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COMPLETE LARVAL DEVELOPMENT OF *GALATHEA INTERMEDIA* LILLJEBORG REARED IN LABORATORY CULTURE (ANOMURA: GALATHEIDAE)

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ABSTRACT

Larvae of the East Atlantic anomuran crab *Galathea intermedia* Lilljeborg were reared in the laboratory from hatching to the first juvenile stage. The larvae were kept in 31–32‰ S sea water at 15°C. The complete larval development consists of 4 or 5 zoeal stages and 1 megalops stage. The larval stages are described and morphological characters are compared with those of the West Atlantic species *Galathea rostrata* A. Milne Edwards described by Gore (1979).

Galathea intermedia Lilljeborg, 1851, occurs along the eastern coasts of the Atlantic from northern Norway (Christiansen, 1972) to Dakar (Zariquiey Alvarez, 1968). The species has also been reported from Angola, and it occurs in the entire Mediterranean (Holthuis, 1961). It is most common in depths between 8 and 100 m (Holthuis, 1950). It is a very common species in all deeper parts of the German Bight (North Sea), living in particularly high numbers between mollusc shells near the island of Helgoland (Caspers, 1950). Its meroplanktonic stages were the most abundant anomuran larvae in this area, occurring from June through October (Fiedler, 1987).

The larvae of *G. intermedia* were dealt with by Sars in 1889. He described the larvae of the three species of *Galathea, G. intermedia, G. nexa* Embleton, and *G. squamifera* Leach together, figuring certain stages, and only the "last larval stage" and the "first postlarval stage" of *G. intermedia.* Webb (1921) gave a short description of "four larval stages" of the genus *Galathea* based on the four species *G. dispersa* Bate, *G. intermedia, G. squamifera,* and *G. strigosa* (Linnaeus) recorded in "Plymouth Marine Invertebrate Fauna," with figures of the "first larval stage" of *G. squamifera,* and telson and uropods of the "fourth larval stage" of *Galathea* sp. Based on larvae hatched from eggs and larvae from plankton, Lebour (1930, 1931) described larval stages of *G. dispersa, G. strigosa, G. squamifera,* and *G. intermedia* and made a key of the zoeal larvae of the four species. Unfortunately, the descriptions and figures by Lebour are of limited value for identifying larvae from plankton. Bull (1937) described the first and second zoeal stages of *G. nexa* and expanded Lebour's key to include the larvae of all five British species of *Galathea.* Gurney (1939, 1942) referred to Sars' and Lebour's descriptions of larvae of *G. intermedia.* Pike and Williamson (1972) made keys to zoeal and megalops stages of Galatheidae in which *G. intermedia* is included.

The first complete description of all larval stages of a species of *Galathea* was published by Gore (1979), who cultured larvae of the western North Atlantic species *G. rostrata* A. Milne Edwards in the laboratory. As he pointed out, "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." The present paper gives a complete description of all larval stages of a second species, *G. intermedia.* The larvae were reared from hatching to the first crab stage under laboratory conditions, and their morphology is compared with that of *G. rostrata.*

MATERIALS AND METHODS

Ovigerous females of *Galathea intermedia* were collected in August 1982, 1983, 1984, and 1987 from a depth of approximately 30–40 m near the island of Helgoland (German Bight, North Sea). The females were maintained in aquaria containing natural sea water (31–32‰ S) at 15°C until the eggs hatched (August/early September). Newly hatched larvae were transferred to glass bowls with approximately 400 ml filtered (1 μm) sea water (31–32‰ S). The initial density of larvae was 50 individuals per bowl. The glass bowls were kept at a constant temperature of 15°C and the larvae were exposed to a light regime of 16 h light and 8 h dark. The larvae were provided daily with a mixture of freshly hatched nauplii of *Artemia* sp. (San Francisco Bay Brand) (approximately 10/ml) and rotifers (*Brachionus plicatilis* (O. F. Müller)) (approximately 100/ml). Molts and dead individuals were recorded daily when water was changed.

In order to verify larval stages and the exact number

Table 1. Duration of stages (days) in larvae from one female of *Galathea intermedia* reared under laboratory conditions at 15°C. Larvae were reared in mass culture until zoea IV. From then on, larvae were reared separately in vials. (N = number of larvae; SD = standard deviation.)

Stages	Days			N
	Minimum	Maximum	Mean ± SD	
Zoea I	6	7	18.1 ± 1.5	78
Zoea II	5	8		
Zoea III	4	10		
Zoea IV → megalopa	8	9	8.7 ± 0.5	15
Zoea IV → zoea V	5	7	5.9 ± 0.6	44
Zoea V	7	10	7.9 ± 0.8	25
Megalopa (from zoea IV)	8	8		1
Megalopa (from zoea V)	9	13	11.0 ± 1.0	15

of molts, larvae were also reared individually in vials with 20 ml of sea water. The time of development given in the present paper is based on larvae from one female. The eggs hatched on 9 September 1987, and the larvae were reared at 15°C in mass culture (see above) until the third zoeal stage. From the fourth stage, the larvae were kept individually in vials.

Larvae and exuviae were preserved in 4% buffered formaldehyde. All stages were examined microscopically, slides prepared, and drawings made as described previously by Christiansen (1973). Descriptions are based on exuviae and preserved larvae. The abbreviations TL and CL refer to total length and carapace length, respectively. TL is measured from the rostral tip to the most posterior edge of the telson (the processes not included); CL is measured from the rostral tip to the posterior midpoint of the carapace. Since the abdomen of the majority of preserved larvae was more or less curved, total length was measured only in a limited number of individuals in the 3 first zoeal stages. Chromatophore color and position in live specimens were not recorded (for description of color see Lebour (1931)).

Results

Ovigerous females of *Galathea intermedia* collected in August hatched their eggs in August or September. The larvae developed through four or five zoeal stages and a megalops stage before metamorphosing to the first crab stage. The survival of zoeal larvae was high both in mass and individual culture, whereas many megalops larvae died during molting to the first crab stage.

The duration of the zoeal and megalops stages in larvae from one female reared at 15°C is shown in Table 1. Larvae which passed slowly through the first three zoeal stages tended to develop through a fifth zoeal stage, whereas larvae which developed quickly through the first three stages tended to go directly from zoea IV to the megalops stage. The duration of the fourth zoeal stage was shorter (5–7 days) for larvae that developed to a fifth zoeal stage than for those molting directly to the megalops stage (8–9 days) (Table 1).

Description of the Larvae

First Zoea

Size.—TL 1.9–2.0 mm, 5 specimens measured; CL 0.9–1.0 mm, 10 specimens measured.

Carapace (Figs. 1A, 2A).—Rostrum well developed, extending almost to level of scaphocerite spine or slightly beyond; carapace produced into spine posteriorly on either side, posterolateral and dorsomedial margins armed with approximately 10–12 small denticles each; eyes sessile.

Abdomen (Figs. 1A, 2A).—Five somites and telson; somite 5 with small lateral spines; somites 2–5 with small paired setae dorsally; no pleopod buds.

Telson (Fig. 3A).—Posterior margin with U-shaped median cleft and 7+7 processes, outermost an immovable naked spine, second an anomuran hair, third to seventh long stout plumodenticulate spines, setae and minute spinules along posterior margin.

Antennule (Fig. 4A).—Elongate, rod-shaped, 3 aesthetascs and 3 setae terminally; 1 long, plumose terminal seta on endopodal bud.

Antenna (Fig. 5A).—Scaphocerite with tip produced into long spine, inner margin with 9 or 10 plumose setae, additional spinules along ventral outer margin; endopod about one-third of scaphocerite length, fused to protopod, rod-shaped with single spine at its tip and long terminal plumose seta; 1 strong protopodal spine ventrally at base of

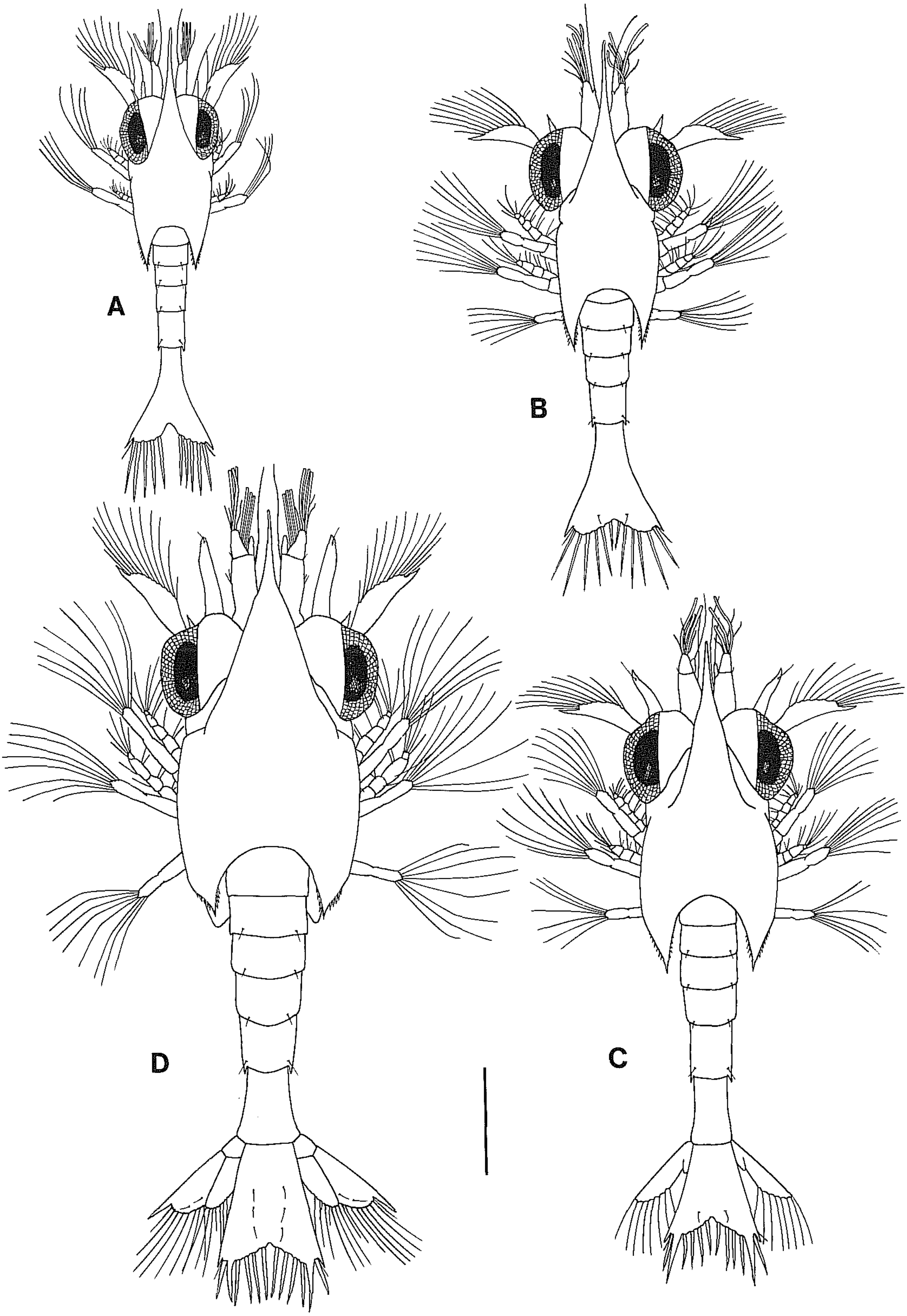

Fig. 1. *Galathea intermedia*: zoeal stages, dorsal views. A, zoea I; B, zoea II; C, zoea III; D, zoea IV. Scale bar = 0.5 mm.

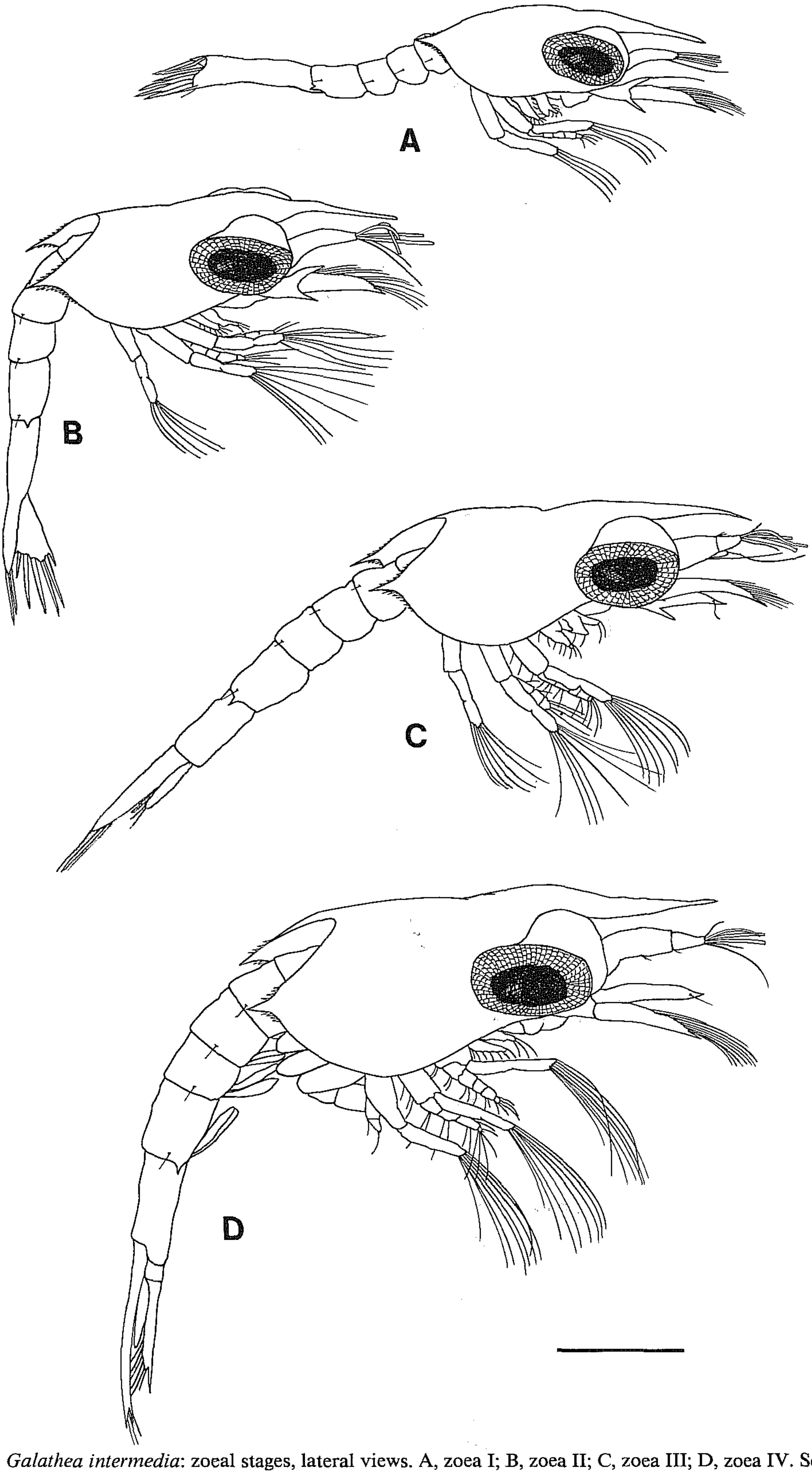

Fig. 2. *Galathea intermedia*: zoeal stages, lateral views. A, zoea I; B, zoea II; C, zoea III; D, zoea IV. Scale bar = 0.5 mm.

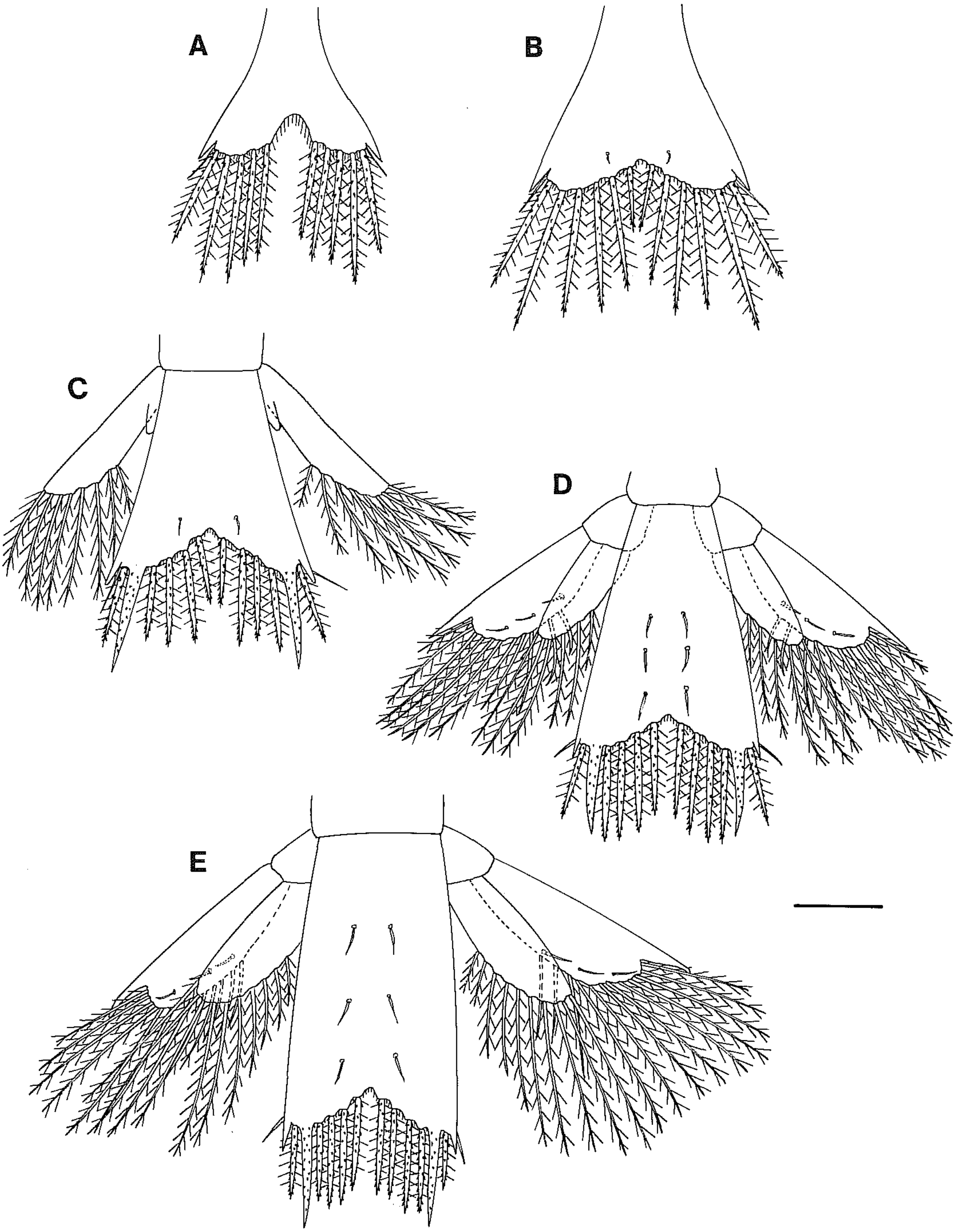

Fig. 3. *Galathea intermedia*: zoeal stages, telsons, dorsal views. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.2 mm.

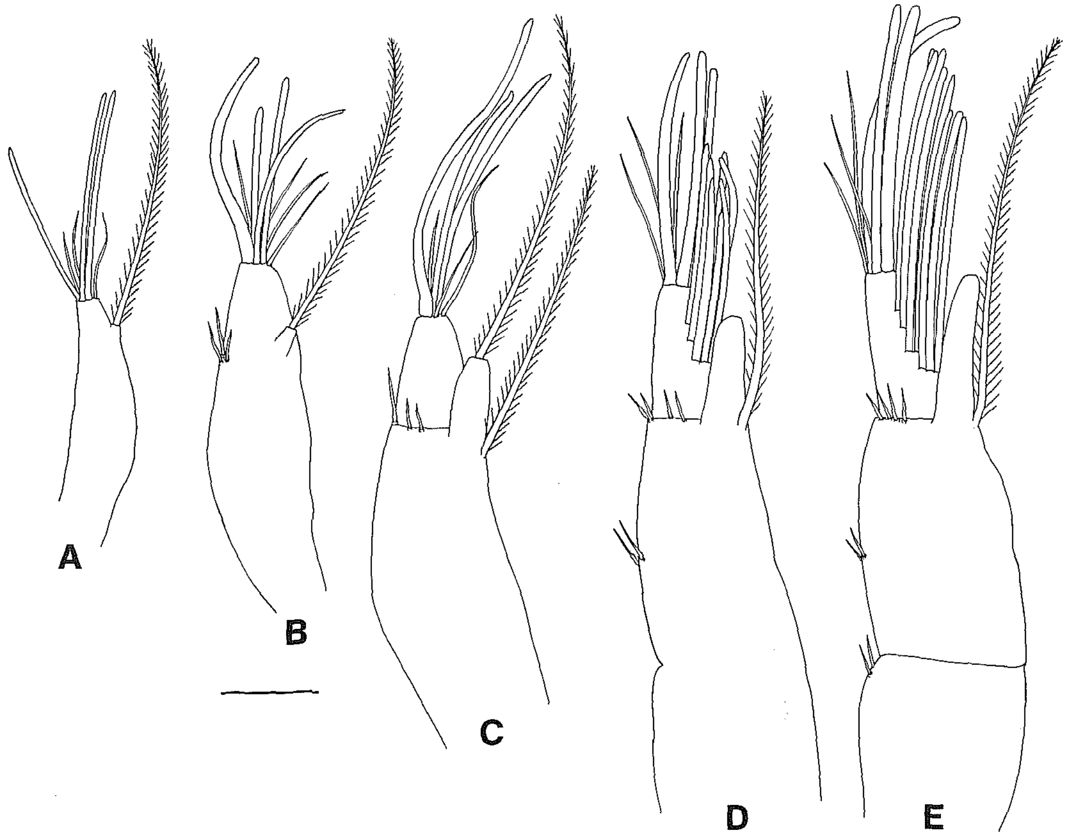

Fig. 4. *Galathea intermedia*: zoeal stages, antennules. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.1 mm.

endopodal junction armed with marginal spinules, spine nearly as long as endopod.

Mandible (Fig. 6A).—Asymmetrical, heavily dentate processes, large teeth on incisor process, smaller ones on molar process; no palp bud.

Maxillule (Fig. 7A).—Endopod 2-segmented, 4 terminal, 1 subterminal setae; coxal endite with 6 or 7 spines/setae, basal endite with 5 spines/setae, 2 of them very strong spines.

Maxilla (Fig. 8A).—Endopodal spines/setae progressing subterminally, 4,2, plus 3 laterally, fine hair along margin as illustrated; coxal and basal endites bilobed, coxal endite with 6 or 7,3, and basal endite with 4,4 spines/setae on proximal and distal lobes, respectively; scaphognathite with 4 lateral plumose setae, plus long plumose posterior process.

Maxilliped 1 (Fig. 9A).—Coxopod with 2 setae; basipod with setal formula 2,3,3,3 progressing distally; endopod 5-segmented, setal formula progressing distally 3,2,1,2,4+I (Roman number denoting dorsal seta); exopod incompletely 2-segmented, 4 plumose natatory setae.

Maxilliped 2 (Fig. 10A).—Coxopod naked; basipodal setae 1,2 progressing distally; endopod 4-segmented, setal formula progressing distally 2,2,2,4+I; exopod incompletely 2-segmented, 4 plumose natatory setae.

Maxilliped 3 (Fig. 11A).—Small unsegmented bud.

Pereiopods.—Small buds.

Second Zoea

Size.—TL 2.3–2.4 mm, 5 specimens measured; CL 1.1–1.2 mm, 10 specimens measured.

Carapace (Figs. 1B, 2B).—Slightly larger and more inflated than in previous stage; posterolateral and dorsomedial margins with approximately 11 and 7 small denticles, respectively; eyes stalked.

Abdomen (Figs. 1B, 2B).—As in zoea I, but slightly larger.

Telson (Fig. 3B).—Median U-shaped cleft on posterior margin reduced from zoea I; posterior marginal formula now 8+8 with addition of pair of median spines shorter than spines 3–7.

Antennule (Fig. 4B).—Four aesthetascs and 4 setae terminally, 3 short marginal setae at level of endopodal bud; endopod retaining long plumose seta.

Antenna (Fig. 5B).—Inner margin of scaphocerite usually with 10 plumose setae; endopod thickened, drawn into point distally, lacking long terminal plumose seta seen in zoea I; protopod now with second spine ventrally, armed as other ventral spine along outer margins but smaller; larger ventral spine slightly shorter than endopod.

Mandible (Fig. 6B).—Nearly as in zoea I, but larger.

Maxillule (Fig. 7B).—Endopod unchanged, coxal endite with 7 spines/setae, basal endite with 7 spines/setae, 4 of them very strong spines.

Maxilla (Fig. 8B).—Endopod unchanged; coxal endite with 7 or 8,3 or 4, and basal endite with 4 or 5,4 spines/setae on proximal and distal lobes, respectively; scaphognathite with 6 lateral plumose setae, plus long plumose posterior process.

Maxilliped 1 (Fig. 9B).—Coxal, basal, and endopodal setation unchanged from zoea I; exopod with 7 natatory setae.

Maxilliped 2 (Fig. 10B).—Basal setation unchanged from zoea I; endopodal formula now 2,2+I,2,4+I; exopod with 7 natatory setae.

Maxilliped 3 (Fig. 11B).—Basipod naked; endopod bud incompletely 2-segmented with 1 plumose seta terminally; exopod indistinctly 2-segmented with 6 natatory setae.

Pereiopods.—Undifferentiated buds.

Third Zoea

Size.—TL 2.5–2.7 mm, 5 specimens measured; CL 1.2–1.4 mm, 10 specimens measured.

Carapace (Figs. 1C, 2C).—Slightly larger than in previous stage, posterolateral and dorsomedial margins with approximately 7 and 5 small denticles, respectively.

Abdomen (Figs. 1C, 2C, 3C).—Six somites; distinct lateral spines only on somite 5; small swellings ventrally on somites 2–5 sometimes present, indicating position of pleopod buds; uropods present at junction of abdominal somite 6 and proximal margin of telson, exopod well developed with usually 8 marginal plumose setae, endopods, if present, naked buds.

Telson (Fig. 3C).—Marginal processes 8+8, fourth pair fused to telson, with minute spinules, processes 3,5–8 armed as in previous stage.

Antennule (Fig. 4C).—Exopod distinctly segmented from protopod, with 3 aesthetascs and 3 setae terminally; endopod enlarged from previous stage retaining long plumose seta terminally; protopod with long plumose seta near base of endopod plus 2 or 3 short setae distally at junction of exopod.

Antenna (Fig. 5C).—Inner margin of scaphocerite with 10 or 11 plumose setae; endopod enlarged from previous stage with subterminal seta; two spines on protopod retained.

Mandible (Fig. 6C).—Generally similar to previous stage, but larger.

Maxillule (Fig. 7C).—Endopod unchanged; coxal endite with 7 or 8, basal endite with 8 spines/setae.

Maxilla (Fig. 8C).—Endopod unchanged, coxal endite with 8,4, and basal endite with 4 or 5,6 spines/setae on proximal and distal lobes, respectively; scaphognathite with 9 or 10 marginal plumose setae, plus long plumose posterior process.

Maxilliped 1 (Fig. 9C).—Coxal, basal, and endopodal setation unchanged; exopod with 8 natatory setae.

Maxilliped 2 (Fig. 10C).—Basal setation unchanged, endopodal formula 2,2+I, 2+I,4+I; exopod with 8 natatory setae.

Maxilliped 3 (Fig. 11C).—Endopod 2-segmented with 1 terminal seta; exopod with 7 natatory setae.

Pereiopods.—More developed than in pre-

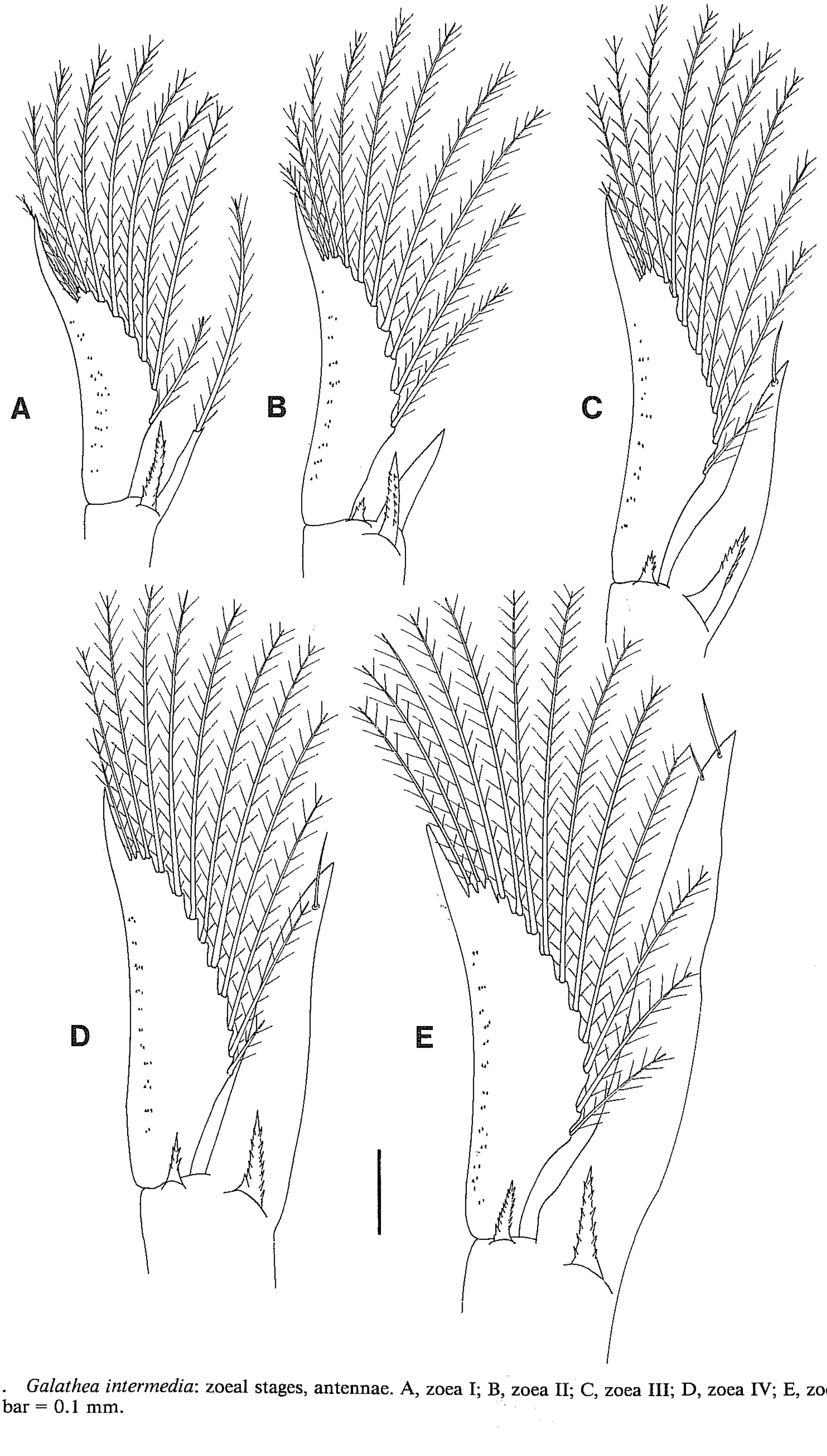

Fig. 5. *Galathea intermedia*: zoeal stages, antennae. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.1 mm.

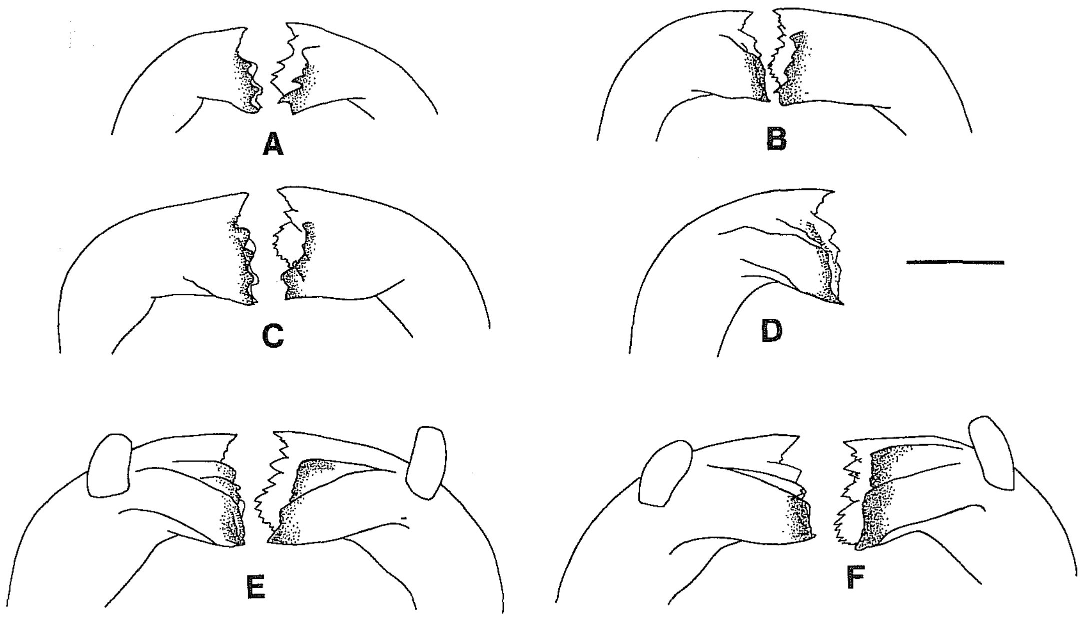

Fig. 6. *Galathea intermedia*: zoeal stages, mandibles. A, zoea I; B, zoea II; C, zoea III; D, zoea IV without palp; E, zoea IV with palp; F, zoea V. Scale bar = 0.1 mm.

vious stage, some with incipient segmentation, partial chelation of first pair.

Fourth Zoea

Description of this stage includes both larvae which molted directly from zoea IV to megalopa as well as zoea IV larvae which went through a fifth zoeal stage before molting to megalopa.

Size.—CL 1.4–1.7 mm, 10 specimens measured.

Carapace (Figs. 1D, 2D).—Enlarged from previous stage; rostrum still extending almost to level or slightly overreaching scaphocerite spine; posterior spines shorter than in previous stage, posterolateral and dorsomedial margins with 4 or 5 and 3 or 4 small denticles, respectively.

Abdomen (Figs. 1D, 2D, 3D).—Pleopod buds present on somites 2–5, length varying between specimens, some with also short endopodal buds on pleopods; uropods completely developed, distal outer tip of exopod produced into long spine, 10 or 11 marginal plumose setae present, endopod with variable number of plumose setae, 3–7; other setae as illustrated. Exuviae of larvae molting from zoea IV to megalopa tending to have higher number of endopodal setae on uropods than exuviae of those larvae passing through fifth zoeal stage.

Telson (Fig. 3D).—Marginal processes as in previous stage; other setae as illustrated.

Antennule (Fig. 4D).—Exopod with 3 rows of lateral aesthetascs, numbering distally 3,2 or 3,2, plus 3 aesthetascs and 3 setae at tip; endopod varying in length from 0.5 to nearly equal length of exopod, terminal plumose seta absent; protopod retaining long plumose seta distally, 4 short setae distally at junction of exopod, plus 2 setae medially.

Antenna (Fig. 5D).—Inner margin of scaphocerite with 11 or 12 plumose setae; endopod enlarged from previous stage, from 0.75 to slightly longer than scaphocerite, retaining subterminal seta; 2 spines on protopod retained.

Mandible (Fig. 6D, E).—Enlarged, heavily toothed processes, some specimens with, others without, palp. Exuviae of larvae molting from zoea IV to megalopa having palp, whereas exuviae of larvae molting to zoea V not having palp.

Maxillule (Fig. 7D).—Endopod unchanged; coxal endite with 8, basal endite with 9–11 spines/setae.

Maxilla (Fig. 8D).—Endopod unchanged,

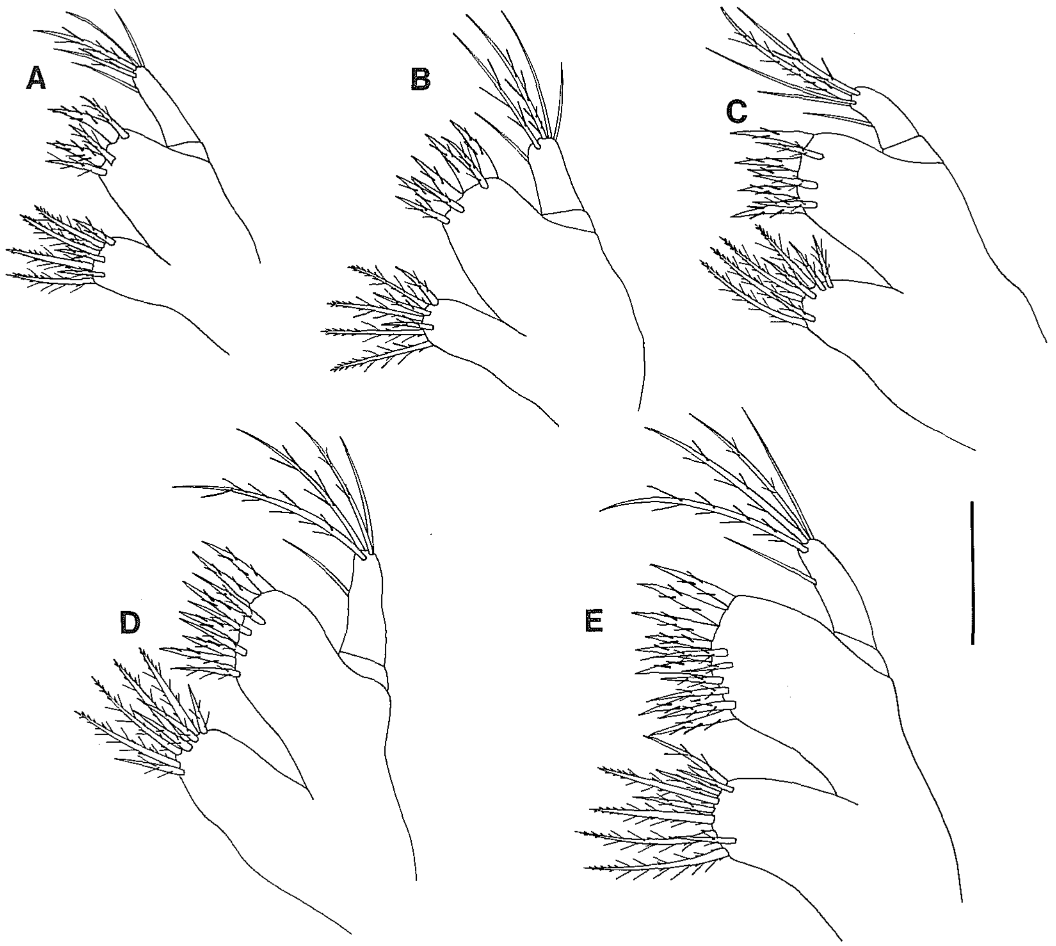

Fig. 7. *Galathea intermedia*: zoeal stages, maxillules. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.1 mm.

coxal endite with 8–11,4, and basal endite with 4–6,5–7 spines/setae on proximal and distal lobes, respectively; scaphognathite with 12–16 marginal plumose setae, including 1 or 2 anteriorly near base, plus long posterior plumose process.

Maxillipeds 1 and 2 (Figs. 9D, 10D).—Unchanged from previous stage.

Maxilliped 3 (Fig. 11D).—Endopod enlarged, overreaching basipod, bearing 2 setae; exopod with 8 natatory setae.

Pereiopods.—More developed than in previous stage, chelation and segmentation more or less apparent.

Fifth Zoea

Size.—CL 1.5–1.6 mm, 10 specimens measured.

Carapace.—As in zoea IV; in some specimens posterolateral and dorsomedial margins unarmed.

Abdomen (Fig. 3E).—Pleopods long bifid buds; uropods with variable number of marginal plumose setae, exopod with 11–13, endopod with 8–11.

Telson (Fig. 3E).—Slightly longer than in previous stage; occasionally 1 or 2 extra plumodenticulate spines on posterior margin, formula then 8+9 or 9+9.

Antennule (Fig. 4E).—Exopod with 4 rows of aesthetascs laterally, numbering distally, 3,2,2,2, plus 3 aesthetascs and 3 setae at tip; endopod from about 0.75 to equal in length to exopod; protopod segmented into basipod and coxopod, former with long plumose seta and 4 short setae distally, plus 2

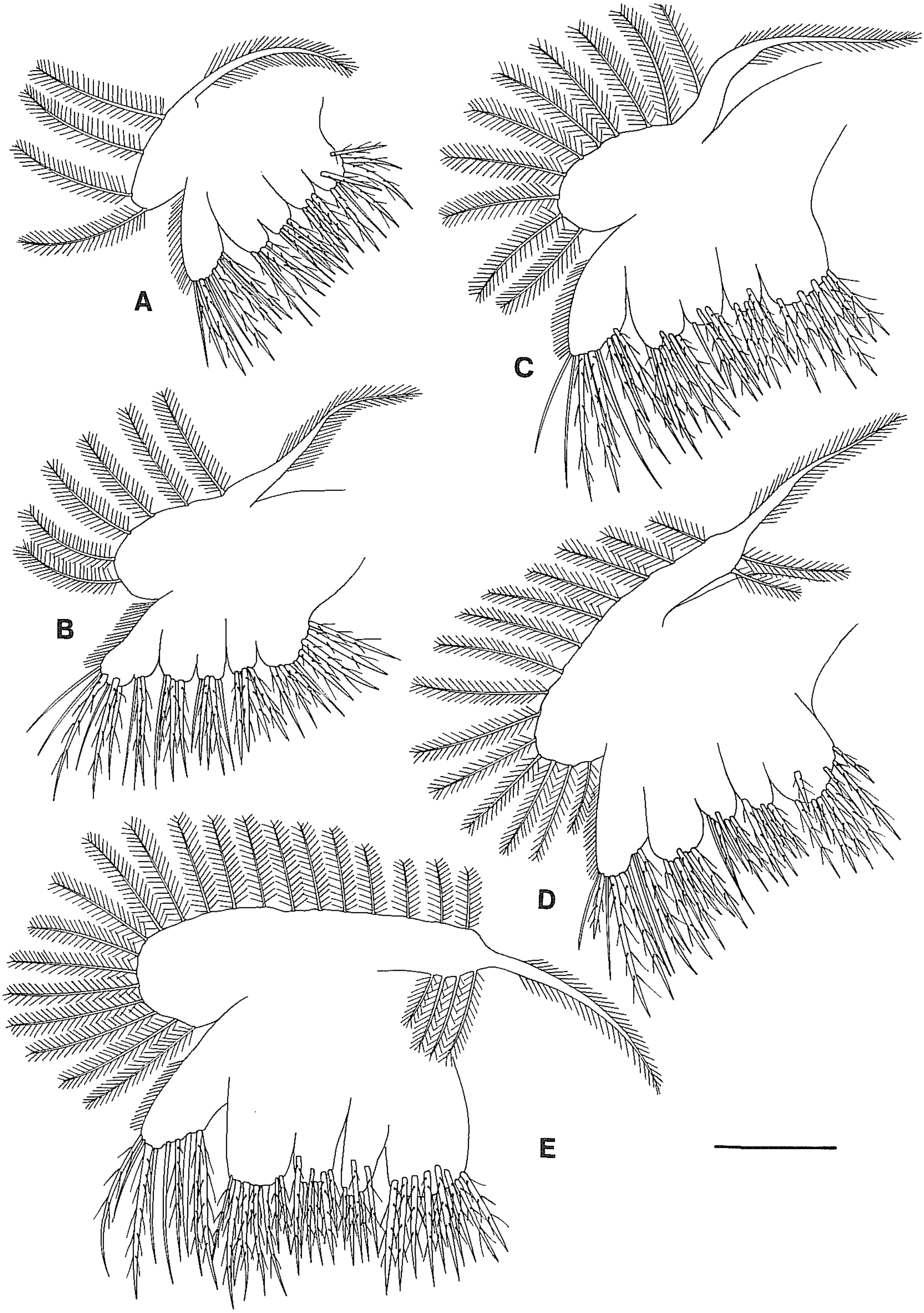

Fig. 8. *Galathea intermedia*: zoeal stages, maxillae. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.1 mm.

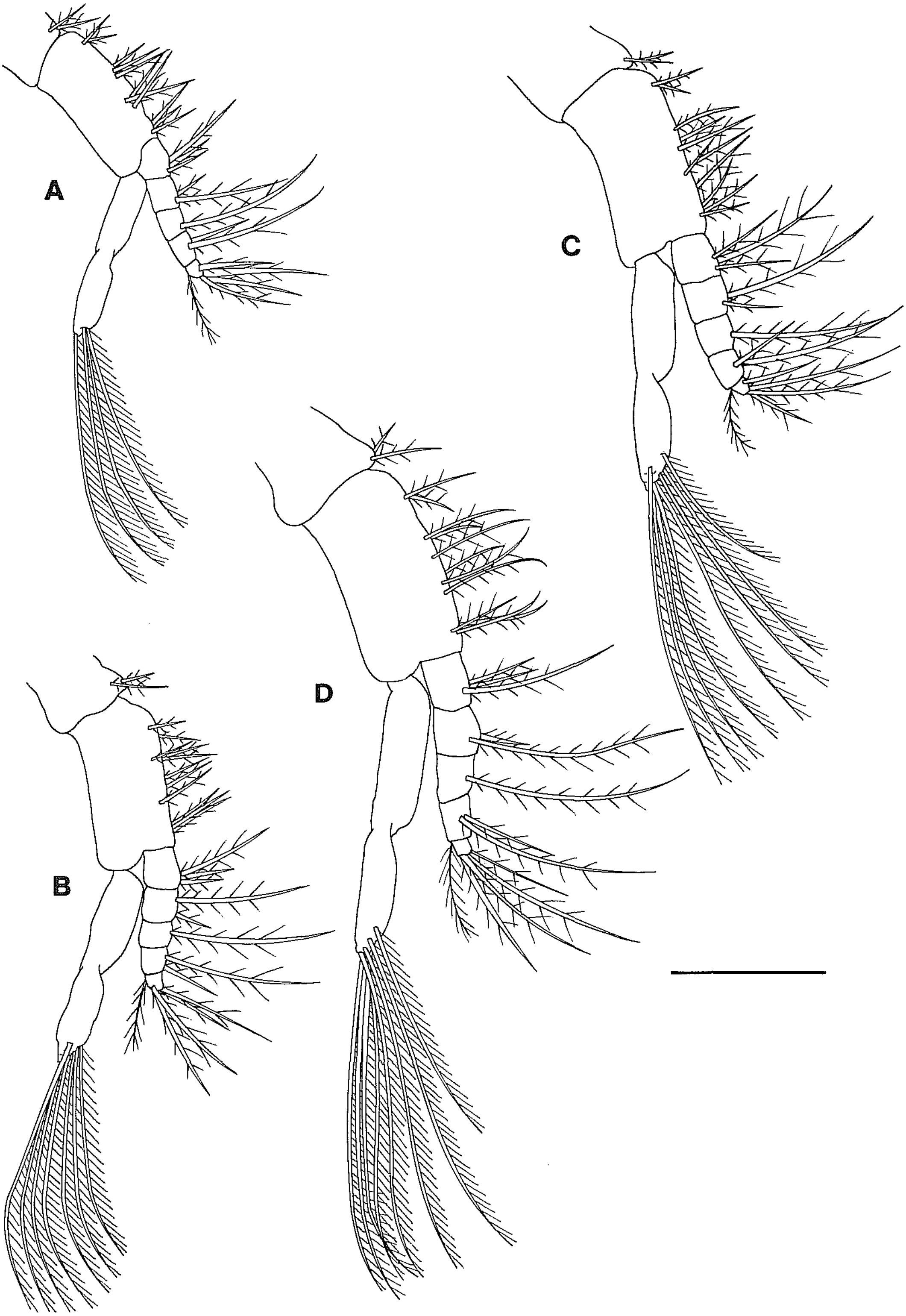

Fig. 9. *Galathea intermedia*: zoeal stages, first maxillipeds. A, zoea I; B, zoea II; C, zoea III; D, zoea IV. Scale bar = 0.2 mm.

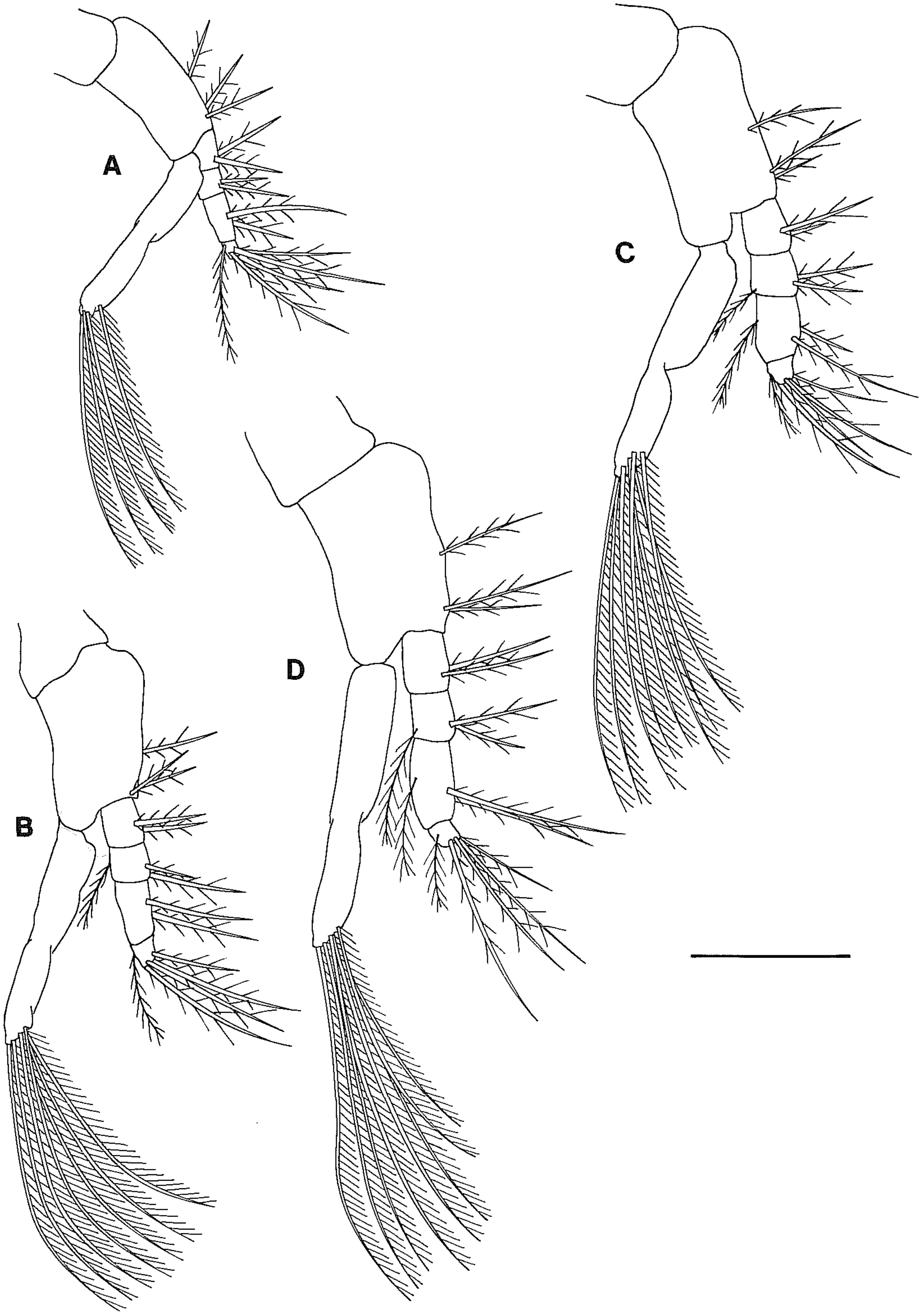

Fig. 10. *Galathea intermedia*: zoeal stages, second maxillipeds. A, zoea I; B, zoea II; C, zoea III; D, zoea IV. Scale bar = 0.2 mm.

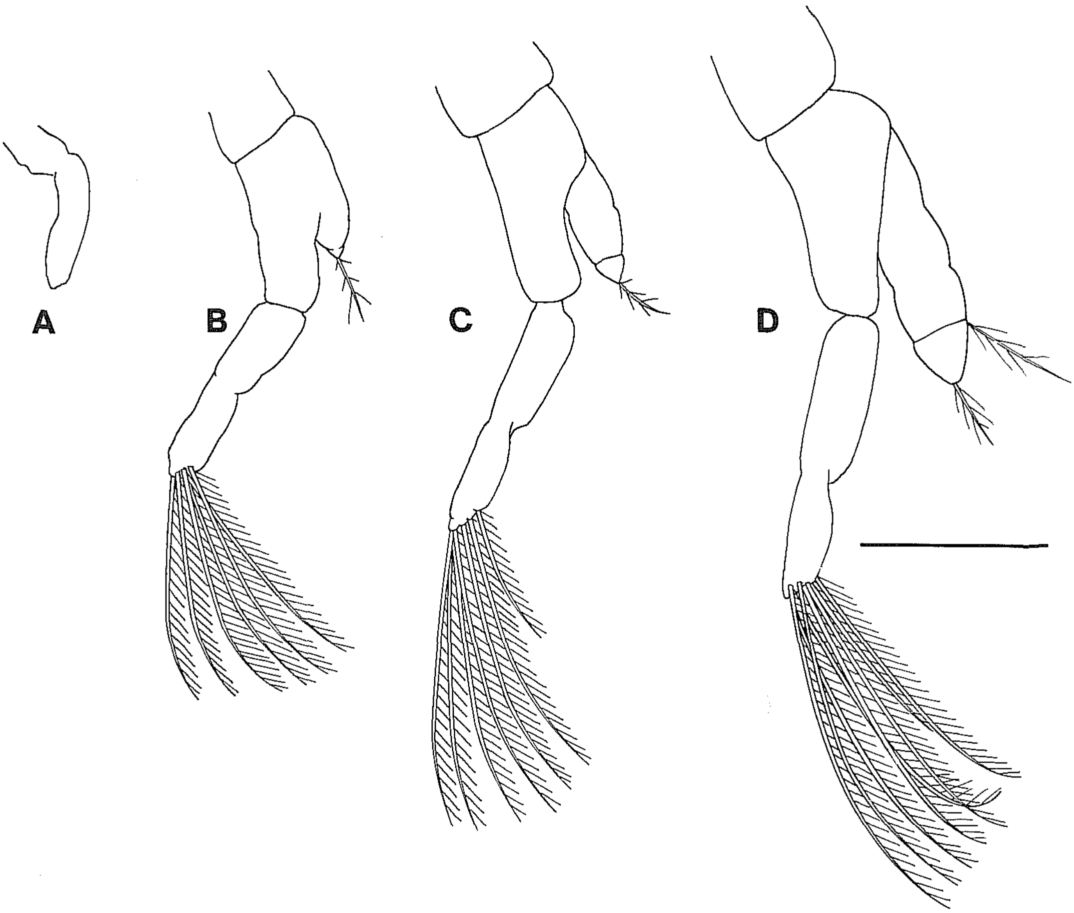

Fig. 11. *Galathea intermedia*: zoeal stages, third maxillipeds. A, zoea I; B, zoea II; C, zoea III; D, zoea IV. Scale bar = 0.2 mm.

setae medially as in previous stage, latter with 2 setae terminally near junction of basipod.

Antenna (Fig. 5E).—Inner margin of scaphocerite with 11–13 marginal setae; endopod noticeably longer than scaphocerite with 1–3 subterminal setae; otherwise as in previous stage.

Mandible (Fig. 6F).—Similar to previous stage, with palp.

Maxillule (Fig. 7E).—Endopod unchanged; coxal endite with 9, basal endite with 13–15 spines/setae.

Maxilla (Fig. 8E).—Endopod unchanged; coxal endite with 8–11,4 or 5, and basal endite with 4–6,7 or 8 spines/setae on proximal and distal lobes, respectively; scaphognathite with 19–24 marginal plumose setae, including 3 or 4 anteriorly near base, plus long posterior plumose process.

Maxillipeds 1 and 2.—Essentially unchanged from previous stage.

Maxilliped 3.—Essentially unchanged, except endopod longer than in previous stage.

Pereiopods.—Enlarged from previous stage, chelation of cheliped and segmentation of walking legs distinctly visible.

Megalopa

Size.—CL 1.6–1.8 mm, 10 specimens measured.

No apparent differences in size were found between megalopa larvae which molted directly from zoea IV and those which went through a fifth zoeal stage.

Carapace (Fig. 12A, B).—Resembling min-

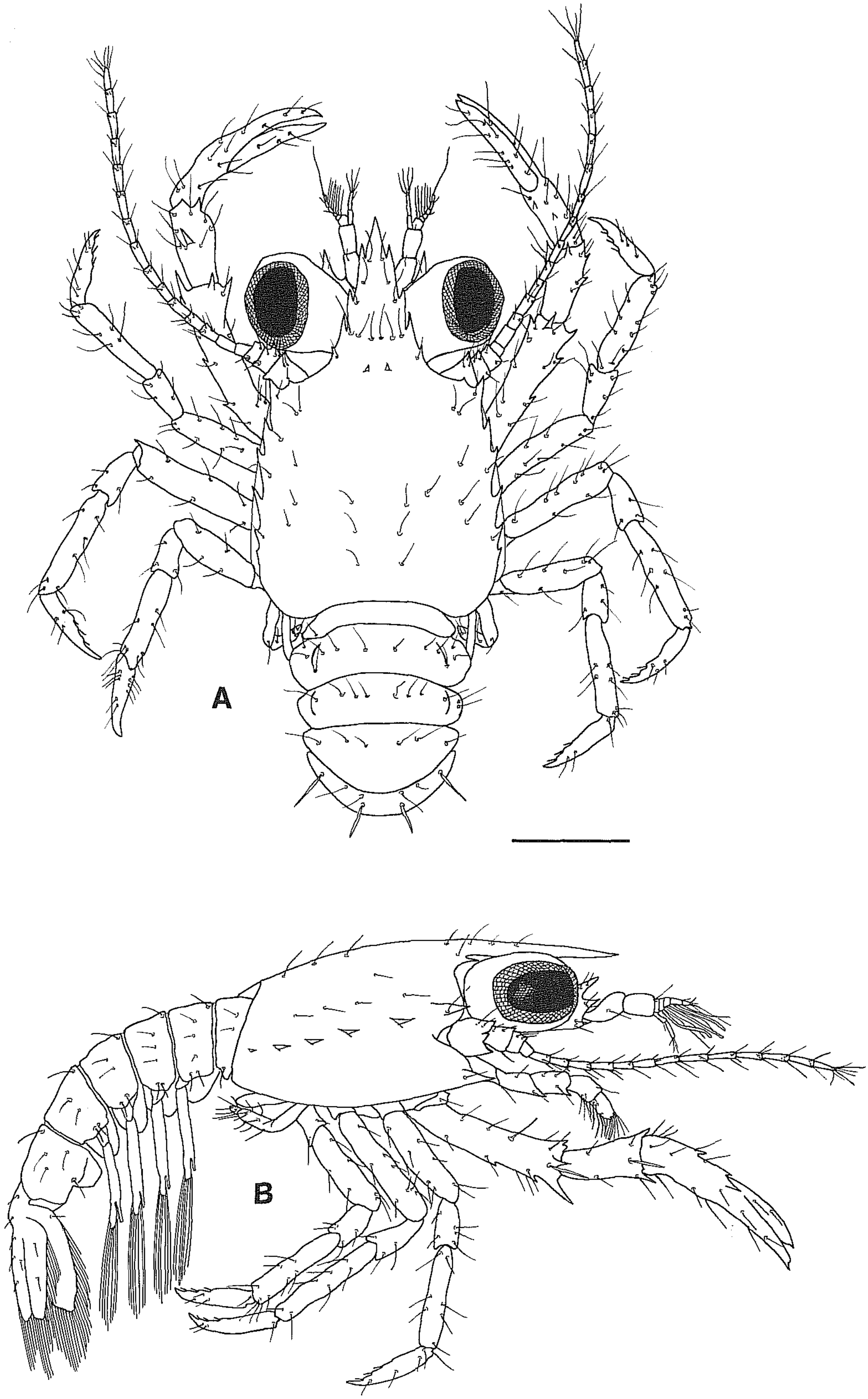

Fig. 12. *Galathea intermedia*: megalops stage. A, dorsal view; B, lateral view. Scale bar = 0.5 mm.

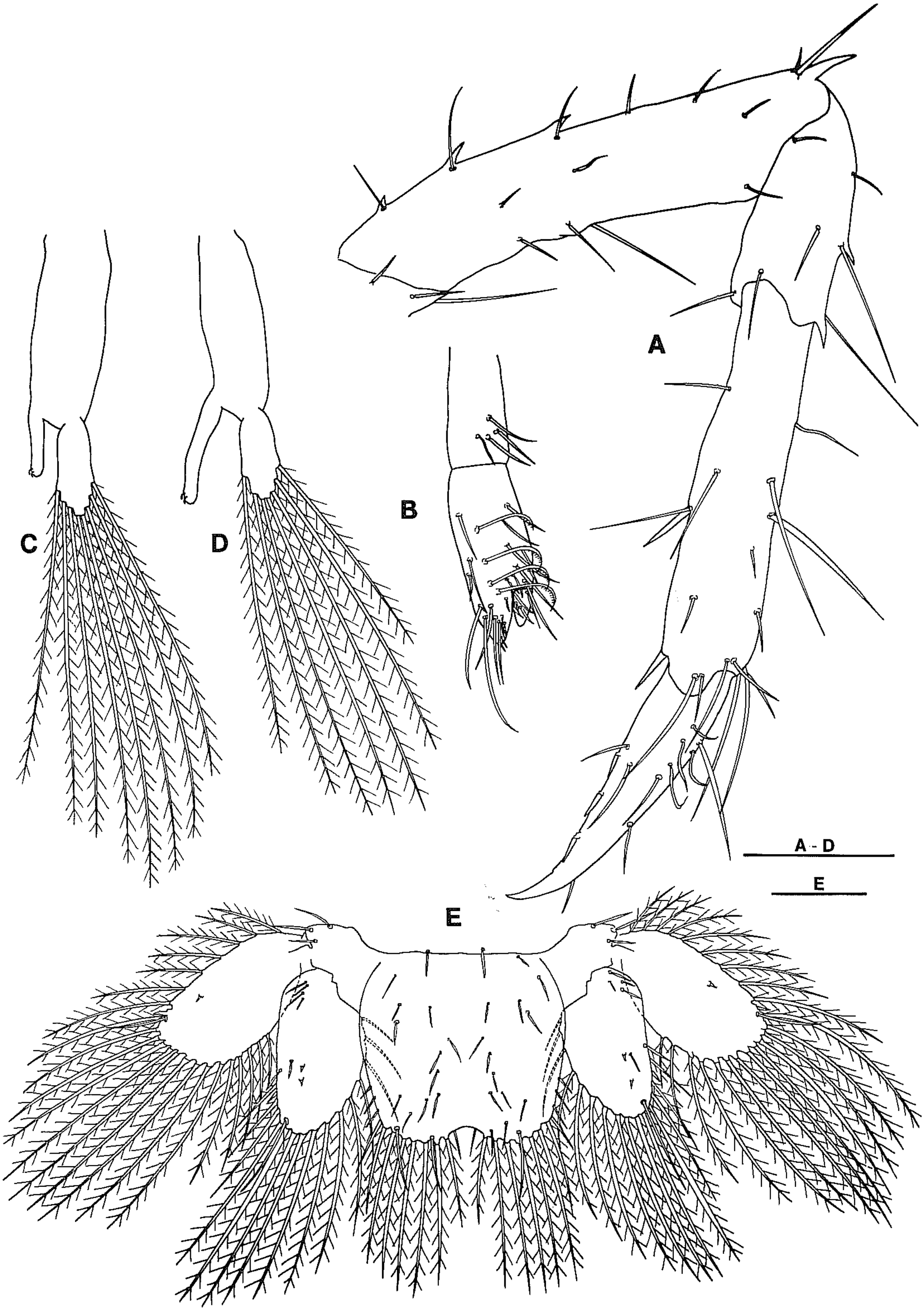

Fig. 13. *Galathea intermedia*: megalops stage. A, pereiopod 2; B, chela of pereiopod 5; C, pleopod 1; D, pleopod 4; E, tail fan. Scale bars = 0.2 mm.

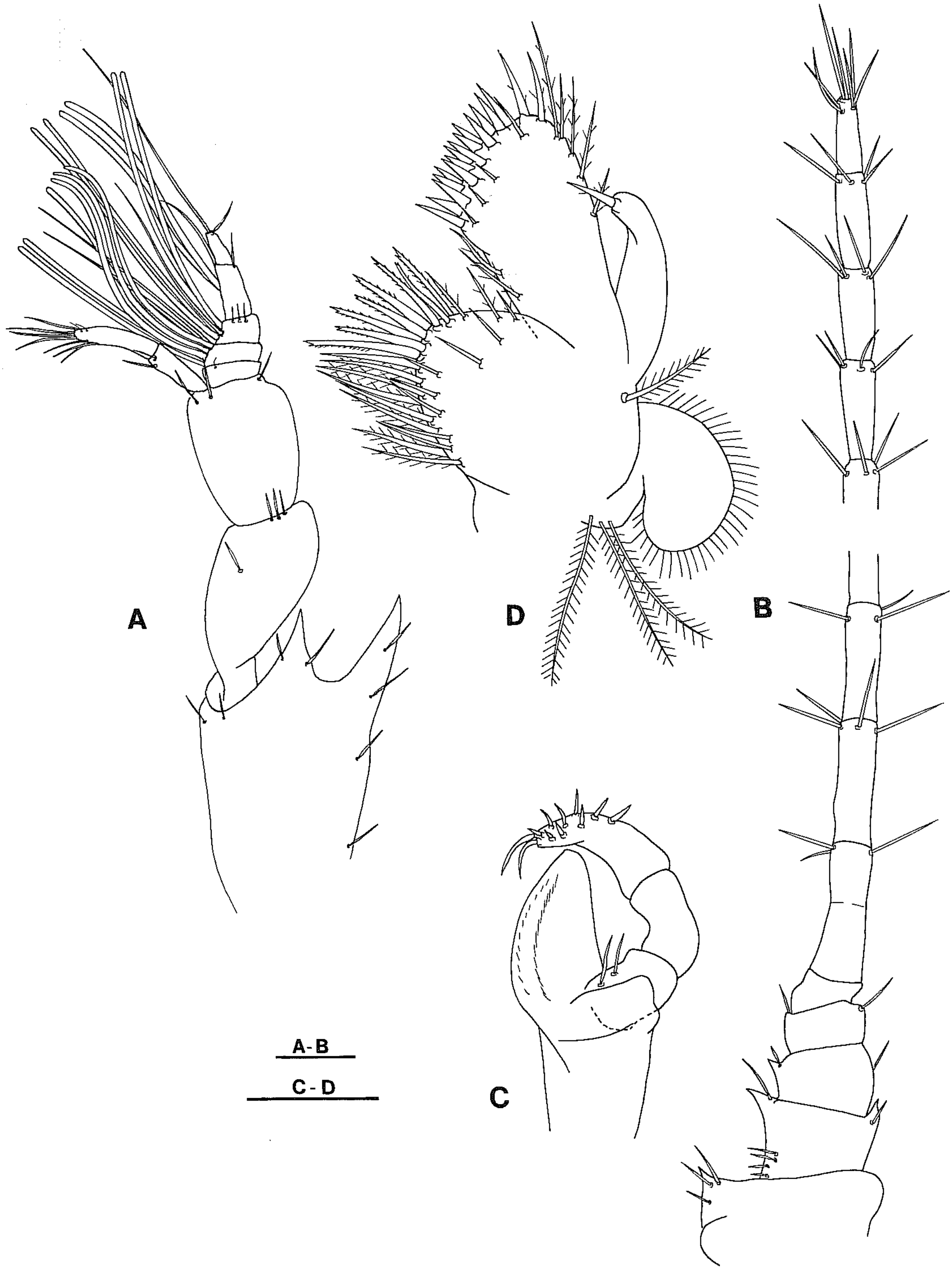

Fig. 14. *Galathea intermedia*: megalops stage. A, antennule; B, antenna; C, mandible; D, maxillule. Scale bars = 0.1 mm.

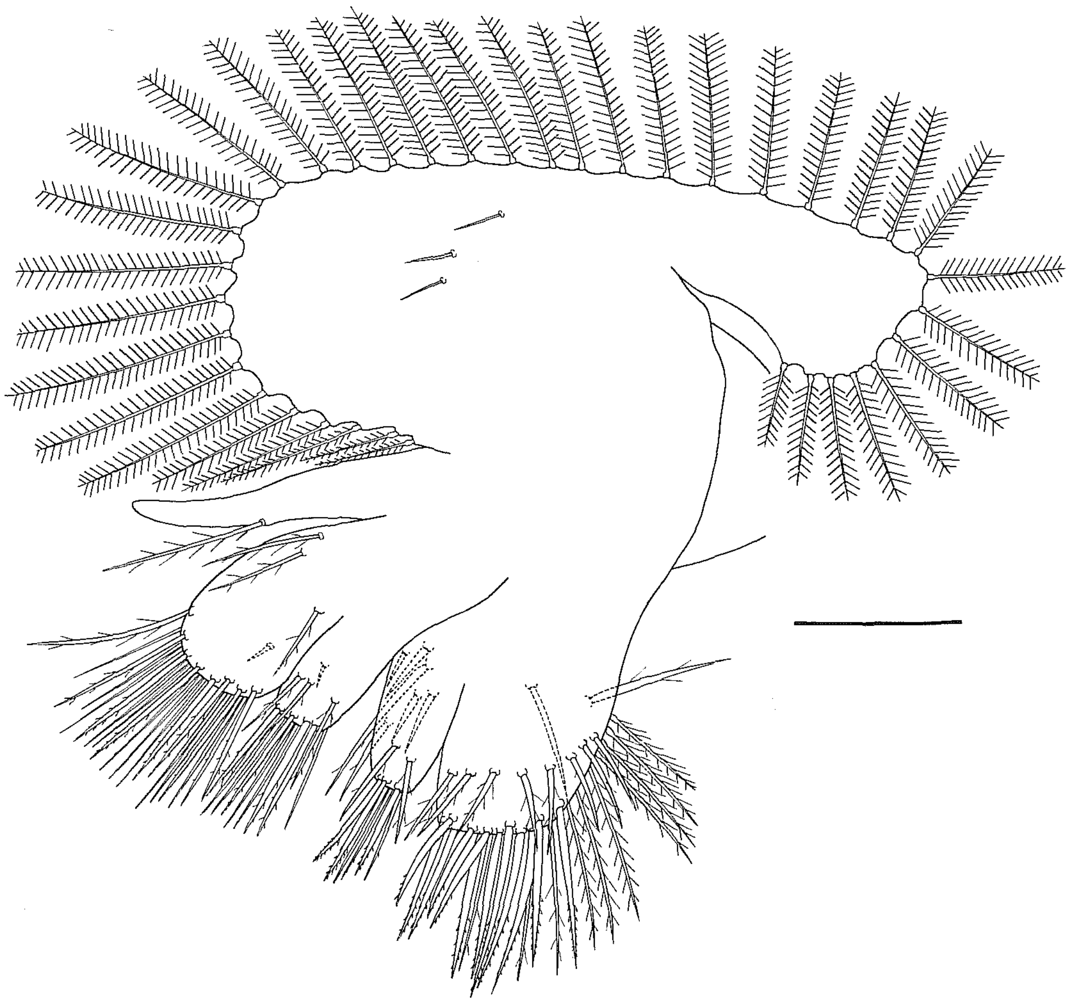

Fig. 15. *Galathea intermedia*: megalops stage. Maxilla. Scale bar = 0.1 mm.

iature adult; length of carapace slightly more than 1.5 carapace width; rostrum triangular with terminal spine and 3 distinct spines plus hindmost smaller spine along lateral margins; 2 small spines medianly on carapace at base of rostrum; 6 spines along lateral margins of carapace, including 1 at anterior angle, posterior spine minute; setae scattered over surface of carapace.

Abdomen (Figs. 12A, B, 13C, D).—Six somites with setae scattered over dorsal surface; biramous pleopods on somites 2–5, exopodal plumose setae progressing toward telson 8,8,8,7 with minor variation of 1 seta less on left or right side in same specimens, endopods with 2 or 3 small hooks on inner surface near tip, endopods increasing in length toward telson from slightly more than half length of exopod on somite 2 to slightly longer than exopod on somite 5.

Tail Fan (Fig. 13E).—Telson with 7+7 (occasionally 1 or 2 more) plumose setae along posterior margin plus few marginal setae, smaller setae/spines scattered on surface and along posterolateral margins; uropods biramous, exopod with approximately 22, endopod with 13–15 plumose marginal setae, smaller setae/spines on surfaces.

Antennule (Fig. 14A).—Biramous; peduncle 3-segmented, basal segment with 2 large forward-directed spines and several setae scattered on surface, remaining 2 segments with few setae; upper ramus (exopod) 5-seg-

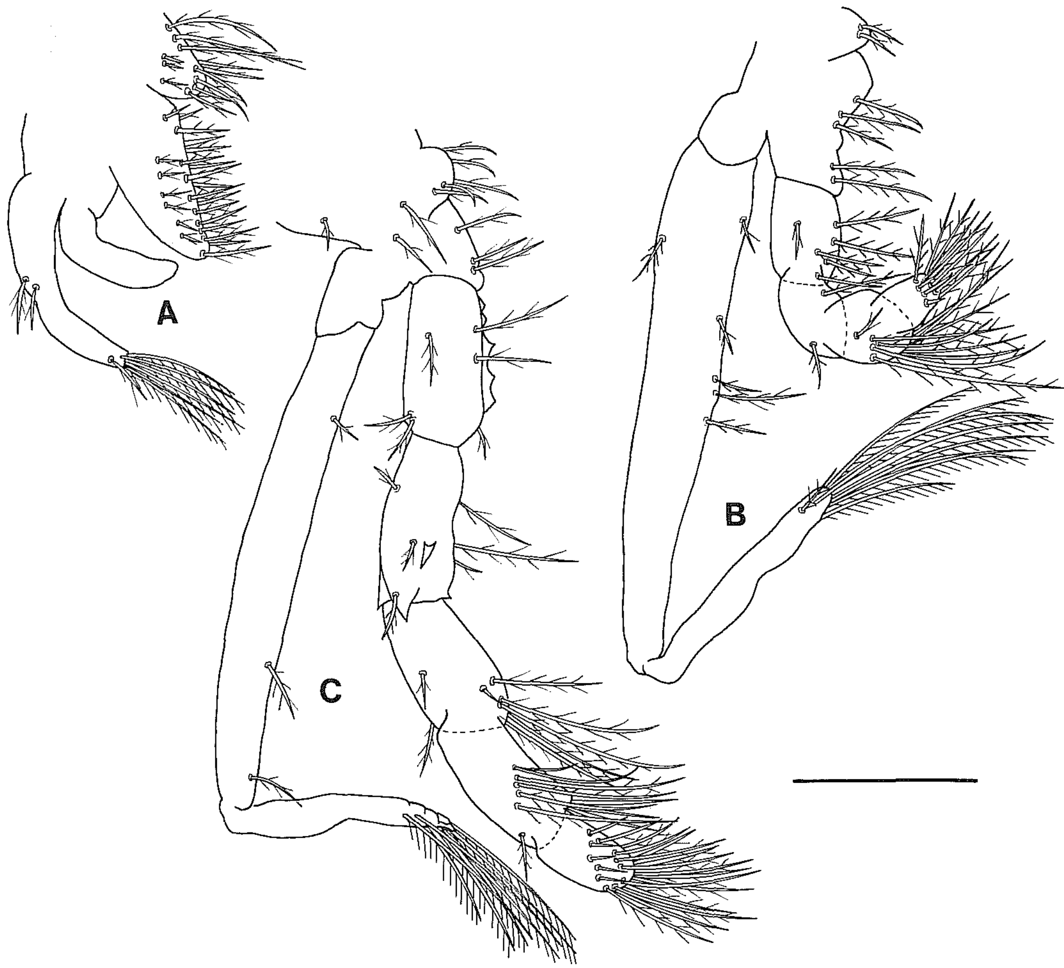

Fig. 16. *Galathea intermedia*: megalops stage. A, maxilliped 1; B, maxilliped 2; C, maxilliped 3. Scale bar = 0.2 mm.

mented (occasionally indistinctly 6-segmented), 5 or 6 rows of aesthetascs on segments 2–4(5) with 2 or 3 aesthetascs in each row, plus 2 and 1 setae in rows 3(4) and 4(5), respectively, segments 2–4 with few additional setae, segment 5(6) with 1 elongate terminal seta plus approximately 1–3 shorter setae; lower ramus (endopod) 2-segmented, basal segment with approximately 2 or 3, distal segment with approximately 7–9 setae.

Antenna (Fig. 14B).—Peduncle 4-segmented (including coxopod) with scattered setae; flagellum with variable number of articles (16–19) (few indistinctly subdivided) bearing from 0–6 (often 4) setae distally, terminal segment usually with 5–7 setae.

Mandible (Fig. 14C).—Scoop-shaped process; palp 3-segmented, basal segment with 2 setae, third segment with 11 or 12 stout setae/spines.

Maxillule (Fig. 14D).—Endopod with no apparent segmentation, possessing only single terminal spine; coxal endite with 24–27 spines/setae, lower portion of coxal endite extended into lobe fringed with fine setae; basal endite with 27–29 spines/setae and single seta basally as illustrated.

Maxilla (Fig. 15).—Endopod with single subterminal seta; large number of spines and setae on coxal and basal endites difficult to determine, coxal proximal lobe with 12–14 spines/setae more or less terminally, approximately 8 and 17 spines/setae subter-

Table 2. Setal formulae for larval characters of *Galathea intermedia* (*G.i.*) and *G. rostrata* (*G.r.*). For setal arrangements, see description of larvae (*G. rostrata* from Gore, 1979).

	Zoea I		Zoea II	
Characters	*G.i.*	*G.r.*	*G.i.*	*G.r.*
Antennule				
Aesthetascs	3	3	4	4
				exopod
Setae	3	3	4,3	4,4
Endopod	1	1	1	1
				protopod
Antenna				
Scaphocerite	9 or 10	9	10	10
Endopod	1	1	0	0
Maxillule				
Endopod	4,1	3,1	4,1	4,1
Coxal endite	6 or 7	7	7	7
Basal endite	5	5	7	7
Maxilla				
Endopod	4,2,3	3 or 4,3,3	4,2,3	4,2,3
Coxal endite	6 or 7,3	8,4	7 or 8,3 or 4	8,4
Basal endite	4,4	4,4	4 or 5,4	4 or 5,6
Scaphognathite	5	5	7	7
Maxilliped 1				
Coxopod	2	2	2	2
Basipod	2,3,3,3	2,3,3,3	2,3,3,3	2,3,3,3
Endopod	3,2,1,2,4 + I	3,2,1,2,4 + I	3,2,1,2,4 + I	3,2 + I,1 + I,2,4 + I
Exopod	4	4	7	7
Maxilliped 2				
Basipod	1,2	1,2	1,2	1,2
Endopod	2,2,2,4 + I	2,2,2,4 + I	2,2 + I,2,4 + I	2,2 + I,2,5 + I
Exopod	4	4	7	7
Maxilliped 3				
Endopod	—	—	0	2
Exopod	—	—	6	6

minally on exterior and interior surfaces, respectively, plus few spines/setae scattered on surface, coxal distal lobe with approximately 6 spines/setae more or less terminally, plus approximately 8 scattered on surface; basal endite proximal lobe with 9 or 10 spines/setae more or less terminally, plus 3 or 4 spines/setae scattered on surface, basal distal lobe with 20–26 spines/setae terminally/subterminally, plus few scattered on surface; scaphognathite with 35–38 marginal plumose setae.

Maxilliped 1 (Fig. 16A).—Coxal and basal endites of protopod with 11–15 and 22–25 setae, respectively; endopod unsegmented, naked; exopod 2-segmented with 6 terminal setae, plus few other setae as illustrated.

Maxilliped 2 (Fig. 16B).—Coxopod and basipod with few setae as illustrated; endopod 4-segmented, setal number on endopod varying, setal formula approximately 4–8,4–6,11–14,14–17 progressing distally, including some daggerlike spines on 2 distal segments; exopod 2-segmented, 8 terminal plus other setae as illustrated.

Maxilliped 3 (Fig. 16C).—Coxopod and basipod with several setae; endopod 5-segmented, first segment (ischium) with crista dentata, second segment (merus) with strong median and strong terminal spine, plus sev-

Table 2. Continued.

Zoea III		Zoea IV		Zoea V	
G.i.	*G.r.*	*G.i.*	*G.r.* (regular)	*G.i.*	*G.r.*
3	2,3	3,2 or 3,2,3	2 or 3,3,2 or 3,3	3,2,2,2,3	2,3,3,3,2,3
3	3 or 4	3	3	3	3
1	1	0	0	0	0
1,2 or 3	1,4,2	1,4,2	1,4,3,2		
				coxopod 2	2
				basipod 1,4,2	1,4,3
10 or 11	9–11	11 or 12	10–12	11–13	12–14
1	1	1	1	1–3	1
4,1	4,1	4,1	4,1	4,1	4,1
7 or 8	8	8	8 or 9	9	9
8	8	9–11	10	13–15	11
4,2,3	4,2,3	4,2,3	4,2,3	4,2,3	4,2,3
8,4	8,4	8–11,4	11,5	8–11,4 or 5	13,6
4 or 5,6	4 or 5,6	4–6,5–7	7 or 8,8	4–6,7 or 8	10,11
10 or 11	11	13–17	18–21	19–24	22–25
2	2	2	2	as in stage IV	as in stage IV
2,3,3,3	2,3,3,3	2,3,3,3	3,3,3,3		
3,2,1,2, 4 + I	3,2 + I,1 + I, 2,4 + I	3,2,1,2, 4 + I	3,2 + I,1 + I, 2,4 + I		
8	7	8	8		
1,2	1,2	1,2	1,2	as in stage IV	as in stage IV
2,2 + I,2 + I, 4 + I	2,2 + I,2, 5 + I	2,2 + I,2 + I, 4 + I	2,2 + I,2 + I, 5 + I		
8	7	8	8		
1	2	2	3	as in stage IV	as in stage IV
7	7	8	8		

eral long setae on both segments, segments 3,4, and 5 (carpus, propodus, and dactylus) with numerous long setae, latter 2 segments also with daggerlike spines; exopod 2-segmented, 8 terminal plus few other setae as illustrated.

Pereiopods (Figs. 12A, B, 13A, B).—Chelipeds equal, with stiff setae and few spines, fingers of chelae bifid at tips; ambulatory legs with stiff setae, dactylus with 3 movable spinules on ventral margin; pereiopod 5 chelate, manus of chela with 4 long scythe-like, pectinate setae, number of other setae additionally.

Discussion

Lebour (1931) separated the zoeal larvae of the four East Atlantic species of *Galathea, G. strigosa, G. squamifera, G. dispersa,* and *G. intermedia,* by the number of lateral spines on the abdominal somites. The two first-mentioned species have lateral spines on somites 4 and 5, whereas the other two species have lateral spines on somite 5 only. Further, she distinguished between *G. dispersa* and *G. intermedia* by the size of the larvae (*G. intermedia* being the smallest, approximately 2 mm or less in the first zoea), and by the presence or absence of pigment

Table. 3. Differences and similarities in zoeal features for larvae of *Galathea rostrata* (*G.r.*) and *G. intermedia* (*G.i.*) (*G. rostrata* from Gore, 1979).

Stages		Antennule	Antenna	Mandible	Abdomen	Uropods	Telson
Zoea I	*G.r.*	simple rod endopod reduced	endopod 0.4 scaphocerite length	without palp	5 somites, lateral spines on somite 4 and 5; pleopods absent	absent	7 + 7 processes, fourth process movable
	G.i.	as in *G.r.*	endopod approximately one-third scaphocerite length	as in *G.r.*	as in *G.r.*, but lateral spines only on somite 5	as in *G.r.*	as in *G.r.*
Zoea II	*G.r.*	as in stage I; endopod more developed	endopod approximately 0.3 scaphocerite length	as in stage I	as in stage I, but spines on somite 4 reduced	as in stage I	8 + 8 processes, fourth process movable
	G.i.	as in *G.r.*	as in *G.r.*	as in *G.r.*	as in stage I	as in *G.r.*	as in *G.r.*
Zoea III	*G.r.*	exopod segmented from protopod	endopod 0.5–0.6 scaphocerite length	as in stage I	6 somites, spines on somite 4 vestigial	exopods present; endopods rudimentary	8 + 8 processes, fourth process fused
	G.i.	as in *G.r.*	endopod more than one-half scaphocerite length	as in *G.r.*	6 somites	as in *G.r.*	as in *G.r.*
Zoea IV (regular)	*G.r.*	endopod one-half exopod length	endopod subequal to scaphocerite	without palp	spines on somite 4 absent; pleopods may be present	exopods and endopods developed	as in previous stage
Zoea IV (advanced)	*G.r.*	endopod subequal to exopod	endopod overreaching scaphocerite	palp present	as in zoea IV regular, but pleopods present, undivided	as in zoea IV regular	as in zoea IV regular
	G.i.	endopod one-half to subequal exopod length	endopod from three-fourths to overreaching scaphocerite	without palp or palp present	pleopod buds varying in length, may be bifid	as in *G.r.*	as in *G.r.*
Zoea V	*G.r.*	endopod subequal to exopod; protopod segmented	endopod noticeably longer than scaphocerite	palp present	pleopods bifid	as in previous stage	as in previous stage
	G.i.	as in *G.r.*	as in *G.r.*	as in *G.r.*	as in *G.r.*	as in *G.r.*	as in *G.r.*, occasionally 8 + 9 or 9 + 9 processes

Table 4. Differences in morphological features between the megalopa larvae of *Galathea intermedia* (*G.i.*) and *Galathea rostrata* (*G.r.*) (*G. rostrata* from Gore, 1979).

Features	*G.i.*	*G.r.*
Antennule		
Exopod	5-segmented, occasionally indistinctly 6-segmented	6-segmented, occasionally indistinctly 7-segmented
Endopod	2-segmented	3-segmented
Antenna		
Flagellum	about 16–19 articles, few indistinctly subdivided	2 or 3 articles fused plus about 24 shorter articles
Maxilliped 1		
Exopod	6 terminal setae	3 more or less terminal setae
Chelipeds	moderately spined	heavily spined
Pereiopods 2–4 dactylus	3 large movable spinules, no distinct fixed triangular tooth on ventral margin	3 large movable spinules plus one fixed triangular tooth on ventral margin

on angles of the telson (*G. intermedia* having orange red pigment). The zoeal larvae of a fifth East Atlantic species, *G. nexa,* has, according to Bull (1937), lateral spines on somites 4 and 5.

The zoeal larvae of the West Atlantic *Galathea rostrata* described by Gore (1979) and the East Atlantic *G. intermedia* are very similar. Only slight differences in morphological characters are found between the two species (see Tables 2 and 3 for comparison of setal formulae and some other larval features). A noticeable difference in the first zoeal stage is the lack of lateral spines on somite 4 in *G. intermedia,* whereas *G. rostrata* has lateral spines on both somites 4 and 5. The spines on somite 4 are, according to Gore, reduced in stage II of *G. rostrata,* and absent in stage IV. From the second zoeal stage, slight differences in setation of the three maxillipeds are noticeable between the two species. In zoeae III and V, larvae of *G. rostrata* also have one more row of aesthetascs on the antennular exopods than larvae of *G. intermedia.*

Lebour (1930) described and figured a fifth zoeal stage of *Galathea dispersa.* According to Lebour, the species has "Four or five larval stages. Five is probably normal, but the young *Galathea* has been seen to emerge from the fourth stage, and the normally fifth stage has been seen to emerge from the third stage with no spines on the inner branch of the uropods; thus the fourth or fifth stage may be omitted." Gore (1979) described a regular and an advanced fourth zoeal stage and found that "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." In the present investigation, fourth zoeal larvae of *G. intermedia* could be separated into two groups. The less advanced larvae molted to the fifth zoeal stage, whereas the more advanced fourth stage larvae skipped the fifth stage, as found by Gore for *G. rostrata.* Although slight differences in setation between the two species exist in the fourth and fifth zoeal stages, the larvae of the two species are very similar. The fifth stage larvae of both species have increased numbers of antennular aesthetascs, a remarkable elongation of the antennal endopod, a mandibular palp, and slight changes in setal number on the maxillule, maxilla, and uropods as compared with larvae in the previous stage.

Like the zoeal larvae of the two species, the megalopa larvae of *G. intermedia* and *G. rostrata* are morphologically very similar. A few distinct differences between the megalopa of the two species are listed in Table 4.

A close relationship between the larvae of the East Atlantic species of *Galathea* was demonstrated by Sars (1889) and Lebour (1930, 1931). The same close relationship is now also shown between the larvae of an East Atlantic and a West Atlantic species of the genus *Galathea.* Two morphological characters which are important for identifying adult *G. intermedia* were found in the megalops stage. These characters are: 2 large forward-directed spines on the basal segment of the antennular peduncle, and a strong median and a strong terminal spine on the merus of maxilliped 3.

Variability in the morphology and number of larval stages has been described very frequently in caridean shrimps (e.g., Broad and Hubschman, 1962, 1963; Fincham, 1979; Haynes, 1979). It is influenced by external factors such as food, temperature, and salinity (e.g., Knowlton, 1974; Sandifer and Smith, 1979; Criales and Anger, 1986). In brachyuran species, variability in the number of developmental pathways has also been reported (Costlow, 1965; Yang, 1971; Gore and Scotto, 1982; Diaz and Bevilacqua, 1987). Additional larval stages occurred mainly under conditions of chemical, nutritional, hormonal, or other stress (Costlow, 1963; Bookhout *et al.,* 1972; Sulkin, 1978; McConaugha, 1982). Furthermore, lobsters passed through a supernumerary stage after hormonal manipulation (Snyder and Chang, 1986; Charmantier and Aiken, 1987). In the Anomura, variability in the number of larval stages was found in larvae belonging to the families Hippidae (Rees, 1959; Diaz and Costlow, 1987), Paguridae (Gore and Scotto, 1983), Diogenidae (Provenzano and Dobkin, 1962; Provenzano, 1967), Lithodidae (Kurata, 1960), and Galatheidae (Lebour, 1930; Boyd and Johnson, 1963; Fagetti and Campodonico, 1971; Gore, 1979; present study).

This brief review shows that variability is a rather common feature in the larval development of decapod crustaceans. It has been found also in the natural pelagic environment (Haynes, 1979; Criales, 1985), and it may be a mechanism that improves the chances for survival and recruitment in a variable environment (see Sandifer and Smith, 1979, for discussion). During the present study, the degree of variability appeared to differ greatly among hatches from different females. This may corroborate the hypothesis proposed by Sandifer and Smith that the number of stages in an individual larva might be inheritable, whereas external factors act as selective forces favoring different developmental pathways under different conditions.

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