genus *Galathea*, remain undescribed.

This paper provides the first description and illustration of the complete larval development of *G. rostrata*, as well as the first report on any species of *Galathea* reared totally under laboratory conditions, from hatching to megalopal stage. The larvae and postlarvae are compared with larval stages known from other members of the Galatheidea throughout the world, and shared features are briefly summarized.

MATERIALS AND METHODS

Eight ovigerous females of *G. rostrata* were obtained on 15 April 1977 by lockout diver from the

¹Scientific Contribution No. 100, from the Smithsonian Institution-Harbor Branch Foundation, Inc., Scientific Consortium, Link Port, Ft. Pierce, Fla. This report is Article IX. Studies on Decapod Crustacea from the Indian River Region of Florida.

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Research Submersible *Johnson-Sea-Link II*, of the Harbor Branch Foundation, Inc. The adult galatheids inhabited a large clump of ivory tree coral which grew in 80 m of water on Jeff's Reef, lat. 27°32.8'N, long. 79°58.8'W, located about 17 n. mi. (27 km) northeast of Ft. Pierce Inlet, Fla. The entire coral colony was collected and returned to the surface inside of a 500- μ m mesh cloth bag. Ambient seawater temperature on Jeff's Reef was 12°C at time of collection. The galatheids were immediately placed in compartmented plastic trays containing recently collected neritic seawater previously chilled to 10°C. Upon return to the laboratory each adult specimen was transferred to individual 100 × 80 mm covered glass laboratory dishes filled with approximately 340 ml of seawater previously chilled to 15°C. Each isolated female was maintained at this temperature, provided a change of chilled seawater, and fed freshly hatched *Artemia salina* nauplii, daily. All specimens were exposed to a 12-h light-12-h dark illumination program in a controlled temperature unit (CTU) until hatching occurred. Five females survived in this regimen and yielded larvae over a period from 16 April to 6 May 1977.

Seven larval series were initiated. Using methodology previously described by Gore (1968), five such series were cultured in 24-compartmented plastic trays. These consisted of two series of 8 and 24 larvae, held in the CTU at 15°C ($\pm 0.5^\circ\text{C}$), and three series of 24 larvae each, maintained at cool laboratory room temperature (ca. 20°C, $\pm 1^\circ\text{C}$). Two mass culture series of about 30 larvae each were also established in individual 100 × 80 mm glass dishes at cool laboratory room temperature, which was controlled by reverse-cycle air conditioning, and was monitored daily with a 7-day recording thermometer. Fresh surfzone seawater (35.5-36‰) was collected weekly, filtered through glass wool, stored in 14-gal (ca. 56-l) polypropylene carboys, and used throughout the rearing period.

All larval series were checked daily, and any molts or dead individuals were recorded and preserved in 70% ethanol. Specimens were examined microscopically, slides prepared, and drawings made as described in previous studies by Gore (1968). Measurements given below are the arithmetic average of all specimens examined in any particular stage. A complete series of larvae, or their molts, is deposited in the National Museum of Natural History, Washington, D.C. (USNM 170862); the Allan Hancock Foundation, Univer-

sity of Southern California, Los Angeles (AHF 1028-01); the British Museum (Natural History), London (BMNH 1978:103); and the Rijksmuseum van Natuurlijke Historie, Leiden (D 31735).

RESULTS AND DISCUSSION OF THE REARING EXPERIMENT

Galathea rostrata passes through four or five morphologically distinct zoeal stages and a single megalopal stage, before completing development in the laboratory. Culture temperature undeniably affects duration of development, and perhaps larval survival as well. While the duration of the zoeal and megalopal stages differed at each rearing temperature, it was nevertheless generally consistent within each of the temperature series, as will be discussed below.

At 15°C five morphologically distinct zoeal stages were observed for those larvae surviving to metamorphosis. The minimum time required to pass through these stages and attain megalopal stage was 52 days. Most larvae remained in each zoeal stage approximately 9-11 days through the first four stages. Only two stage V zoeae survived, and they remained as such 14 and 16 days before molting to megalopa. However, neither of these specimens survived longer than 6 or 7 days as megalopae, so the mean duration of the postlarval stage at 15°C remains unknown (Table 1). With the minimum noted period of 6-7 day duration for megalopae at this temperature, completion of development and metamorphosis to first crab stage

TABLE 1.—Duration of larval and postlarval development in *Galathea rostrata* under laboratory conditions at the indicated temperatures.

Temp and stage	Days required to attain next stage			
	Min	Mean	Mode	Max
15°C:				
I	10	10.8	10	14
II	8	9.7	10	16
III	9	10.5	9	17
IV	8	9.4	9	11
V	14	—	—	16
Mg	6-7	(Both megalopae died in stage)		
20°C:				
I	5	5.8	6	7
II	4	4.2	4	5
III	4	4.1	4	5
IV (regular)	5	5.7	6	6
V (regular)	5	5.8	6	6
IV (advanced)	3	3.3	3	4
Mg (combined) ²	12	12.6	13	13
III-IV (intermediate)	7	—	—	8 (Died in stage)

¹One zoea remained 30 days in stage II, dying 13 days later in stage III.
²Combined megalopae data include stages obtained from both IV (advanced) and IV (regular).

is conservatively estimated to take well over 60 days (Figure 1).

At 20°C either four or five morphologically distinct zoeal stages occurred. The minimum time required to complete larval development and reach megalopa was 18 days. Most larvae remained in each zoeal stage from 3 to 6 days and as megalopae from 12 to 13 days. The total duration of development from hatching to first crab stage spanned a minimum of 30 days at 20°C, if only four zoeal stages were required, but took at least 37 days with five zoeal stages (Figure 1, inset).

The larvae generally fared well at both culture temperatures. Although the larvae at 15°C took longer to complete their development, they initially appeared to survive better than their counterparts at 20°C (Figure 1). At 15°C, at least 50% larval survival occurred through stage IV, before a rapid decrease occurred in stage V and megalopa. Larvae reared at 20°C exhibited a steep decline after stage I, to about 35% survival, and showed a continual decline thereafter. The precipitous decline in larval survival at this temperature from stage I to stage II was the result of an almost complete mortality in one culture tray, for unknown reasons.

At 15°C ecdysis in the earlier zoeal stages (I-III) generally was a less critical period than at 20°C, although the larvae at the latter temperature were still able to complete most molts. The larvae at 20°C attained subsequent stages more rapidly than did those at 15°C, and some were able to complete zoeal development, although overall larval mortality was relatively higher. On the other hand, at 15°C larval survival may have been enhanced by lower temperature, but the major difficulty then seemed to be the attainment of stage V and megalopa. Only two megalopae were obtained in the 15°C program and neither was able to molt to the succeeding first crab stage. In contrast, four megalopae survived at 20°C, and molted to crab stage I; three of these specimens were maintained in the laboratory to crab stages XII and XIV.

Ecdysial and Sequential Variation in *Galathea rostrata*

Two modes of developmental variation were noted in *G. rostrata* at 20°C. In one mode, some zoeae III molted to an instar which, for purposes of discussion, is labelled "regular" stage IV. This stage was characterized, among other features, by

a reduced number of antennular aesthetascs and was always without well-developed pleopod buds on the abdominal somites. Zoeae remained in this stage for 3-4 days before molting to stage V, an instar possessing distinct, well-developed, pleopod buds and an increased number of antennular aesthetascs. The duration of stage V lasted 5-6 days and was followed by the molt to megalopa. One of these postlarvae subsequently molted to first crab stage.

In the second mode of variation, some zoeae III molted to an "advanced" stage IV, with some, but not all, of the features as noted above for stage V. Zoeae remained longer in the advanced stage (5-9 days) before molting directly to megalopa. Three of these megalopae went on to attain first crab stage. The two types of development are compared in the inset of Figure 1.

Two other stage III zoeae, which remained in stage III 7-8 days (instead of the usual 4-5), molted to what appeared to be an intermediate stage IV. These zoeae exhibited some stage V zoeal features in size, maxillipedal setae numbers, and in possessing pleopod buds, although the latter were only rudimentary. A reduced number of antennular aesthetascs similar to that of regular stage IV zoeae was also seen. The two specimens survived only 4-5 days in this stage before dying. This mode of variation was not considered as important as the previous two modes and will not be discussed further.

Remarks

The regular and advanced fourth stages cannot be equated to an early and late fourth stage, nor to substages IVa and IVb, because no molt occurred from one fourth stage or substage to another. If the molt from stage III was to regular stage IV, this was invariably followed by an ecdysis to stage V, and then a subsequent molt to megalopa. If the molt from stage III produced an advanced stage IV, this in turn molted directly to megalopa, skipping stage V altogether. At 15°C the regular stage IV and stage V appear to be necessary plateaus in larval development, whereas at 20°C development may proceed in some zoeae without resorting to either of these instars.

The regular fourth zoeal stage (as defined above), therefore, appears to be a true sequential stage of development, inasmuch as it was seen in larvae at both 15°C and 20°C programs. However, it is also a stage which can occasionally be skipped

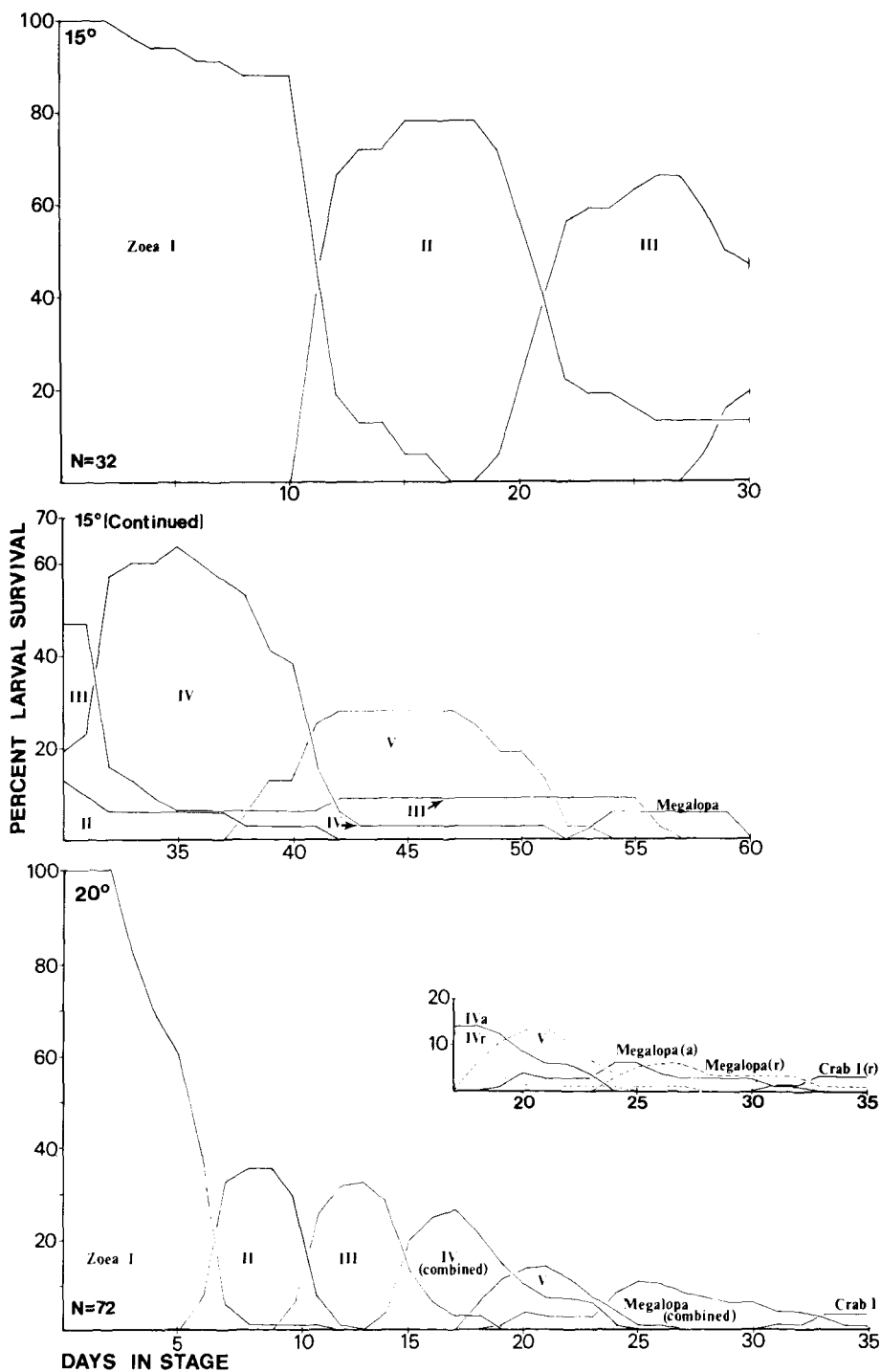


FIGURE 1.—Percentage survival and duration of stages in larvae of *Galathea rostrata* reared under laboratory conditions at 15°C (upper 2 graphs) and 20°C (lower graph). Inset at 20°C gives duration and survival of regular (IVr, dashed line) and advanced (IVa, solid line) stages; number of days the same as in larger graphs.

by some 20°C larvae, and thus could be thought of as an intercalated stage, if the advanced stage IV be considered more indicative of the developmental sequence. Other features shared between the advanced fourth and regular fifth zoeal stages (besides the presence of well-developed pleopod buds noted earlier) include increased numbers of antennular aesthetascs, a remarkable elongation of the antennal endopodite, the appearance of a mandibular palp, and slight changes in setae number on maxillulae, maxillae, maxillipeds, and telsonal uropods (see section on Description of the Larvae). Moreover, the advanced stage IV zoeae were always larger than the regular stage IV zoeae.

It will probably remain a question of semantics whether the regular stage IV is considered an intercalated stage or one that occasionally may be skipped. It could just as well be asked whether the advanced stage IV was an intercalated stage because it embodies many of the features of regular stage IV, plus some seen only in stage V zoeae in the developmental sequence. What is of more importance in the development of *G. rostrata* is that the substitution of an advanced stage IV and the subsequent elimination of the regular stages IV and V allows earlier postlarval metamorphosis. The resultant early benthic crab stages may be reached in a shorter period of time by the species, thereby reducing the time spent in the plankton.

Discussion

It is, of course, conjectural as to whether the larvae of *G. rostrata* skip stages in their development in the natural environment or are ever subject to constant low (e.g., 15°C) or intermediate (20°C) seawater temperatures. The adults of the species, found in deeper continental shelf waters, presumably are often exposed to cool seawater temperatures, as was noted, e.g., during the time the adult females for this study were collected. It is not unreasonable to assume that developmental stages may occasionally be subjected to relatively constant cool temperatures as well, either immediately after hatching or just prior to postlarval metamorphosis when the megalopae settle to the sea floor. In addition, should the larvae become entrained in cyclonic cold core rings of Gulf Stream origin (see Richardson 1976; Wiebe 1976; Wiebe et al. 1976), they would presumably be subjected to relatively constant cold water (at least 17°C) for at least part of their developmental

period. Delayed metamorphosis provides an alternative hypothesis against the more traditional "stepping-stone" idea, to account for the rather extensive distribution of the species along the Middle and North American continental shelves.

There is some evidence that larvae of other species of *Galathea* may skip stages in the plankton (Lebour 1930, 1931) and that other galatheids may intercalate substages (e.g., Boyd and Johnson 1963). For example, the larvae of four of the five British galatheids described by Lebour, viz. *Munida rugosa* (Fabricius 1775 [as *M. bamffica* = *M. bamffica* (Pennant 1777)]), *Galathea intermedia* Lilljeborg 1851, *G. squamifera* Leach 1814, and *G. strigosa* (Linnaeus 1767) developed through four zoeal stages, whereas *G. dispersa* Bate 1859, exhibited four or five stages. Lebour (1930) considered five stages in the latter species as "probably normal" but pointed out that the megalopa could be obtained from the fourth [numerical] stage, and "the normally fifth [numerical] stage has been seen to emerge from the third stage." She stated that the fourth or fifth stage may therefore be omitted in *G. dispersa*, but made no mention of intercalated stages or substages.

The developmental situation in *G. dispersa* is quite similar to that noted in this report for *G. rostrata*, in which an advanced fourth stage replaces the regular fourth and fifth stages, thereby causing them to be omitted from the developmental sequence. Lebour's (1930) "fifth stage. . . from third" is probably equivalent to what is termed in this report the advanced fourth stage. Her statement that long, unjointed pleopods appear in the "last" stage of *G. dispersa* indicates that either the fourth stage (or advanced) or fifth stage (or regular) possess these appendages, depending on whichever stage is "last." It also indicates that the molt to megalopa does not occur without the appearance of pleopods in the "last" larval stage. However, North Sea species of *Galathea* differ from *G. rostrata* in possessing pleopod primordia "in the third stage" which are "long but unjointed in the last stage" (Lebour 1930). In addition, Sars (1889) had also noted and illustrated pleopod development in the "last" stage of larvae attributed to *G. intermedia*, *Munida rugosa*, and *Munidopsis* [as *Galathodes*] *tridentata* (Esmark 1857). The latter species will be considered further below.

Rayner (1935), using planktonic stages from Argentinian waters, described the larvae he attributed to *Munida gregaria* (Fabricius 1793) and

M. subrugosa (White 1847). Rayner did not note any substages or skipped stages in the five instars he described for the two species, and was not certain whether additional stages followed. By analogy with *M. rugosa* [as *M. bamffica*] he thought it possible that the next stage would be postlarval. In this he was probably correct, but it seems strange in retrospect that Rayner did not attach importance to the well-developed pleopods on the larvae before him, a feature by which he earlier characterized the fifth zoeal stage. These appendages in other galatheid larvae are quite obviously developed at stage V (see Lebour, Sars, Boyd and Johnson, and others), and Sars (1889) even drew attention to them when describing his "last zoeal stage."

Intercalation of substages, however, is known in the genus *Pleuroncodes*, as was specifically discussed by Boyd and Johnson (1963) in the larvae of *P. planipes* Stimpson 1860.³ Five zoeal stages had been initially noted in this species (Boyd 1960), but a sixth stage, apparently unnatural and not known to occur in the plankton, could be induced in the laboratory. Boyd and Johnson thought this stage was due to the presence of penicillin pills or to the CaCO₃ buffer in the pills, used to control bacterial growth in the cultures. These authors also stated that numerical stage IV could be subdivided into a complex of from four to nine substages, each represented by a molt, all without pleopods, but otherwise morphologically similar to each other. Although no sequential substages were skipped (e.g., a molt from substage IVa to IVh), one or more substages could be omitted terminally, with a subsequent molt to the morphologically discrete stage V, which possessed pleopods (Boyd 1960). Boyd and Johnson suggested that in *P. planipes* the number of substages in stage IV was probably influenced by temperature, with higher culture temperatures (e.g., 16°-20°C) producing faster development but causing more substages to occur before the molt to stage V. They noted, however, that other factors such as food supply or crowding of larvae might also exert an effect on the number of substage instars, but neglected to consider the possibility that the large number of induced substages in stage IV might also be due to the use of antibiotics in the cultures, as suggested by Fagetti and Campodonico (1971).

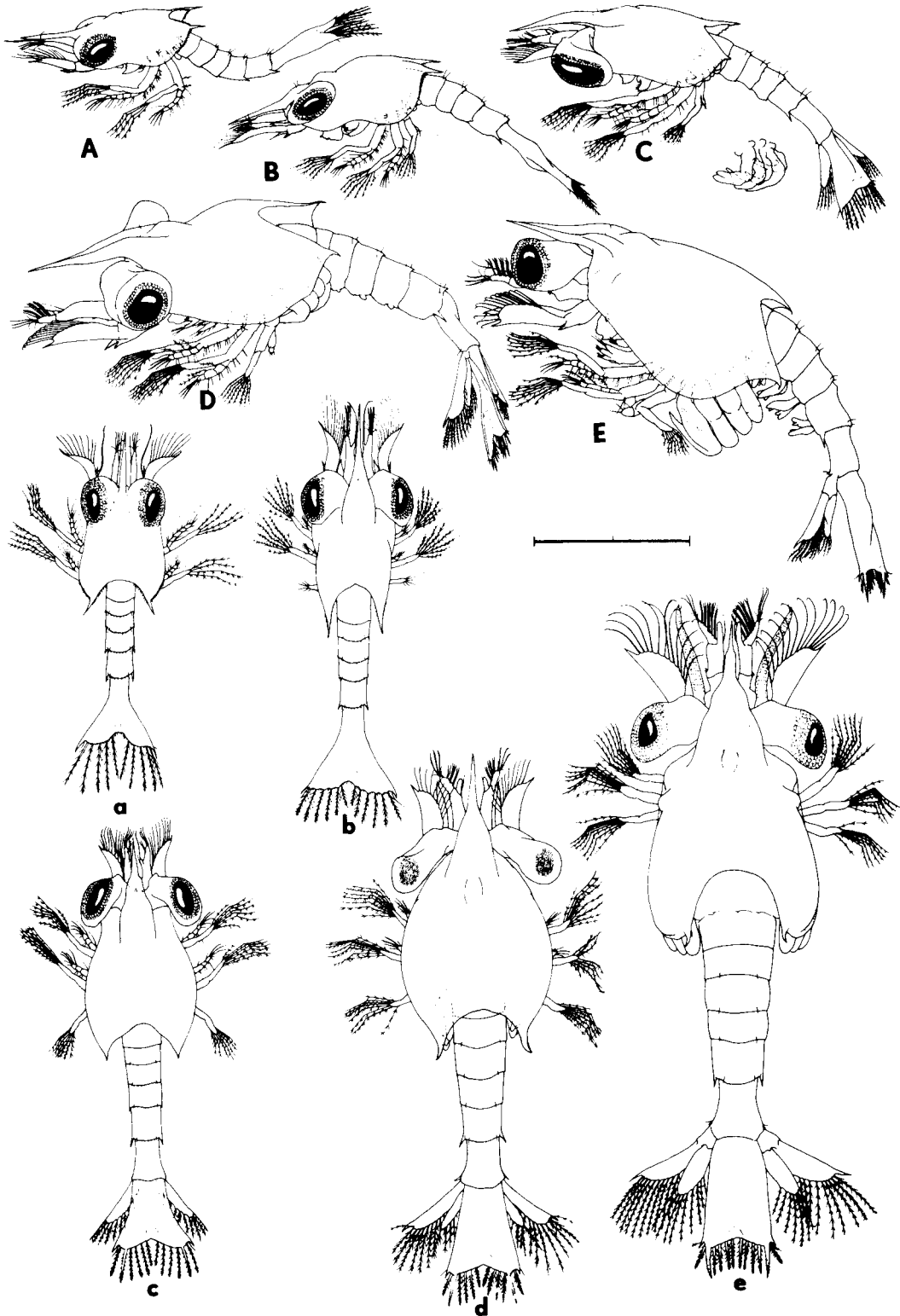
³Both Stimpson (1860) in his original description of *Pleuroncodes planipes* and Haig (1955) have suggested that the species may prove to be only a northern Pacific form of the Chilean *P. Monodon*.

FIGURE 2.—*Galathea rostrata*, zoeal stages in lateral and dorsal view: (A, a) First zoea; (B, b) second zoea; (C, c) third zoea; (D, d) fourth zoea (regular); (E, e) fifth zoea. Scale line equals 1.0 mm.

The Chilean congener, *Pleuroncodes monodon* Milne Edwards 1837, also was found to have intercalated substages (Fagetti and Campodonico 1971). At 15°C, substage IVa-d were followed by a molt to stage V, possessing pleopods; at 20°C a fifth substage (IVe) was attained instead of zoeal stage V. Whether stage IVE would be followed by ecdysial stage V is not known because all larvae in stage IVE died. However, the lack of pleopods in stage IVE implies that stage V should occur, with pleopods, before the molt to megalopa takes place. Whether such substages occur in the plankton is conjectural, but they certainly would present some difficulty in separation because of their great similarity to each other in samples collected from the plankton.

Abbreviated larval development is also known to occur in at least two galatheids. Sars (1889), in describing the prezoel, "first" and "last" zoeal stages of *Munidopsis tridentata* from Norwegian waters suspected that development time was shorter than that seen in *Galathea*, but came to no conclusion as to the total number of stages. He commented on the remarkably advanced features exhibited in the early zoea, an observation later supported by Samuelsen (1972). Samuelsen determined that only three zoeal stages exist for *M. tridentata* and further suggested that the megalopal stage followed stage III because the latter stage was in the same relative state of development as some fourth zoeae which preceded the megalopae in other galatheids. Samuelsen noted that the presence of a mandibular palp, pleopod primordia, antennular aesthetascs, antennal setae, and scaphognathite setae in the early zoeal stages were all advanced features usually restricted to later zoeae in other galatheid larvae. The relatively nonsetose feeding appendages and endopodites of the natatory appendages indicate that the larvae may not feed, although they can swim well.

Al-Kholy (1959) described and figured larvae attributed to a "*Galathea* sp." which apparently developed through only three zoeal stages. However, no methodology was given, nor indication as to whether the larvae were cultured in the laboratory or collected from the plankton. It is doubtful whether the species will ever be identi-



fiable based on his incomplete descriptions and rather stylized illustrations.

Advanced development⁴ is implied in but one galatheid, the cave-dwelling *Munidopsis polymorpha* Koelbel 1892. This species is presently known only from a littoral cave formed by lava tunnels which connect to the sea in the Canary Islands (Fage and Monod 1936). These authors never found more than five, extremely large (1.5-1.8 mm in diameter) eggs on an individual female. No larval stages were described, but it was hypothesized that the young *Munidopsis* was well advanced in development inside the egg and probably hatched into a form nearly like the adult. Given the rather unique habitat for a *Munidopsis*, advanced development in *M. polymorpha* would not be surprising. The vast majority of other species of *Munidopsis* are deep-sea forms, most of which occur below 500 m (Mayo 1974) in the Atlantic Ocean, although some species occur in shallower waters on the continental shelf.

In summary, it is apparent that larval development in the Galatheidae is quite diverse, including advanced development (i.e., with imminent metamorphosis) in the cave dwelling *M. polymorpha*, abbreviated development with as few as three larval stages (*M. tridentata*, Al-Kholy's *Galathea* sp.), to "normal" development of four-five zoeal stages (e.g., *Munida*, *Galathea*). Substage intercalation is known in the genus *Pleuroncodes*, but seems to be restricted to the fourth, or penultimate, ecdysial stage. Intercalation of a sixth zoeal stage, perhaps only a laboratory artifact, is also known in one species of this genus. Skipped stages appear only in two species of *Galathea*, and perhaps one of *Munida*, at present, and these result in the elimination of regular zoeal stages IV and V and their replacement by an advanced stage IV which subsequently molts directly to megalopa.

Developmental variation such as that just discussed allows some interesting speculation as to its evolutionary consequences in view of the fact that the phylogenetically closely related anomuran family Porcellanidae generally undergo a re-

duced developmental sequence of usually no more than two zoeal stages. These stages appear to be morphologically equivalent in most respects to *Galathea* stages I and IV, sensu lato. Substages have been postulated for some porcellanid larvae, notably Indo-Pacific species, but are not positively known to occur in Atlantic and eastern Pacific species. Previously postulated substages in Atlantic species have been shown to be the result of accelerated morphological development without an ensuing molt and have been seen primarily in larvae collected from the plankton (Gore 1968 and others). However, the larvae of the western Pacific genus *Petrocheles* apparently do reflect their galatheid ancestry by undergoing five zoeal stages during development. Morphological features of the telson, uropods, and antennal scale in these larvae all resemble, to a greater or lesser degree, their counterparts in larvae of *Galathea* and *Munida* (Wear 1965). Further studies along these lines should be most interesting and productive.

DESCRIPTION OF THE LARVAE

First Zoea

Carapace length: 1.0 mm.

Number of specimens examined: 10.

Carapace: (Figure 2A, a). Typically galatheid, somewhat inflated; rostral spine horizontal, little expanded proximally, straight, extending to level of scaphocerite spine, or slightly beyond, about $0.5 \times$ carapace length (CL), unarmed; posterolateral carapace margins armed with a series of about 15 small denticles placed before large, posterior spine; latter slightly more than $0.1 \times$ CL; dorsomedial carapace margin excavated, with about 13 small denticles along sinus margin. Two small setae medially above eyes; latter sessile.

Antennule: (Figure 3A). A simple rod, both endopodite and exopodite fused to protopodite; former with 1 elongate plumose seta, latter with 3 aesthetascs and 3 setae.

Antenna: (Figure 3B). Endopodite rodlike, about $0.4 \times$ scaphocerite length, fused to protopodite, a single distinct spine at its tip, plus a long plumose seta; scaphocerite usually with 9 setae along margin, tip produced into long daggerlike spine about $0.3 \times$ total scale length; protopodite

⁴The term "direct" development is restricted in this paper to those larvae which hatch from the egg in a form morphologically similar to the adult and undergo no further metamorphosis. Larvae exhibiting "advanced" development usually hatch in the penultimate or ultimate zoeal stage and thus may undergo additional ecdysis prior to metamorphosis. Larvae with "abbreviated" development hatch as early zoeae (often with a pre-zoeal or first zoeal stage present), but may dispense with one or more intermediate stages in completing their larval develop-

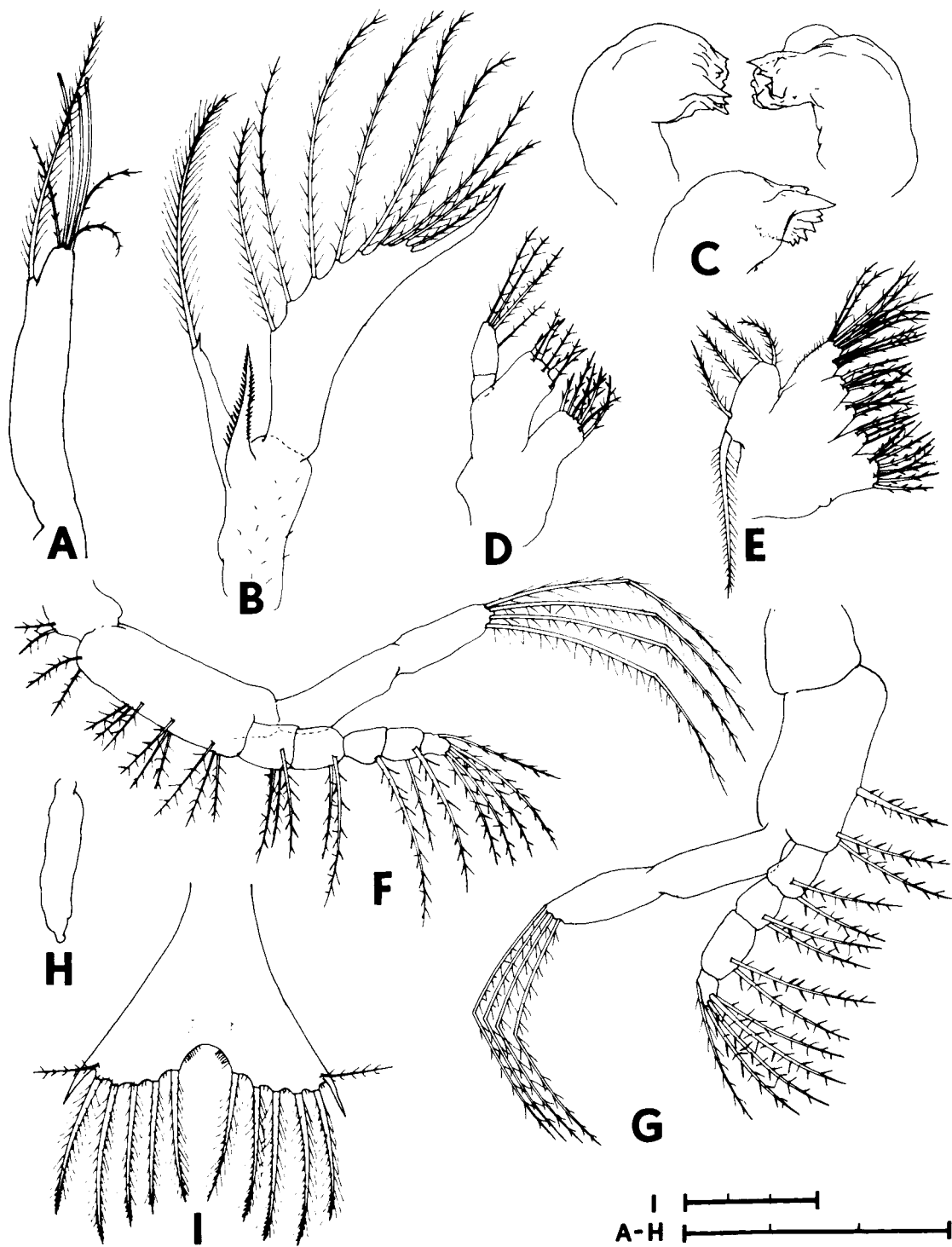


FIGURE 3.—*Galathea rostrata*, first zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated interiorad to zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

with sharply pointed spine ventrally, armed along either side with distinct acute spinules; this spine falling short of distal tip of endopodite; scattered setae basally on protopodite.

Mandibles: (Figure 3C). Asymmetrical dentate and spined processes, as shown.

Maxillule: (Figure 3D). Endopodite segmented, 3 terminal, 1 subterminal seta. Basal endite with 2 large, widely separated strong spines, plus 3 setae; coxal endite with 4 spines, 3 strong setae.

Maxilla: (Figure 3E). Endopodite setae, progressing subterminally, 3-4, 3, plus 3 laterally, and additional fine hairs as illustrated. Basal endite proximal and distal lobes each with 3 regular and 1 spinelike seta; coxal endite proximal and distal lobes with 8, and 4 spinelike setae, respectively. Scaphognathite with 4 lateral, 1 stout elongate apical seta.

Maxilliped 1: (Figure 3F). Coxopodite with 2 setae. Basipodite setae formula progressing distally 2, 3, 3, 3. Endopodite five-segmented, setae progressing distally 3, 2, 1, 2, 4 + I (Roman numeral denotes dorsal setae); all endopodal and basipodal setae heavy, spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 2: (Figure 3G). Coxopodite naked. Basipodite setae 1, 2, progressing distally. Endopodite four-segmented, setal formula 2, 2, 2, 4 + I; all spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 3: (Figure 3H). A small, unsegmented amorphous bud.

Pereiopods: Appear as small and undifferentiated buds, gradually enlarging as stage progresses.

Abdomen: (Figure 2A, a). Five somites; last 2 with large lateral spines; somites 2-5 each with paired setae dorsally, plus a series of small distinct spinules along posterior margin of somite; somite 6 fused to telson. Pleopods absent.

Telson: (Figure 3I). Setal formula on margin 7 + 7; all plumose setae (= processes 3-7) with small, hooklike spinules progressing down their

length; other setae and hairs as illustrated. Anal spine absent.

Color: Zoea transparent; frontal region of carapace diffused with orange, brighter orange dorsally on midgut region. Chromatophores as follows: orange on protopodite of antennule, faintly orange on scaphocerite of antenna; red-orange around inner oral region; mandibles and labrum outlined in red, interiorly orange; basipodites of maxillipeds 1 and 2 red-orange along dorsal and ventral margins; red spiderlike chromatophores dorsally in longitudinal line on abdominal somites 3-5; orange chromatophores ventrally placed in a similar manner. Eyes black, with bluish highlights in reflected light.

Second Zoea

Carapace length: 1.2 mm.

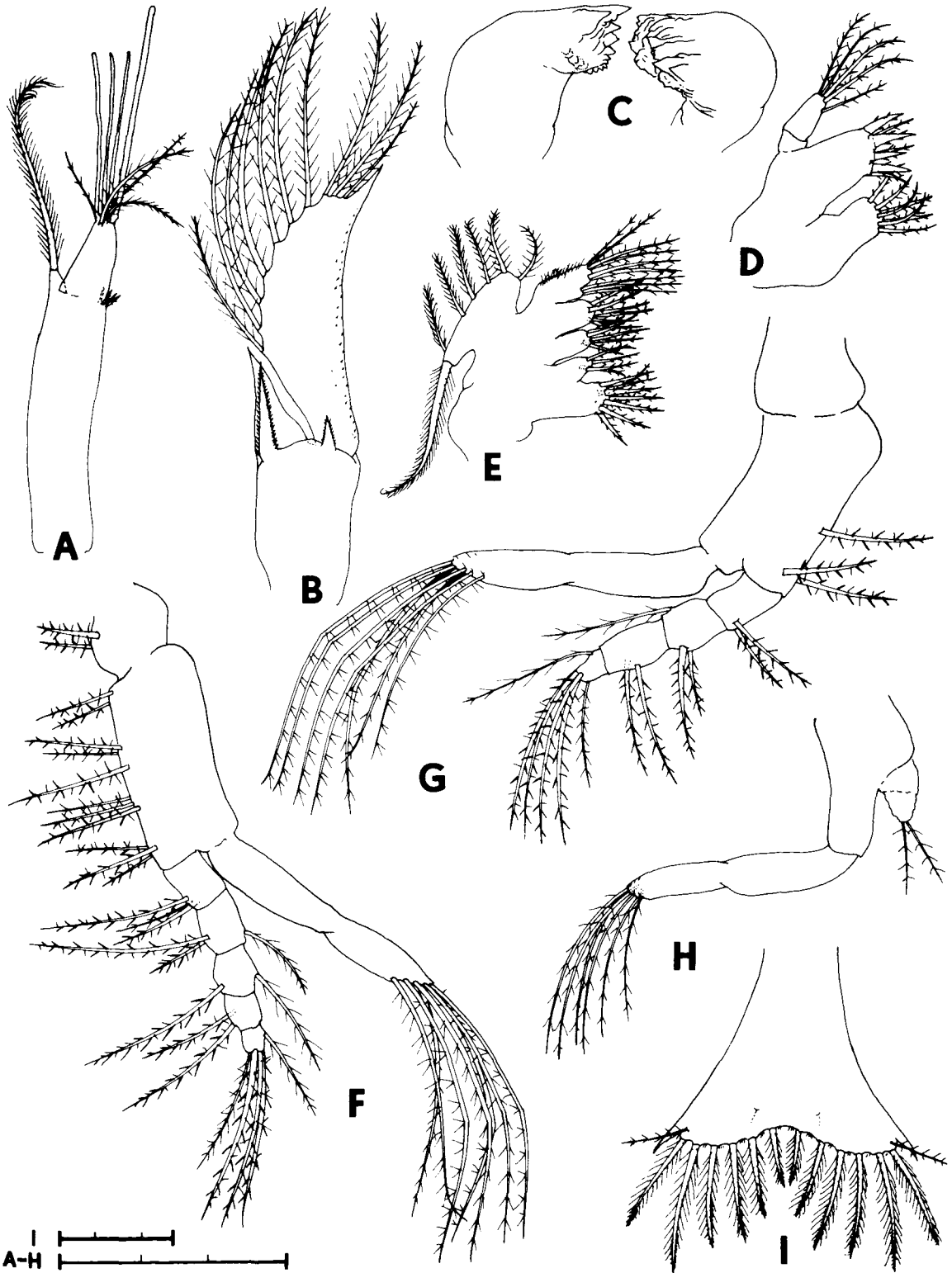
Number of specimens examined: 8.

Carapace: (Figure 2B, b). More inflated; rostral spine more or less knifelike in lateral view, noticeably expanded proximally in dorsal view; about $0.5 \times$ CL, overreaching distal tip of antennal scaphocerite spine in several specimens, unarmed; posterolateral margins of carapace with about 14 small denticles or spinules, dorsomedial margin possessing only scattered nubs or with denticles totally absent; posterior spines remain slightly more than $0.1 \times$ CL; eyes now stalked.

Antennule: (Figure 4A). Incipient segmentation seen at junction of exopodite with protopodite; former usually carrying 4 aesthetascs and setae, with 4 small thick setules on junction with protopodite. Endopodite retains single long plumose seta.

Antenna: (Figure 4B). Endopodite thickened, drawn into point distally, appearing conical, about $0.3 \times$ scaphocerite length, incompletely fused to protopodite, now lacking elongate plumose seta seen in first stage. Scaphocerite usually with 10 marginal setae, plus numerous small spinules ventrally along outer margin; distal spine about

FIGURE 4.—*Galathea rostrata*, second zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.



0.2× scale length. Protopodite now carries second sharp spine ventrally, armed as first along outer margins; larger ventral spine now shorter than endopodite; ventral spinulelike setae inconspicuous or lacking.

Mandibles: (Figure 4C). Dentition now larger, more complex. No palp.

Maxillule: (Figure 4D). Endopodite unchanged from stage I. Basal endite with 4 large spines, 3 setae; coxal endite processes stronger, but number unchanged, from stage I, appearing to be 5 spines, 2 strong setae.

Maxilla: (Figure 4E). Endopodite setal formula progressing subterminally 4, 2, plus 3 laterally, and fine hairs as shown. Basal endite proximal and distal lobes with 4-5, 6 processes, respectively, former as 3-4 spinelike and 1 thin seta, latter as 1 strong and 1 regular spine, 4 thin setae. Coxal endite distal lobe with 3 spines, 1 strong seta, proximal lobe with 8 spines or strong spinelike setae. Scaphocerite with 6 lateral, plus usual elongate apical seta.

Maxilliped 1: (Figure 4F). Coxopodite and basipodite setae unchanged from stage I. Endopodite setal formula now 3, 2 + I, 1 + I, 2, 4 + I. Exopodite remains two-segmented throughout later development, now with 7 natatory setae.

Maxilliped 2: (Figure 4G). Coxopodite and basipodite as in stage I. Endopodite setal formula 2, 2 + I, 2, 5 + I. Exopodite as above and for later stages, carrying at this stage 7 natatory setae.

Maxilliped 3: (Figure 4H). Remarkably developed; incompletely two-segmented exopodite with 6 natatory setae; endopodite poorly calcified, originating about half way up basipodite, two-segmented, with 2 terminal setae.

Pereopods: (Figure 2B). Undifferentiated, but enlarging buds throughout stage.

Abdomen: (Figure 2B, b). Five somites, sixth still fused to telson; lateral spine on somite 5 distinct, that of somite 4 reduced, even vestigial; paired dorsal setae on posterior dorsal margins of somites 2-5 remain, and are present throughout later zoeal stages; posterior marginal spinules much reduced in size and number.

Telson: (Figure 4I). Marginal setal formula 8 + 8, additional pair added in medial sinus; latter reduced from distinct U-shaped notch seen in stage I. Armature on plumose processes as before, but distal tips with hooklike processes more distinct; other setae and hairs as shown.

Color: Similar to stage I, but with less diffusion of orange frontally; internal midgut region, mandibles and maxillipedal basipodites retain red-orange color, mandibles showing noticeable red outline, maxillipedal color appearing more diffused than stage I; abdominal somites 4-5 with red dorsal and lateral chromatophore lines, plus orange line ventrally, all connecting to single orange ring of spiderlike chromatophores around each anterior margin of somites 4 and 5. Eyes electric blue to black in reflected light.

Third Zoea

Carapace length: 1.3 mm.

Number of specimens examined: 8.

Carapace: (Figure 2C, c). Proximal margins of rostral spine more developed laterally when seen dorsally, in this and subsequent stages; length remains about 0.4-0.6× CL, distal tip reaches to about tip of scaphocerite spine or slightly beyond; posterolateral margins of carapace with denticles much reduced, becoming irregular nubs; dorsomedial margin with only poorly developed, ragged nubs, almost totally obsolete; posterior carapace spines considerably shortened, less than 0.1× CL. Eyes much enlarged, basal peduncles elongate.

Antennule: (Figure 5A). Exopodite segmented from protopodite, bearing 2 lateral aesthetascs in addition to 3 terminal, plus 3 or 4 setae, at tip. Endopodite slightly enlarged, retaining long plumose seta. Protopodite carries single long lateral seta distally, plus 2 short fine setae, placed medially, and basally, and 4 short stout setae distally.

Antenna: (Figure 5B). Endopodite continues to develop, but remains incompletely segmented from protopodite, now about 0.5-0.6× scaphocerite length, a thin seta just below spinous tip. Scaphocerite with 9-11 marginal setae, number somewhat variable on left and right appendages in same specimen, plus additional shorter spinules

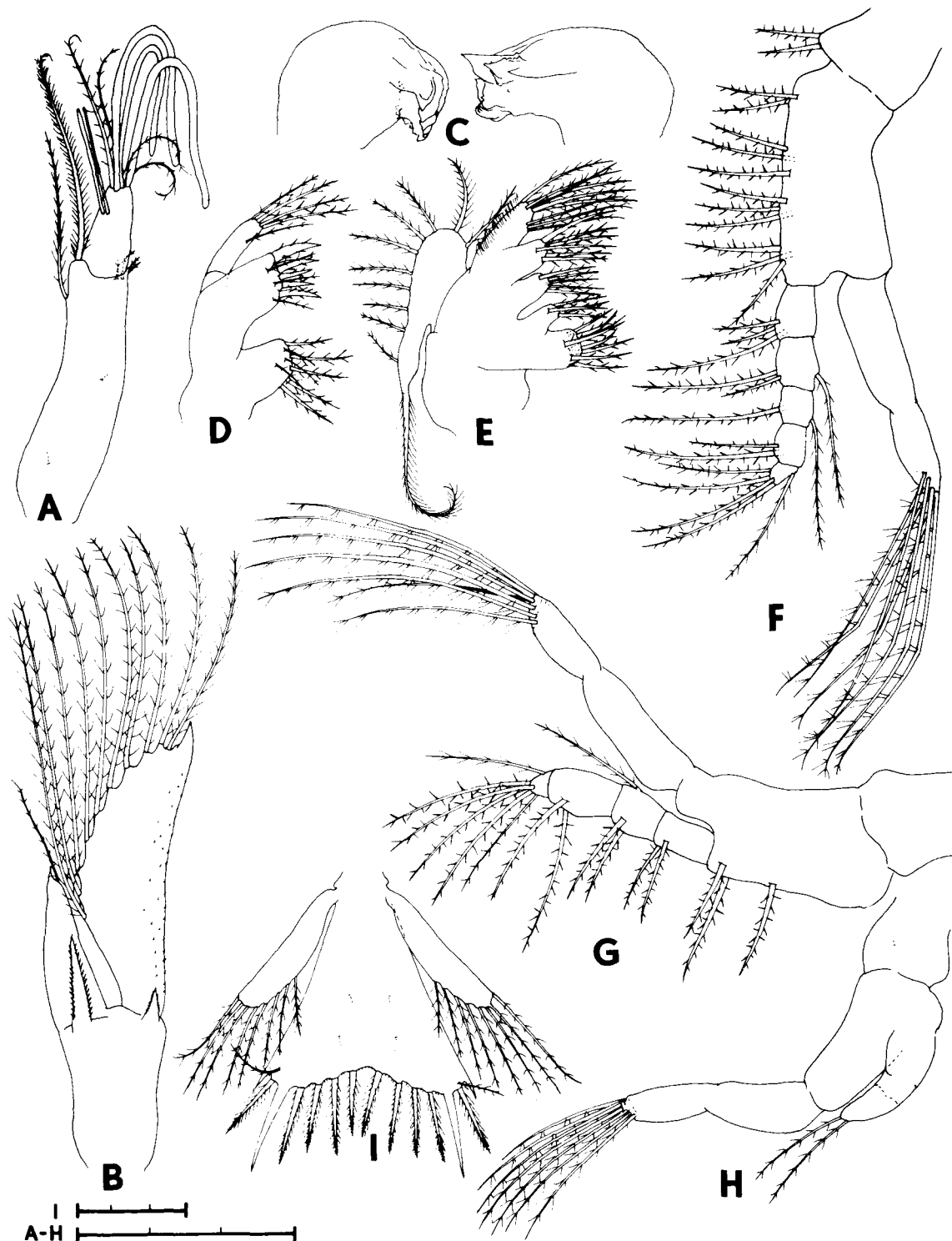


FIGURE 5.—*Galathea rostrata*, third zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

along ventral outer margin; distal spine shortened to about $0.1 \times$ scale length. Protopodite retains 2 sharp ventral spines, larger about $0.6 \times$ endopodite length, smaller about $0.3 \times$ length of larger.

Mandibles: (Figure 5C). Incisor and molar processes more developed; no palp.

Maxillule: (Figure 5D). Endopodite unchanged. Basal and coxal endites both with 5 spines, 3 setae.

Maxilla: (Figure 5E). Endopodite unchanged. Numbers and form of processes on either endite little changed from earlier stage, with exception of basal endite distal lobe; latter now with 1 spine, 4 strong setae, 1 thin seta. Scaphognathite with 10 marginal setae and usual thick apical seta.

Maxillipeds 1 and 2: (Figures 5F, G). Coxal, basipodal, dorsal and ventral endopodal, and exopodal natatory setae as in previous stage.

Maxilliped 3: (Figure 5H). Endopodite bud now subequal to basipodite length, incipient segmentation more prominent in some specimens than others; exopodite with 7 natatory setae.

Pereiopods: (Figure 2C, and detailed inset). More developed, many with incipient segmentation; partial chelation of protochela often visible.

Abdomen: (Figure 2C, c). Six somites present, sixth divided from telson; distinct lateral spine remains only on somite 5; spinules on dorsal posterior margins vestigial, ragged and irregular. In some specimens small, amorphous swellings occur ventrally on somites 2-5, signifying future position of pleopod buds.

Telson: (Figure 5I). Marginal setal formula remains $8 + 8$; fourth pair of processes elongate spines fused to telson; processes 3, 5-8 retain noticeable hooklike spinules distally; other dorsal setae as illustrated. Uropods present at junction of abdominal somite 6 and proximal margin of telson; exopods of same well developed, with variable number of marginal plumose setae (usually about 8); endopods, if present, merely foreshortened naked buds.

Color: More distinctly colored than stage II.

Orange chromatophores: dorsally on interior margin of eyestalks, a single orange spot on carapace laterally, just above each maxilliped 1, another small grouping laterally on abdominal somite 2; diffused orange on antennular peduncle, ventrolaterally on carapace below eyes, interiorly on mouthparts and within gut region, and on endopodites of maxillipeds 1-3. Red chromatophores: on cutting edge of mandibles, dorsomedially and laterally on abdominal somite 4, laterally on somite 5, the latter appearing as if small drops of blood.

Fourth Zoea (Regular)

Carapace length: 1.4 mm.

Number of specimens examined: 10.

Carapace: (Figure 2D, d). Rostral spine with noticeably raised lateral margins, greatly expanded basally at point of attachment to carapace, slightly overreaching scaphocerite spine and antennular exopodite; carapace posterolateral and dorsomedial margins unarmed; posterior spines quite short, hooked downward. Eyes large, on elongated stalks.

Antennule: (Figure 6A). Exopodite with three rows of lateral aesthetascs, numbering distally 2-3, 3, 2-3, in addition to usual 3, plus 3 setae, at tip. Endopodite about $0.5 \times$ length of exopodite, plumose seta absent. Protopodite retains distal lateral setal, plus usual 4 stout setae at junction of exopodite; 3 medial, 2 basal setae now also present.

Antenna: (Figure 6B). Endopodite elongate subequal to scaphocerite length; latter bearing 10-12 (numbers variable on left and right appendages in same specimen) marginal setae plus numerous ventral spinules on outer margin. Larger protopodal ventral spine about $0.3 \times$ endopodite length, smaller about half size of larger; armature of both remains as in earlier stages.

FIGURE 6.—*Galathea rostrata*, fourth zoeal appendages: (A) Antennule, regular stage; (a) same, advanced stage; (B) antenna, regular stage; (b) same, advanced stage; (C) mandibles, regular stage; (c) same, advanced stage; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; all regular stage; (i) detail, fifth telsonal process, $40 \times$ objective. See text for discussion. Scale lines total 0.3 mm.



Mandibles: (Figure 6C). Molar and incisor processes acutely spinous, otherwise unchanged from earlier stages; no palp.

Maxillule: (Figure 6D). Endopodite unchanged, but may have small seta at base of segment. Basal endite with 7 stout spines, 3 setae; coxal endite with 5 or 6 long spines, 3 strong setae, and occasional small tooth.

Maxilla: (Figure 6E). Endopodite unchanged. Basal endite distal lobe with 6 spines, 2 setae, proximal lobe with 7 or 8 spines and strong setae intermixed; coxal endite distal lobe with 4 terminal spines, 1 lateral seta, proximal lobe with 11 spines, placed 5 terminally, 4 subterminally, 2 laterally. Scaphognathite with 17-20 marginal setae, including 2 or 3 anteriorly near base, plus usual long apical plumose seta, as shown.

Maxilliped 1: (Figure 6F). Basipodite adds a single small seta proximally, ventral formula now 3, 3, 3, 3. Endopodal and coxal setae unchanged; 8 exopodal natatory setae.

Maxilliped 2: (Figure 6G). Coxal and basipodal setae unchanged. Endopodite setal formula 2, 2 + I, 2 + I, 5 + I. Exopodal natatory setae 8.

Maxilliped 3: (Figure 6H). Endopodite overreaches basipodite, bearing 3 setae. Exopodite with 8 natatory setae.

Pereiopods: (Figure 2D). Chelation and segmentation more or less apparent, progressing rapidly throughout stage; entire pereiopodal mass hangs from beneath posterolateral carapace region in later stage.

Abdomen: (Figure 2D, d). Lateral spine present only on somite 5; dorsal spinulation on posterior margins of somites nearly absent; paired dorsal setae remain. A short, sharp spine on posterolateral margin of somite 6, just above insertion of uropodal basipodite. Pleopod primordia may be present in some specimens, but development is weak and occurs slowly, if at all, throughout stage.

Telson: (Figure 6I, i). Uropods completely developed, exopodite distal outer tip produced into long spine, 8-11 long marginal setae present; endopodites with 4 or 5 setae; with shorter setae on

both rami. Telson marginal setal formula 8 + 8, fused fourth process now heavily spinulose, other movable processes (except process 2, which, as in other anomurans, remains a simple seta) carry distinctive, sharp, separated, spinules along their length (Figure 6i; 40 \times objective), these spinules much more hooklike distally, more spinous proximally. Other dorsal and ventral setae on telson as illustrated.

Color: Similar to stage III; quite developed and noticeable along anterior and internal margin of eyestalks; interiorly on midgut, and bases of maxillipeds; single red chromatophores now basally on antennular protopodite, on posterior margin of maxillipedal basipodites, and laterally on abdominal somites 3-5; eyes blue, reflecting green highlights.

Remarks: This stage, with limited aesthetasc numbers, reduced antennular endopodite and unsegmented protopodite, lacking mandibular palps, and with developing pereopods and usually only pleopodal primordia, always molted to zoeal stage V.

Fourth Zoea (Advanced)

Carapace length: 1.6 mm.

Number of specimens examined: 12.

Carapace: Differs little from regular stage IV except being larger, more inflated; armature similar to regular stage zoea.

Antennule: (Figure 6a). Endopodite about 0.75 \times to nearly equal to length of exopodite; latter with four rows of aesthetascs laterally, as 1, 3, 3, 2, plus usual 3, plus 3 setae terminally. Other setae as illustrated.

Antenna: (Figure 6b). Endopodite distinctly overreaches (1.2 \times) scaphocerite; latter with 12-14 marginal setae; larger ventral propodal spine about 0.25 \times endopodite length, remaining half again as long as smaller propodal spine.

Mandibles: (Figure 6C). Large, heavily toothed processes, distinguished now by undivided simple palp.

Maxillule: May add one more process on basal endite; tooth on coxal endite usually distinct.

Pereiopods: Well formed, completely segmented and chelated, protruding almost totally from under posterolateral carapace margins.

Abdomen: Somites 2-5 each with a pair of undivided pleopod buds, gradually lengthening as stage progresses, but never becoming bifid.

Color: Similar to regular stage IV zoeae.

Remarks: The zoeae in this stage are much more developed morphologically, possessing a different arrangement of antennular aesthetascs, a well-developed antennal endopodite, mandibular palps, segmented and chelated pereiopods, and distinct (but undivided) pleopod buds. These zoeae molt directly to megalopae, bypassing stage V completely.

Fifth Zoea

Carapace length: 1.6 mm

Number of specimens examined: 8.

Carapace: (Figure 2E, e). Rostral spine with lateral margins appearing somewhat embossed at posterolateral angle of zoeal orbit; carapace lateral margins deeply rounded, convex posterolaterally, unarmed; posterior spine recurved ventrally in some specimens, nearly straight in others, inner margin of same curving regularly inward to deeply excavated dorsomedial margin of carapace; latter entirely without armature. Eyes large, ovoid, on well-developed elongate stalks.

Antennule: (Figure 7A). Exopodite with five rows of aesthetascs laterally: 2, 3, 3, 3, 2, plus 3 and 3 setae at tip. Endopodite from about 0.75 \times to just subequal in length to exopodite. Protopodite segmented into elongate basipodite and truncated coxopodite; former with a single long plumose seta distally, plus 4 stout setae terminally at exopodite junction, 3 more medially; latter with 2 stout setae ventrally near line of segmentation.

Antenna: (Figure 7B). Endopodite very noticeably longer than scaphocerite (1.3-1.4 \times); latter bearing 12-14 plumose marginal setae plus additional ventral marginal spinules as in earlier stages. Larger propodal ventral spine less than 0.2 \times endopodite length, smaller remains about half the size of larger, both armed similarly as

illustrated. Toward end of larval stage transparent endopodite reveals distinctly segmented megalopal antennal flagellum within endopodal sheath.

Mandibles: (Figure 7C). Noticeably dentate, each with simple, distinct palp.

Maxillule: (Figure 7D). Endopodite unchanged from regular stage IV; basal setule may not be present. Basal endite with 8 stout spines, 3 setae; coxal endite with 6 long spines, 3 strong setae, and small tooth, placed as illustrated.

Maxilla: (Figure 7E). Endopodite unchanged. Basal endite distal lobe with 8 spines and strong setae, 2 thin setae terminally, one regular seta laterally; proximal lobe with 6 terminal, 2 subterminal, 2 lateral processes, most appearing to be strong setae and spines. Coxal endite distal lobe with 2 spines, 2 strong apical setae, 2 thinner subapical or lateral setae; proximal lobe with about 13 spines and strong setae, progressing terminally to laterally as 7, 4, 2. Scaphognathite with about 22-25 marginal setae, including enlarged plumose seta apically; 2 small setules present, positioned laterally.

Maxilliped 1 and 2: (Figures 7F, G). Little changed from previous stage.

Maxilliped 3: (Figure 7H). Little changed in form from previous stage, except endopodite now much larger, longer, extending well past distal margin of basipodite; 3 setae as before.

Pereiopods: (Figure 2E). Extremely large, appearing to be nearly functional, protruding beneath, and forcing posterolateral margins of carapace, outward; walking leg segmentation and cheliped chelation distinctly visible.

Abdomen: (Figure 2E, e). Lateral spine on somite 5, and that on posterodistal angle of somite 6, the only armature. Pleopods present as well-developed, bifid, buds.

Telson: (Figure 7I, i). Uropods well-developed, both endopodite and exopodite with variable number of marginal setae, usually 8-10, and 10-13 or occasionally 14, respectively. Telsonal fused and movable processes as illustrated; fourth process distinctly spinulose; occasionally an extra

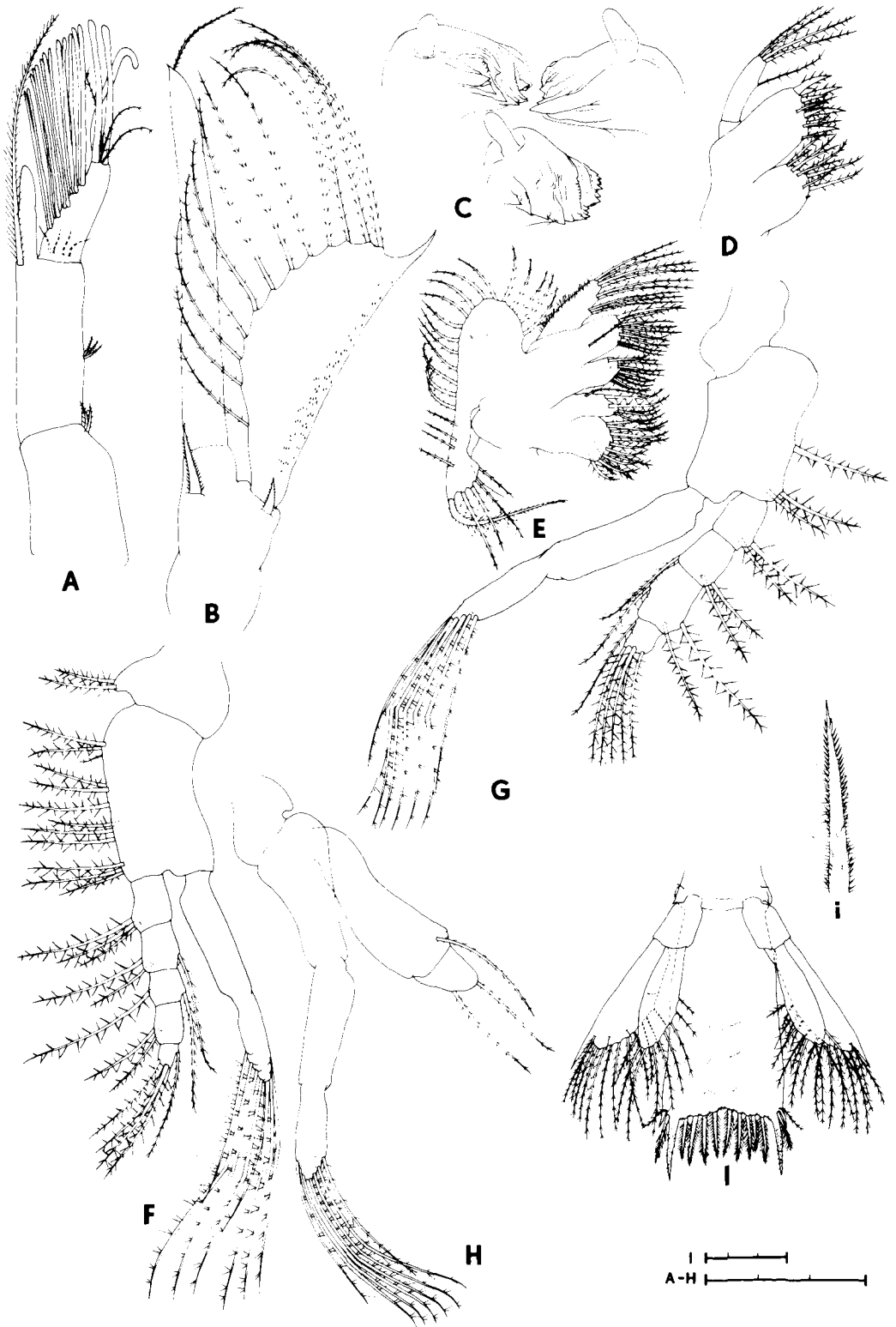


FIGURE 7.—*Galathea rostrata*, fifth zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated exteriorad of zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; (i) detail (40 × objective), fifth telsonal process. Scale lines total 0.3 mm.

plumose process appears making telson marginal setal formula 8 + 9 as shown.

Color: Chromatophores as follows: Red, on anterior margin of eyestalks, paired on carapace dorsally just behind eyes on frontal region, single ventrolaterally beneath each eyestalk just above mandibular region, ventrally on both antennular and antennal peduncles at junction with carapace, laterally on carapace above insertion of maxilliped 2; interiorly on mouth region on outer margin of mandible, posterior to mandible on maxillule, and on midgut; abdominal somites 3-5 with several groups laterally, plus a reddish-orange line above hindgut of same. Orange chromatophores in elongate streaks longitudinally on basipodite of maxillipeds 1-3, more diffused on maxillipedal endopodites, and in lateral groupings on abdominal somites 3-5. Eyes blue-green in reflected light, corneas dark, probably black.

Remarks: This stage followed the regular stage IV and invariably molted to megalopal stage.

Megalopa

Carapace length × width: 1.7 × 1.2 mm.

Number of specimens examined: 4.

Carapace: (Figure 8A, B). Resembling miniature adult; rostrum triangular proximally, drawn into sharp point distally, armed along lateral margins with 4 distinct spines, some smaller spinules occasionally interspersed; frontal region with additional spinules as illustrated; 2 elongate thickened setae on gastric region, plus other setae and spinules as shown; lateral margins with 4 large spines, including 1 at epibranchial angle, 2 placed about equidistant behind, and the fourth at junction with cervical groove; a variable number, usually 3, smaller spines laterally between larger spines; a fifth large spine on posterolateral margin, followed by another, smaller, dorsally and posteriorly. Numerous small setae scattered over entire carapace; eyes each with 2 large, feathery setae on anterodorsal margin.

Antennule: (Figure 9A, a). Biramous; peduncle large, three-segmented; basal segment inflated, with 2 large forward-directed spines dorsally, another, smaller, distoventrally; other setae as shown; remaining two segments nearly smooth, sparsely setose. Lower ramus three-segmented, tip with 2 spinules (see detail, Figure 9a), other setae as shown. Upper ramus six- or occasionally indistinctly seven-segmented; aesthetascs on segments two through five in the following sequence of rows and numbers: one row (2), two rows (3, 3, + 2 setae), two rows (3, 2, + 1 seta), one row (2); sixth segment with a single elongate terminal seta plus other smaller setae.

Antenna: (Figure 9B). Peduncle three-segmented, heavily spined; flagellum with 2 or 3 fused segments plus a variable number (about 24) shorter segments each bearing 5 or 6 setae distally; terminal segment with 7 longer setae, as illustrated.

Mandible: (Figure 9C). Symmetrical, scoop-shaped process, chitinized along leading margin; a three-segmented palp, basal segment of which bearing 2 short, spinelike setae, third segment with about 13 or 14 stout, toothed spines.

Maxillule: (Figure 9D). Endopodite now possessing but a single short, terminal seta. Basal endite with 4 strong terminal setae, followed by 16 short, stout spines, 4 subterminal and 3 lateral setae; a single seta basally as shown; coxal endite lower portion extended into elongate, weakly chitinized, lobe fringed with fine hairs; 3 basal setae, 3 lateral setae, followed by 11 stout spines and 8 strong setae terminally.

Maxilla: (Figure 9E, e). Endopodite with a single, long subterminal seta. Coxal and basal endites heavily spinose and setose, numbers and position difficult to discern, but approximately as follows: basal distal lobe, about 14 terminally, 4 + 2 subterminally, 2 laterally; proximal lobe, about 6 terminally, 3 + 1 subterminally, 1 + 2 laterally; coxal distal lobe, about 3 each, terminally and subterminally, 2 + 8 in irregular row laterally; proximal lobe, about 11 placed more or less terminally, 8 subterminally, 22 in a row encircling lobe laterally, 1 + 2 beneath these; for exact positioning refer to outer (Figure 9E) or inner (Figure 9e) views of lobes. Scaphognathite with about 40

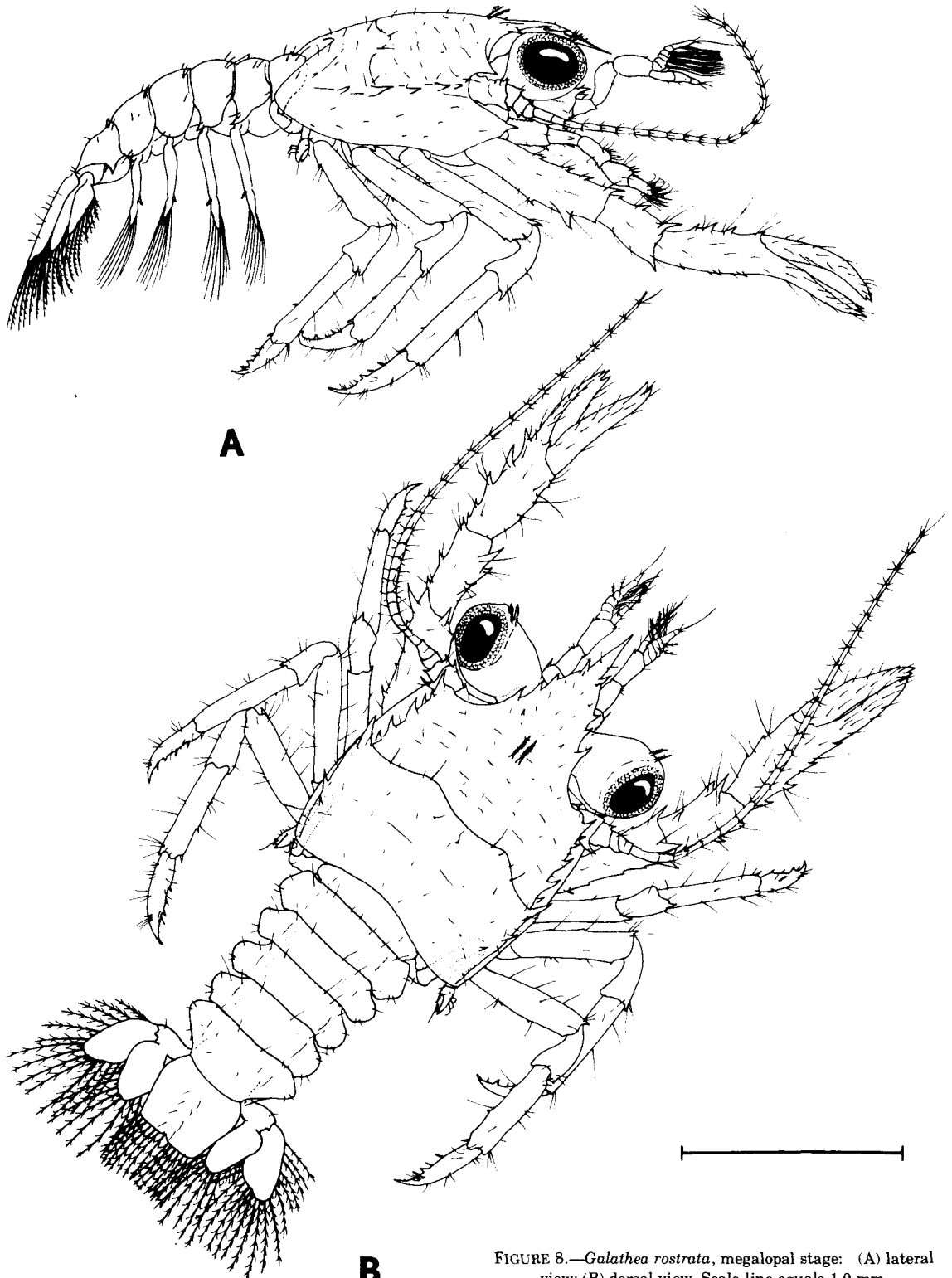


FIGURE 8.—*Galathea rostrata*, megalopal stage: (A) lateral view; (B) dorsal view. Scale line equals 1.0 mm.

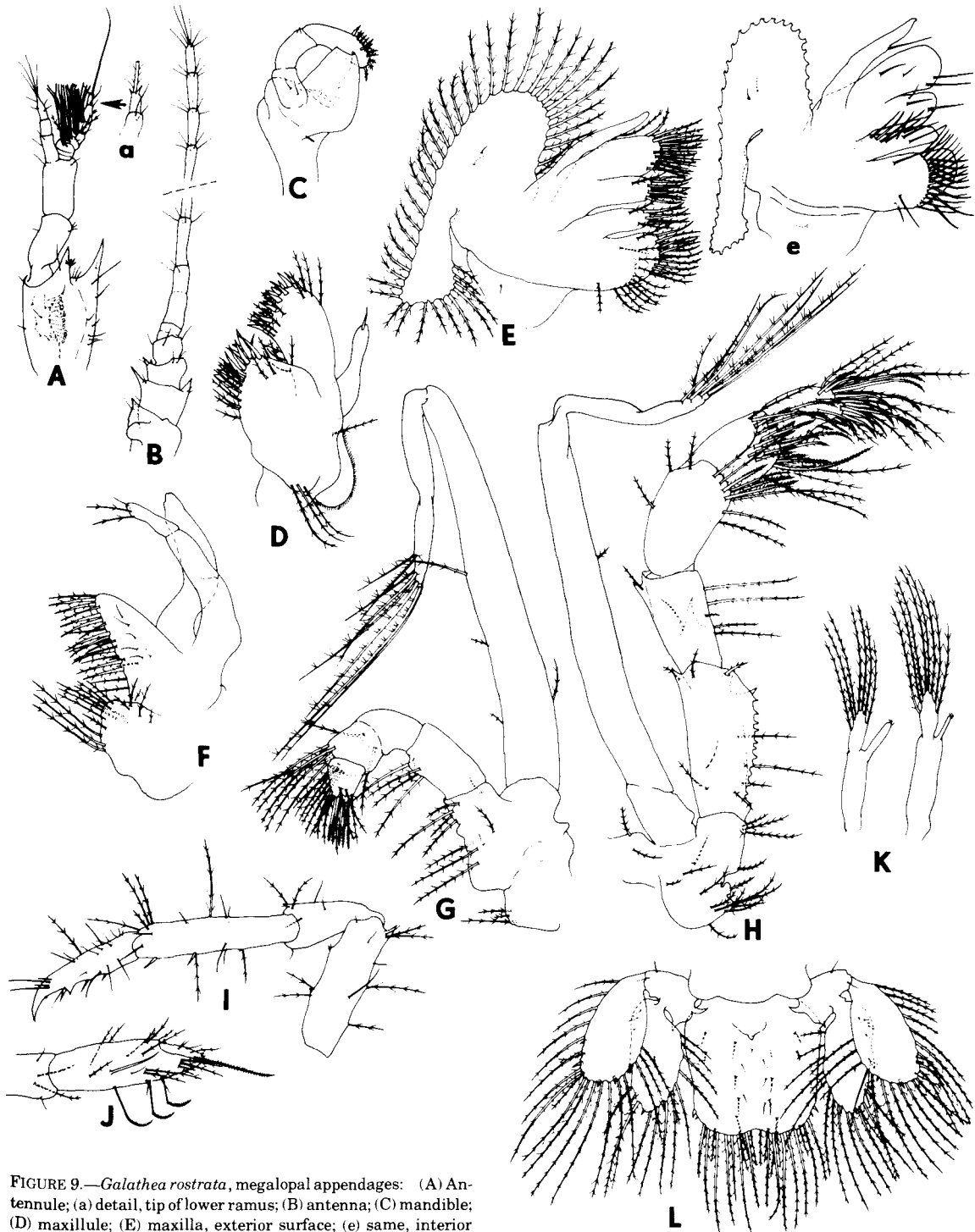


FIGURE 9.—*Galathea rostrata*, megalopal appendages: (A) Antennule; (a) detail, tip of lower ramus; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla, exterior surface; (e) same, interior surface showing only inner setation; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) pereopod 4; (J) cheliped, pereopod 5; (K) pleopod 1 (right) and 4 (left); (L) tail fan. Scale lines total 0.3 mm.

A,B,J,K,L ————
 a,C-H,J ————

marginal setae plus finer setules on either side of upper lateral surface.

Maxilliped 1: (Figure 9F). Exopodite and endopodite weakly chitinized; former two-segmented, with 3 more or less terminal setae; latter naked. Protopodite with about 27 and 15 setae on basal and coxal endites, respectively, placed as illustrated.

Maxilliped 2: (Figure 9G). Exopodite two-segmented, 8 terminal, plus other setae, as shown. Endopodite four-segmented, proximal two with 4 and 2 setae, respectively, distal two each with about 12 processes, including 5 daggerlike spines terminally. Setae on basipodite and coxopodite as illustrated.

Maxilliped 3: (Figure 9H). Exopodite two-segmented, 8 terminal setae. Endopodite five-segmented; ischium and merus each with strong, sharp triangular spine, plus a shorter spine at anterodistal angle; ischium also with prominent crista dentata; last three segments (carpus, propodus, dactylus) with 3, about 15, about 18 long daggerlike spines plus numerous longer setae interspersed among them. Several setae on coxopodite and basipodite.

Pereiopods: (Figures 8A, B; 9I, J). Chelipeds rounded, equal, elongate, heavily spined, covered with long, stiff bristlelike setae, these more prominent in gape of fingers and on outer surface of manus; fingers of each hand trifold at tips. Merus and carpus with marginal spines. Walking legs thin, elongate; merus, carpus, and propodus covered with setae plus small spinules ventrally along margins, these often difficult to discern except under higher ($40\times$ objective) magnification; propodus with 2 larger spinules ventrally; dactylus with 3 large movable spinules plus one fixed triangular tooth on ventral margin; a second, very small, almost vestigial tooth may appear about midway between larger fixed tooth and dactylar tip. Pereiopod 5 chelate, 1 long serrated seta, 3 scythelike pectinate setae quite noticeable, plus additional numerous setules on manus; 2 very small, spinulelike teeth on distal tip of dactylus.

Pleopods: (Figures 8B, 9K). Occur on somites 2-5; biramous, greatly elongate; exopodal setae progressing toward telson 8, 8, 8, 7, with minor variation of 1 or 2 occasionally seen on left or right

side in same specimen; endopodites not as long as exopodites, thin, naked, but each with appendix interna of 2 or 3 small hooks developed at tip.

Tail Fan: (Figure 9L). Telson with 6 or 7 long plumose setae, and several shorter marginal setae interspersed among these, numbers of latter inconsistent in same specimen; 1 or 2 small toothlike spines laterally, as shown. Uropods biramous, each with 4 widely separated marginal spines, that on outer lateral margin of endopodite the strongest; exopodite with about 18-20, endopodite blade with 11-14 plumose marginal setae, numbers again variable in same specimen. Smaller setae on dorsal and ventral surfaces of tail fan as illustrated.

Color: Megalopa beautifully colored. Carapace and abdomen overall red-orange, dorsolateral carapace margins and spines darker red; an irregular longitudinal white, or semitranslucent stripe extends dorsally from just behind frontal region along entire length of carapace and abdomen; this stripe bordered with darker orange-red chromatophores along its length; a similar white stripe appears laterally, below which carapace becomes translucent, but covered with numerous red spiderlike chromatophores; a third stripe appears ventrally on sternum, extending to junction of abdomen. Numerous pale blueish-white dots interspersed over dorsal surface of carapace, especially on either side of previously noted longitudinal stripe. Eyestalks orange-red, with regular white band longitudinally, this meeting second band which encircles distal margin of eyestalk just before cornea; latter black, overlain with dark red maculations. Chelipeds with distal margin of merus, entire carpus, propodus, and all but distal tip of dactylus ivory white; merus proximally red-orange; cheliped finger tips orange. Walking legs translucent, speckled with many red-orange chromatophores, these coalescing to form irregular bands on outer segments; dactyli of latter clear, or light horn color.

DISCUSSION

In the western North Atlantic Ocean the family Galatheidae is represented by four genera: *Galathea* (2 species), *Munida* (31 species), *Munidopsis* (48 species), and *Phylladorhynchus* (1 species). With the exception of the present report, the larval development of the remaining 81

galatheid species known to occur in the western Atlantic is unknown.

The majority of our knowledge on galatheid larvae comes from studies conducted on species from the eastern Atlantic and Pacific Oceans, and associated seas such as the Red, Mediterranean, or North Seas. Lebour (1930) first characterized larvae in the family Galatheidae, and Gurney (1942) was the first to provide a synopsis of larval features based on Lebour's work and studies he made on western Pacific galatheid larvae. As might be expected, only some of the characters considered important by Gurney in 1942 remain valid today, and the lack of detailed descriptions in earlier studies on galatheid larval morphology prevents comparative statements to be made among most of the species for which the larvae are known. Nevertheless, morphological differences in rostral, carapacial, antennal, abdominal, and telsonal features continue to be of some value in distinguishing the larvae of at least five galatheid genera.

In general, the larvae so far described for species of *Munida* share several features with those known from *Galathea* and *Pleuroncodes*, and are thus somewhat indicative (as seems true for the adults) of close relationships among the three genera. *Pleuroncodes*, an eastern Pacific genus, is morphologically very similar to *Munida* in several larval features, more so than are larvae of *Galathea* as presently described. As noted in the following synopses, the larvae of the three genera can be easily separated. The adults, based on present taxonomic criteria, are distinct and generic status is undoubtedly warranted.

The genus *Munidopsis*, on the other hand, is a heterogeneous grouping of forms, some adults bearing little resemblance to others in the taxon (see Mayo 1974, for discussion). The larvae from the sole species so far described, however, are certainly distinctive and do not resemble those from other genera. The genus *Munidopsis*, as presently constituted, would seem to provide an ample example of a taxon wherein the relationships among the various species (and perhaps their elevation to generic status) might be clarified on the basis of morphological relationships among their larvae.

The first zoeal larvae of the eastern Pacific species *Cervimunida johni* (Fagetti 1960) are quite spinose but could perhaps be confused with either *Munida* or *Pleuroncodes* larvae (Fagetti and Campodonico 1971). It remains to be seen

whether later larval stages would be more distinctive. The presence of a single ventral antennal spine (instead of two as seen in other genera) is of limited value, because *Galathea* and *Munida* exhibit a single spine in stage I and two spines in later stages (see below).

In the genus *Galathea*, larvae are principally known from northeastern Atlantic species described by Lebour (1930, 1931) and Sars (1889). Live specimens of these species may be separated from larvae of *G. rostrata* by chromatophore color and position, but unfortunately no further detailed comparison is possible until the former species are completely redescribed and illustrated. This holds true for most of the studies by the 19th and early 20th century authors which were listed in Gurney (1942). The "*Galathea* sp." briefly described and illustrated by Al-Kholy (1959) from the Red Sea agrees in several respects with "typical" *Galathea* larvae, but differs in others. Whether it may be equated with Gurney's (1938) *G. longimana* remains uncertain as the brief descriptions and illustrations of both authors prohibit meaningful comparison between the two studies, and those on other *Galathea* larvae.

In order to facilitate comparison between the two western Atlantic *Galathea* species a summary of larval features exhibited by *G. rostrata* is provided in Table 2. These may be applied both to *G. agassizii*, when its larvae become known, and to other *Galathea* larvae when expanded or more complete descriptions are provided. In addition, a provisional synopsis of larval characters for the five genera discussed above is also presented. The summaries have been extracted from the more reliable larval descriptions, as so noted, and may allow distinction among the more typical larvae in each genus. As our knowledge increases further modification may be required.

SYNOPSSES OF GALATHEID LARVAE

In the following section, emphasis is placed on the setal-spinal formulae of the larval telson. Conventionally, this formula may be expressed thusly: 8 + 8, indicating that eight telsonal processes, consisting of fixed and movable spines, setae, and thin hairs, occur on each side of the telsonal midline. It is apparent now that the type of these processes may provide a useful reference feature in distinguishing between the various galatheid larvae. Accordingly, spines (whether movable or fixed) are herewith denoted by Roman

TABLE 2.—Summary of zoeal features in the larval stages of *Galathea rostrata*.

	Zoea I	Zoea II	Zoea III	Zoea IV (regular)	Zoea IV (advanced)	Zoea V
Rostral spine	Not expanded proximally	Expanded proximally	Expanded proximally	Raised lateral margins	As in regular stage	Expanded proximally
Posterior carapace spines	Elongate	Elongate	Reduced	Slightly hooked	Slightly hooked	Hooked
Eyes	Sessile	Stalked	Stalked, enlarged	Stalked, elongate	Stalked, elongate	Stalked, greatly developed
Antennule	Simple rod, no lateral aesthetascs Endopod reduced	As in stage I Endopod more developed Protopod lacks lateral seta	Exopodite segmented, 2 lateral aesthetascs Protopod with 1 lateral seta	3 lateral rows aesthetascs Endopod ½ exopod length Protopod unsegmented	4 lateral rows aesthetascs Endopod subequal to exopod	5 lateral rows aesthetascs Endopod subequal to exopod Protopod segmented
Antenna	Exopod with seta Scaphocerite spine elongate	Exopod lacks seta Scaphocerite spine reduced	Exopod ½ scaphocerite length, with apical seta	Exopod subequal to scaphocerite, with apical seta	Exopod longer than scaphocerite with apical seta	Exopod much longer than scaphocerite with apical seta
Mandibles	Without palp	Without palp	Without palp	Without palp	Palp present	Palp present
Maxillipeds:						
Endopod (1)	3.2, 1.2, 4 + 1	3.2 + 1.1 - 1.2, 4 - 1	As in previous stage	and thereafter		
Endopod (2)	2.2, 2.4 + 1	2.2 + 1.2, 5 + 1	2.2 + 1.2, 5 + 1	2.2 + 1.2 + 1.5 + 1	As in previous stage	and thereafter
Endopod (3)	Bud	Less than basipod, 2 seta	Subequal to basipod, 2 seta	Longer than basipod, 3 seta	As in regular stage	Much longer than basipod, 3 seta
Exopods (1, 2)	4	7	7	8	8	8
(3)	0	6	7	8	8	8
Pereiopods	Amorphous buds	Developing buds	Developing buds	Well-formed buds	Segmented, chelated buds	Large, nearly functional
Abdomen	5 somites, lateral spines 4, 5 Pleopods absent	5 somites, spine on 4 reduced Pleopods absent	6 somites, spine on 4 vestigial Pleopods absent	6 somites, spine on 4 absent Pleopod primordia may be present	6 somites Pleopods present, undivided	6 somites Pleopods present, bifid
Uropods	Absent	Absent	Exopods present Endopods rudimentary	Exopods and endopods developed	As in previous stage	and thereafter
Telson	7 + 7 setae 4th process movable	8 + 8 setae 4th process movable	8 + 8 setae 4th process fused	8 + 8 setae As in previous stage and thereafter	8 + 8 setae	8 + 8 setae

numerals, setae by Arabic numerals, and fine hairs by lower case Roman numerals. It should also be remembered that previously movable setae may, in a subsequent stage, become fixed spines and the setal formulae will change accordingly. Thus, a setal configuration proceeding medially of a fixed spine (I), a thin hair (ii), a regular seta (3), a previously movable seta now a fixed spine (IV), followed by four movable setae (5-8) results in the telsonal formula of I + ii + 3 + IV + 5-8. While somewhat more ponderous than the previously used formula of 8 + 8, it does provide a clearer picture of the type of processes and their changes throughout subsequent larval development.

Cervimunida (Fagetti 1960)

Rostrum elongate, needlelike, noticeably denticulate; carapace posterolateral and posterior margins dentate; posterior spines extremely elongate, reaching fifth abdominal somite; antennal scaphocerite elongate, aciculate, distinctly spined along outer margin, and upper surface, basal segment with a single dorsal spine, unarmed ventrally (thus differing noticeably from other galatheids where the situation is exactly the reverse); abdominal somites spined dorsally, somites 4 and 5 with large lateral spines; telson deeply bifurcate, furcae heavily armed; setal for-

mula I + ii + 3-7 (based on first stage zoeae). Presumably four or five larval stages.

Galathea (Sars 1889; Lebour 1930, 1931)

Rostrum acute, often expanded at base, may be armed distally; carapace posterolateral margin usually spinulate or denticulate, posterior spine rarely exceeding third abdominal somite; antennal scaphocerite broad, flattened, basal segment with single spine ventrally in stage I, two spines in all other stages; posterodorsal margins of abdominal somites minutely denticulate, but may become unarmed in later stages; distinct posterolateral spines on somites 4, 5, or both but may be absent later; no median dorsal spine on somite 6; telson triangular, not deeply bifurcate in early stages, becoming more elongate and truncately triangular in later stages; lateral spines may be denticulate; marginal setal formula in stages I and II of I + ii + 3-7, 3-8, respectively, and in all later stages I + ii + 3 + IV + 5-8. Four or five larval stages, pleopods present in last stage, as primordia in penultimate stage on occasion.

Munida (Sars 1889; Lebour 1930, 1931; Rayner 1935)

Rostrum elongate, needlelike, spinulate on dis-

tolateral margins and tips in early stages, but may be unarmed in later stages; a serrated posterolateral carapace margin with noticeable posterior spine, latter often extending to about fourth abdominal somite; antennal scaphocerite elongate, thin or even noticeably aciculate, often spined; basal segment with a single ventral spine in first stage, 2 in later stages; abdominal somites 2-5 with two or more spines or spinules dorsally, margin of somite 6 with a single larger median spine from stage III onward; telson originally deeply bifurcate in early stages of development, but becoming more triangularly truncate later, thus appearing similar to that in *Galathea* in later stages; telson furcae often spined; telson setal formula $I + ii + 3-7$, $3-7$ or -8 in stages I and II and $I + ii + 3 + IV + 5-9$, $5-10$, $5-11$ or -12 in stages III-V, respectively. Four of five larval stages, pleopods present in last stage.

Munidopsis (Sars 1889; Samuelson 1972)

Rostrum broad, flattened, nearly spatulate in all zoeal stages, profusely armed about outer margins; carapace with a large, forward-directed spine on anterolateral margin; entire ventral and posterolateral margins noticeably spinulate, posterior margin rounded, lacking elongate posterior spine otherwise typical of larvae in the family; antennal scaphocerite a flattened blade, two spines ventrally; posterodorsal margins of abdominal somites unarmed, a posterolateral spine present on somite 5; telson broadly spatulate, posterior marginal setal formula $1 + 2 + iii + IV + 5-15$ in stage I, and $I + 2 + iii + IV + 5-15$ in stages II and III; other smaller hairs interspersed among setae 5-15. Three larval stages, pleopods present in each.

Pleuroncodes (Boyd 1960; Fagetti and Campodonico 1971)

Rostrum flattened basally, expanded similarly to that of *Galathea*, distal portion acute, margins noticeably spinulate, especially at tip; posterolateral carapace margins serrated, elongate posterior spines usually extending to fourth abdominal somite; antennal scaphocerite narrow, not as aciculate as in some *Munida*, basal segment with either 1 or 2 ventral spines; abdominal somites 1-5 heavily spined dorsally on posterior margins, becoming somewhat reduced in spination in later stages; somite 6 with a median dorsal spine in stage III

and later; telson deeply bifurcate in stages I and II, becoming more truncately triangular in later stages as in *Munida* and *Galathea*; furcae may be denticulate; marginal setal formula $I + ii + 3-7$, $3-8$ in stages I and II, and $I + ii + 3 + IV + 5-9$, $5-10$, and $5-12$ in stages III-V, respectively. Five larval stages, including up to eight substages in stage IV; stage VI in laboratory culture; pleopods present in stage V. The genus is presently restricted to the eastern Pacific Ocean.

ACKNOWLEDGMENTS

I thank my laboratory assistants Kim A. Wilson and Nina Blum for their aid in field collections and in laboratory culture of the larvae. Robert M. Avent and the Coral Biology Section of the Harbor Branch Science Foundation Laboratory obtained the ovigerous females which provided the larvae used in this study. Susan Bass and Karen Rodman recorded data and helped in the laboratory during their tenure on Harbor Branch Foundation and Smithsonian Institution Fellowships.

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A THEORETICAL EXAMINATION OF SOME ASPECTS OF THE INTERACTION BETWEEN LONGLINE AND SURFACE FISHERIES FOR YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

This paper explores several aspects of a dual fishery (surface and longline) on yellowfin tuna, *Thunnus albacares*. The work is exploratory in nature and results, though indicative, are not conclusive for any specific fishery. Our results indicate that the yield per recruit is higher for the longline fishery than for surface gear if all fish are available to both gears and higher for the combined gears than for either gear fishing alone. The effect of fishing by one gear on yield to the other gear and the effect of the fishery on stock fecundity is shown to be greater for the often assumed 1:1 sex ratio than for the ratios usually observed. A simulation model was used to examine the interrelations of pattern of movement of fish, pattern of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either only along the coast or throughout the fishing area. The results indicated that either of these patterns of recruitment could allow for increased catch as the surface fleet moved offshore. However, location or pattern of recruitment is shown to be important when measuring natural mortality and for examining the potential of a localized fishery, primarily on younger fish, relative to a fishery exploiting the full range of the stocks or to one taking primarily older fish. Tagging and fecundity studies are suggested for further investigation of the questions examined in this paper.

An unsolved problem common to many of the tuna fisheries of the world is the nature of the interaction between longline and surface (i.e., seining, pole and line, and occasionally trolling and shallow handline) fisheries for the same species. Fisheries for yellowfin tuna, *Thunnus albacares*; albacore, *T. alalunga*; bluefin tuna, *T. thynnus*; southern bluefin tuna, *T. maccoyii*; and bigeye tuna, *T. obesus*, are prosecuted by both types of gear in the Pacific, Atlantic, and Indian Oceans. Although there can be considerable overlap of sizes of fish taken by the two types of gear, in general, longline gear takes larger (older) fish. Exploitation of a tuna stock by the two types of gear presents management with the problems of determining the effect of various combinations of fishing effort by the two gears on both yield per recruit to the two gears and recruitment to the stocks. In order to make these determinations, it is necessary to estimate 1) availability of the stock at each age to each of the two gears [The available portion of the stock is subject to both other mortal-

ity (any mortality not caused by gear of concern) and fishing mortality caused by the gear of concern. The unavailable portion of the stock is subject only to other mortality.], 2) fishing mortality of the available portion of the stock caused by each gear, 3) natural mortality, 4) growth, 5) fecundity, and 6) the relationship between egg production and recruitment.

The aim of this paper is to examine the interactions between longline and surface fisheries for yellowfin tuna and to determine the impact such interactions may have on the assumptions often made in assessment of yellowfin tuna fisheries and thus on the assessment calculations themselves. The paper is divided into three major sections. The first section examines the relationship between availability of the stock(s) of yellowfin tuna to surface and longline fishing and yield per recruit to the two gears. This is an important, and to our knowledge unexamined, aspect of all tuna fisheries exploited by both types of gear; the subsequent sections examine two aspects of the biology of tuna that can affect the catch by each type of gear. The second section examines the effect of age specific sex ratios of yellowfin tuna on yield per recruit to the two types of gear and on egg production. The third section examines the effect of

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