



Description of the complete larval development of *Lysmata amboinensis* (De Man) (Decapoda: Lysmatidae) reared under laboratory conditions

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Abstract

Complete larval morphological descriptions are currently only known for three of the 48 species of genus *Lysmata*. The present study describes and illustrates the larval development of *Lysmata amboinensis* (De Man) reared under laboratory conditions. *Lysmata amboinensis* larval development is composed by a total of ten zoea and a decapodite stage.

The first zoeal stage larvae presents sessile eyes, a carapace with a pterigostomial spine and antero-ventral marginal denticles, a long, slender, and pointed rostrum, an antennal exopod terminally articulated, a pleon with five somites, the fifth one bearing a pair of dorso-lateral spines on the posterior margin, and a triangular shaped telson with 7+7 posterior processes. The decapodite resembles a smaller adult and has extremely long antennas (more than twice the total length of the decapodite), the first two pair of pereopods with chela, first four pairs of pereopods with reduced and entire exopods, and fully developed pleopods.

The morphological features of *L. amboinensis* are compared with those currently available for the larval stage of the genus *Lysmata*.

Key words: Larval morphology, Crustaceans, Zoeas, Cleaner shrimp, Decapodite, Caridea

Introduction

Over the past decades the marine ornamental trade has become a growing industry in size and popularity, with capture from the wild being the main source of supply Calado *et al.* (2017b). Within marine ornamental decapods, one of the most traded groups due to their attractive appearance and easy maintenance are shrimp from genus *Lysmata spp.* (Risso) are some of the most exploited organisms for the marine aquarium industry Calado *et al.* (2003). There are major concerns regarding the collection of wild specimens from coral reefs given the generalized lack of traceability in the trade (Cohen *et al.* 2003) and the threat it can pose to these ecosystems, especially when considering “cleaner” organisms and their symbiotic relations with other local species (e.g. Vaughan *et al.* 2017). The alternative to their capture lies within aquaculture, but their production has several constrains such as specific environmental requirements to be met, the existence of long life cycles and the ability to perform mark-time molting, which combined lead to an indeterminate delay in the rearing process (Calado 2008). Therefore, methods for aquaculture optimization are being developed alongside the increase of knowledge (Calado *et al.* 2017a) and accurate larval descriptions are urgently required to provide guidance throughout the development of reared larvae.

Known for its bright colours and lifestyles diversity, *Lysmata spp.* (Risso) larvae are easily recognizable by their stalked eyes with a distinct shape (in first zoea eyes are sessile), long rostrum and a long fifth pereopod bearing

a paddle-like propodus with serrated margins (Calado 2008). The genus has 48 extant species (De Grave & Fransen 2011; De Grave & Anker 2018), of which only three have complete larval descriptions known so far. *Lysmata wurdemanni* Kurata (1970) has eleven zoeal stages plus a decapodite described, while both *L. ensirostris* (Bensam & Kartha 1967; Pillai 1974) and *L. seticaudata* Calado *et al.* (2004) have nine zoeal stages plus a decapodite. Despite not being complete morphological development descriptions, there is also information available for five other *Lysmata* species that still provides useful details on the genus. Knowlton & Alavi (1995) have described five zoeal stages plus a ninth zoeal stage for *L. anchisteus*. *Lysmata vittata* first nine zoeal stages were described by Yang & Kim (2010), seven zoeal stages are known for *L. galapagensis* and the first four stages plus the last zoea for *L. moorei* were described by Bartilotti *et al.* (2012) and the first three zoea of *L. lipkei* were described by Almeida *et al.* (2021). Finally, a study evaluating the resistance to starving of newly hatched *Lysmata* larvae, a brief description of some morphological and biometrical features was made for *L. amboinensis*, *L. ankeri*, *L. debelius* and *L. seticaudata* by Calado *et al.* (2008a).

Lysmata amboinensis larval development was initially studied by Wunsch (1996). Using material reared in the laboratory the author described seven zoeal stages, after which records were made considering the larva's number of days after hatching, achieving a decapodite, which the author termed as post-larva, after 142 days.

Lysmata amboinensis (De Man), also known as “scarlet skunk cleaner shrimp”, is a medium size shrimp presenting two longitudinal dorsal red stripes, with a white one in the middle, a see-through yellow ventral body and long white antennae. Inhabiting the Indo-Pacific coral reefs (*e.g.* Poupin 2010), these shrimps commonly live in pairs and establish cleaning stations where they feed of ectoparasites that they remove from several different fish species Militz & Hutson (2015). These caridean shrimps are protandric simultaneous hermaphrodites, as reported by Fiedler (1998), individuals that first develop as males and later can also reproduce as females, but not being able to self-fertilize. Throughout their development larvae can perform mark-time molting Gore (1985), *i.e.* having a molt only increasing its size but not developing new morphological characters, which enables them to delay their zoeal development depending on the environmental conditions. Its evolutionary background has attracted some attention and larval development descriptions may help to better understand phylogenetic relationships amongst the genus (*e.g.* Baeza 2010).

For the present study, larvae from six females of *Lysmata amboinensis* were reared under laboratory conditions and their complete larval cycle was accomplished. Their morphological description is here presented, followed by a comparison and discussion on the morphological characters for genus *Lysmata* known to date.

Materials and methods

Larval culture techniques. *Lysmata amboinensis* brood stock was acquired through TMC Iberia, and as far as was possible to know, captured in the Indian ocean. Brood stocks were kept in a recirculation system similar to the one described by Calado *et al.* (2007), and fed with Ocean Nutrition™ Formula One pellets, mussels, squid and cod roe. Spawn occurred during night, every 18 days, spawning 1283 ± 469 larvae. Only larvae with positive phototaxis were selected for assay. The larvae were reared in 2 litre cylindrical tanks (21 cm height x 15 cm diameter) at a density of 30 larvae per litre with gentle aeration until third zoea stage after which they were transferred to 1.5 litre kreisel tanks (U shaped, 15 cm height x 13.5 cm top length x 12 width), at the same density, for the rest of their larval development. Temperature was kept at 25 ± 1 °C, salinity 35 and nitrogenous compounds remained below detectable levels through monitorization with API® test kits. The water was renewed daily, and larvae fed on newly hatched *Artemia nauplii ad libidum* conditions (around 10 nauplii ml⁻¹). The decapodite stage was achieved in 90 to 120 days post hatching.

Larval drawings and measurements. Drawings and measurements were made following the methods and equipment described by Bartilotti *et al.* (2012). Measurements were made using a stereomicroscope Olympus SZX12, considering total length (TL) as the distance between tip of rostrum to posterior margin of telson, carapace length (CL) as the distance from tip of rostrum to posterior margin of carapace and rostrum length (RL), as the distance from the rostrum tip to the eye socket. Drawings were made with aid of a *camera lucida* on an Olympus BX51 microscope and were later edited with the use of GIMP software The GIMP Development Team (2019). Setules from setae were omitted from drawings for clarity. All used and stored larvae have been deposited in IPMA under the reference (IPMA/H/La/11/2013).

Results

Larvae from 6 females were reared in laboratory and reached the eighth zoeal stage in 33 days post hatching (with an average of 4 days per moult/ zoeal stage), with the decapodite stage appearing 90 to 120 days after hatch. Ten zoeal stages plus a decapodite stage were analysed, the first and last zoeal stages were described in detail, while for other stages only the morphological differences recorded from the previous stage are presented. Table 1 presents a comparison of selected morphological characters of known *Lysmata* larval descriptions up to date.

Morphological description of larval stages of *Lysmata amboinensis*

(Fig 1–7)

First Zoea (Figure 1A–J)

Size: TL= 2.86±0.04 mm; CL= 0.95±0.02 mm; RL= 0.30±0.03 mm; N = 10

Carapace (Figure 1A, A'): rostrum slender and pointed, reaching half the size of the antennular peduncle, eyes compound and sessile; carapace smooth with 1 pterigostomial spine, followed by 3–5 denticles along anterior ventral margin.

Antennule (Figure 1B): peduncle entire, with endopod represented by 1 long plumose setae, and exopod with 1–2 plumose setae and 3 aesthetascs.

Antenna (Figure 1C): peduncle entire; endopod apically with 1 long plumose setae and 1 short spine; exopod with 5-articles, with 9 plumose setae on inner side and 2 plumose setae on outer side, plus a simple setae on apex.

Mandible (Figure 1D): asymmetrical, palp absent, left mandible bearing 3 teeth and right mandible with 5 teeth, both with 1 *lacinia mobilis*, molar process as illustrated.

Maxillule (Figure 1E): coxopodite with 7 cuspidate setae, basipodite with 6 cuspidate setae; endopod with 2 strong subterminal serrulate setae and 3 strong terminal serrulate setae.

Maxilla (Figure 1F): coxopodite bilobed with 8–9 (3 serrulate and 5–6 pappose) and 4 pappose setae, respectively; basipodite bilobed with 3 pappose setae and 4 pappose setae, respectively; endopod entire bearing 3+2+4 pappose setae; exopod with 5 marginal plumose setae.

First maxilliped (Figure 1G): coxopodite with 2+1+2 serrulate setae; basipodite with 12 (4 serrulate and 8 pappose) setae; endopod with 4 articles with 3,1,2, 4–5 pappose setae; exopod entire, with 1+2+1 plumose setae.

Second maxilliped (Figure 1H): coxopodite unarmed; basipodite with 1+2+2 serrulate setae; endopod with 3 articles with 1–3 (2 simple and 1 plumodenticulate) + 0–1 simple, 0–3 (0–2 simple and 0–1 plumodenticulate), 4+1 (2 simple and 3 plumodenticulate) setae; exopod entire bearing 2+2+2+2+1 plumose setae.

Third maxilliped (Figure 1I): coxopodite unarmed; basipodite with 2+1 serrulate setae; endopod with 4 articles with 2+1 simple, 0, 1+4 plumodenticulate, 2–3 (0–1 simple and 2 plumodenticulate) setae; exopod entire bearing 2+2+2+2+1 plumose setae.

First pereopod (Figure 1A): as bud

Second to fifth pereopods: absent

Pleon (Figure 1A): 5 somites; 1 pair of dorso-lateral spines on posterior margin of the 5th somite.

Pleopods: absent

Uropod: absent

Telson (Figure 1A, 1J): triangular, indented medially with 7+7 posterior processes; minute spines between setae.

Second Zoea (Figure 2A–F)

Size: TL= 3.16±0.10 mm; CL= 0.85±0.11mm; RL= 0.38±0.03 mm; N = 10

Carapace (Figure 2A): rostrum slender and pointed, reaching half the size of the antennular peduncle, eyes compound and stalked; 1 supraorbital spine, 1 pterigostomial spine, and 3–6 denticles along ventral margin.

Antennule (Figure 2A): peduncle with 2 articles, distal article bearing 2 plumose setae distally; endopod represented by 1 long plumose setae; exopod with 1 simple seta and 4 long aesthetascs.

Antenna (Figure 2A, 2B): peduncle entire; endopod represented by 1 long plumose setae; exopod with 4 articles, with 9 plumose setae on inner side and 2 setae on outer side, plus a simple small setae on apex.

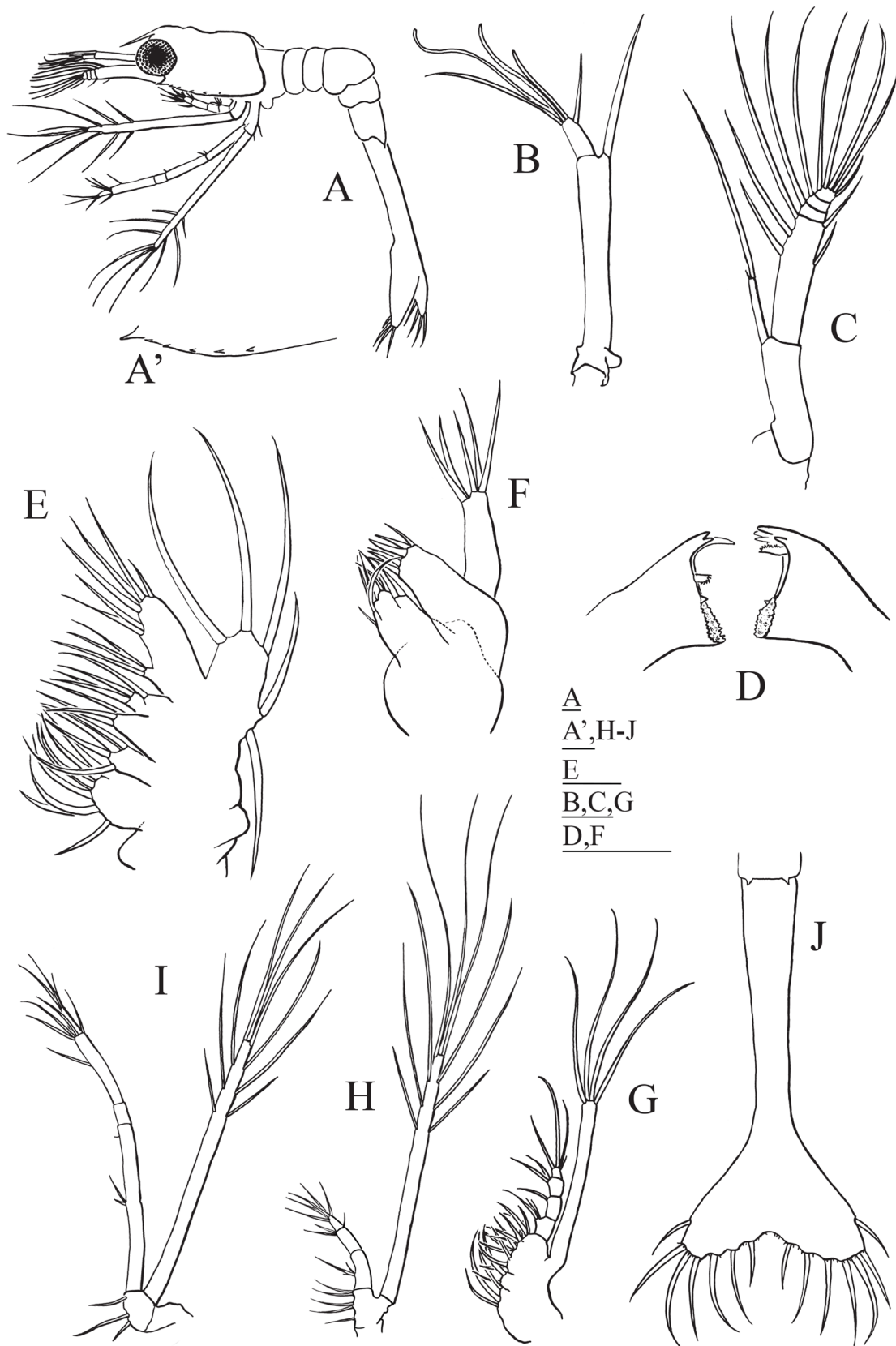


FIGURE 1. First zoea: **A** complete larvae lateral view; **A'** carapace denticles; **B** antennule; **C** antenna; **D** mandibles; **E** maxillule; **F** maxilla; **G** first maxilliped; **H** second maxilliped; **I** third maxilliped; **J** telson. Scale bars: 0.1mm (A–D, F–J); 0.5mm (E).

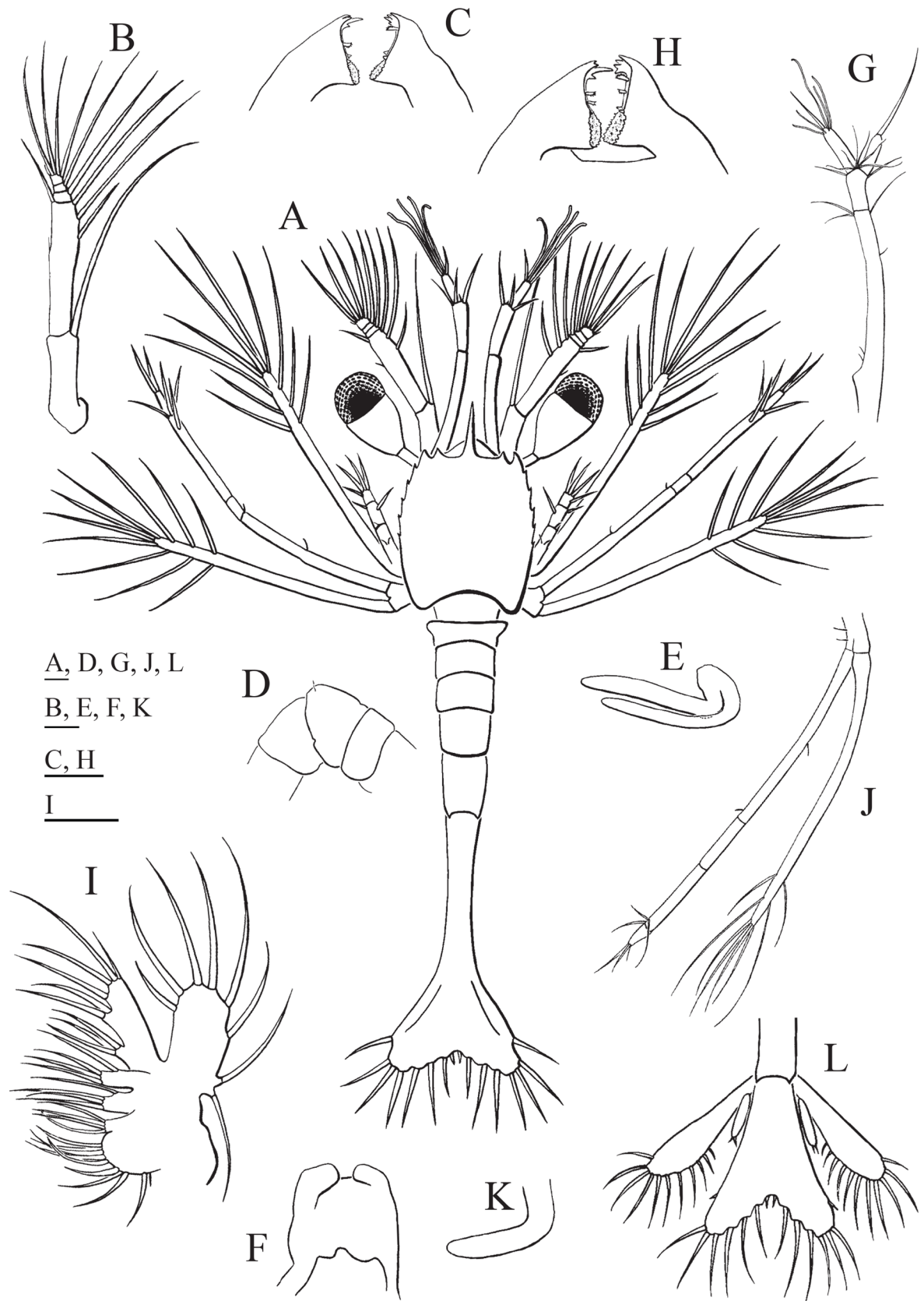


FIGURE 2. Second zoea: **A** complete larvae dorsal view; **B** antenna; **C** mandibles; **D** pleon lateral view; **E** first pereiopod; **F** fifth pereiopod. Third zoea: **G** antennule; **H** mandibles; **I** maxilla; **J** first pereiopod; **K** fifth pereiopod; **L** telson and uropods. Scale bars: 0.1mm.

Mandible (Figure 2C): asymmetrical, both mandibles bearing 4 incisors and 1 *lacinia mobilis*, armature of molar processes as illustrated.

Maxillule: unchanged beside size.

Maxilla: unchanged beside size.

First maxilliped: exopod entire with 1+1+2+1 plumose setae; otherwise unchanged besides size.

Second maxilliped (Figure 2A): coxopodite unarmed; basipodite with 1+2+3 serrulate setae; exopod entire bearing 5 pairs of plumose setae on distal part; otherwise unchanged besides size.

Third maxilliped (Figure 2A): coxopodite unarmed; basipodite with 2+1 serrulate setae; endopod with 4 articles with 2+1 simple, 0, 1+4 plumodenticulate, 2+1 (1 simple and 2 plumodenticulate) setae; exopod entire bearing 5 pairs of plumose setae on distal part.

First pereopod (Figure 2E): biramous bud.

Second to fourth pereopods: absent.

Fifth pereopod (Figure 2F): small bud.

Pleon (Figure 2A, 2D): 1 pair of small setae on the dorso-posterior side of the 3rd somite. Otherwise unchanged, besides size.

Pleopods: absent.

Uropods: absent.

Telson (Figure 2A): triangular, indented medially with 8 + 8 posterior processes.

Third Zoea (Figure 2G–L)

Size: TL= 3.61±0.10 mm; CL= 0.86±0.11 mm; RL= 0.33±0.05 mm; N = 10

Carapace: rostrum reaching a quarter of antennular peduncle; otherwise unchanged.

Antennule (Figure 2G): peduncle with 2 articles, with 2 small simple setae proximally near the stylocerite, 1 small plumose setae in a more distal position, and 2–3+1 distally; distal article bearing 2–3 plumose setae and 5–7 simple setae; endopod with 1 long plumose setae terminally; exopod with 1 plumose setae, 1–2 small plumose setae and 2–4 aesthetascs.

Antenna: peduncle entire; endopod apically with 1 long plumose setae; exopod with 3 articles, with 11–12 plumose setae on inner side and 2 setae on outer side, plus a simple small setae on apex.

Mandible (Figure 2H): asymmetrical, both mandibles bearing 4 incisors, 1 *lacinia mobilis* and 1 submarginal setae; armature of molar processes as illustrated.

Maxillule: unchanged besides size.

Maxilla (Figure 2I): coxopodite bilobed with 9–11 (4 serrulate and 5–7 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; basipodite bilobed, both bearing 4 (1 serrulate and 3 pappose) setae; endopod entire bearing 3 (2 serrulate and 1 simple) +2 serrulate +2 serrulate setae +1–2 serrulate setae; exopod with 8 marginal plumose setae bearing lateral microtricha.

First maxilliped: unchanged besides size.

Second maxilliped: unchanged besides size.

Third maxilliped: coxopodite unarmed; basipodite with 2+1 serrulate setae; endopod with 4 articles with 2+2 simple, 1 simple, 1+4 plumodenticulate, 2+1 (1 simple and 2 plumodenticulate) setae. Otherwise unchanged besides size.

First pereopod (Figure 2J): functional, biramous; coxopodite unarmed; basipodite with 2 setae; endopod: first article with 1–2+1 simple setae, second article without setae, third article with 3–4 plumodenticulate setae, fourth article with 1+2 (1 simple and 2 plumodenticulate) setae; exopod entire with 4 pairs of plumose setae on distal part.

Second to fourth pereopods: absent

Fifth pereopod (Figure 2K): uniramous bud

Pleon: 6 somites; 1 pair of small dorso-lateral spines on posterior margin of 5th somite, 1 pair of small lateral spines on 6th somite and 1 pair small posterior setae on 3rd somite.

Pleopods: absent

Uropod (Figure 2L): biramous, smaller than telson; exopod developed with 11–12 plumose setae; endopod small with 2 small plumose setae apically.

Telson (Figure 2L): first pair of processes in an anterolateral position, about a fifth of total length of telson; otherwise unchanged besides size.

Fourth Zoea (Figure 3A–D)

Size: TL= 3.87±0.15 mm; CL= 0.86±0.08 mm; RL= 0.33±0.03 mm; N = 10

Carapace (Figure 3A): rostrum reaching approximately a third of antennular peduncle; 1 supraorbital spine, 1 antenal spine, 1 pterigostomial spine and 4 denticles along ventral margin.

Antennule (Figure 3A): peduncle with 2 articles, with 2 small simple setae proximally, 3 small plumose setae in a more distal position, and 4 plumose setae distally; distal article bearing 2–4 plumose setae and 3–5 simple setae; endopod with 1 long plumose setae; exopod with 1 plumose setae and 2 aesthetascs.

Antenna (Figure 3B): peduncle entire; endopod apically with 1 long plumose setae; exopod entire, with 13–17 plumose setae on inner side and 1–2 setae on outer side, plus a simple small setae on apex.

Mandible (Figure 3C): asymmetrical, both mandibles bearing 4 incisors, 1 *lacinia mobilis* and 2 submarginal setae; armature of molar processes as illustrated.

Maxillule: unchanged besides size.

Maxilla: exopod with 8–12 marginal plumose setae. Otherwise unchanged besides size.

First maxilliped: unchanged besides size.

Second maxilliped (Figure 3A): endopod with 3 articles with 3 (2 simple and 1 plumodenticulate) +1 simple, 1 simple + 1 plumodenticulate, 1+4+1 (3 simple and 3 plumodenticulate) setae; Otherwise unchanged besides size.

Third maxilliped (Figure 3A): endopod with 4 articles with 2+2 simple, 1 simple, 1–3+4 plumodenticulate, 2+1 (1 simple and 2 plumodenticulate) setae; exopod entire bearing 6–7 pairs of plumose setae on distal part. Otherwise unchanged besides size.

First pereopod (Figure 3A): endopod: first article with 2+2 setae, second article with 1 plumodenticulate setae, third article with 1+4 plumodenticulate setae, fourth article with 2 simple and 1 plumodenticulate setae; exopod entire with 5–7 pairs of plumose setae on distal part; Otherwise unchanged besides size.

Second pereopod (Figure 3A): biramous bud.

Third to fourth pereopods: absent

Fifth pereopod (Figure 3A, 3D): developed, uniramous. Coxopodite unarmed; basipodite bears 1 simple setae; first article with 1 setae; second article with 0–1 setae; third article with 1 setae; fourth article flattened and paddle-like enlarged with margins serrated (6–7 and 5 teeth on each side respectively), bearing 2 setae distally; fifth article small with 2 terminal setae.

Pleon (Figure 3A): 6 somites; 1 pair of small dorso-lateral spines on posterior margin of 5th somite, 1 pair of small lateral spines on 6th somite and 2 pairs small posterior setae on 3rd somite; dorsal region of the 3rd pleomere is slightly curved.

Pleopods: absent

Uropod (Figure 3A): biramous; exopod well developed reaching the end of telson, with 15–19 plumose setae bearing lateral microtricha; endopod with 7–12 plumose setae.

Telson (Figure 3A): unchanged besides size.

Fifth Zoea (Figure 3E–I)

Size: TL= 4.30±0.43 mm; CL= 0.77±0.38 mm; RL= 0.30±0.09 mm; N = 10

Carapace: rostrum reaching a fifth of antennular peduncle; 2 denticles along ventral margin. Otherwise unchanged.

Antennule (Figure 3E): peduncle with 2 articles; proximal article with 4–5 small simple setae on stylocerite and 1+1+2+3–4 plumose setae along the article; distal article with 4–6 plumose setae; endopod with 3 articles, distal article with 1 long plumose setae and 2–3 simple setae; exopod with 3 articles with 2 aesthetascs in the first one and 1 plumose +0–1 simple setae apically.

Antenna: peduncle entire; endopod developing without setae; exopod entire, with 18 plumose setae on inner side, plus simple small setae on apex.

Mandible: asymmetrical, both mandibles bearing 4 incisors and 1 *lacinia mobilis*, right mandible with 2 submarginal setae and left with 3 submarginal setae.

Maxillule: coxopodite with 8 cuspidate setae, basipodite with 8 cuspidate setae bearing lateral microtricha; endopod with 2 strong subterminal serrulate setae and 3 strong terminal serrulate setae.

Maxilla: exopod with 11–13 marginal plumose setae. Otherwise unchanged besides size.

First maxilliped (Figure 3F): basipodite with 13 (4 serrulate and 9 pappose) setae; unchanged besides size.

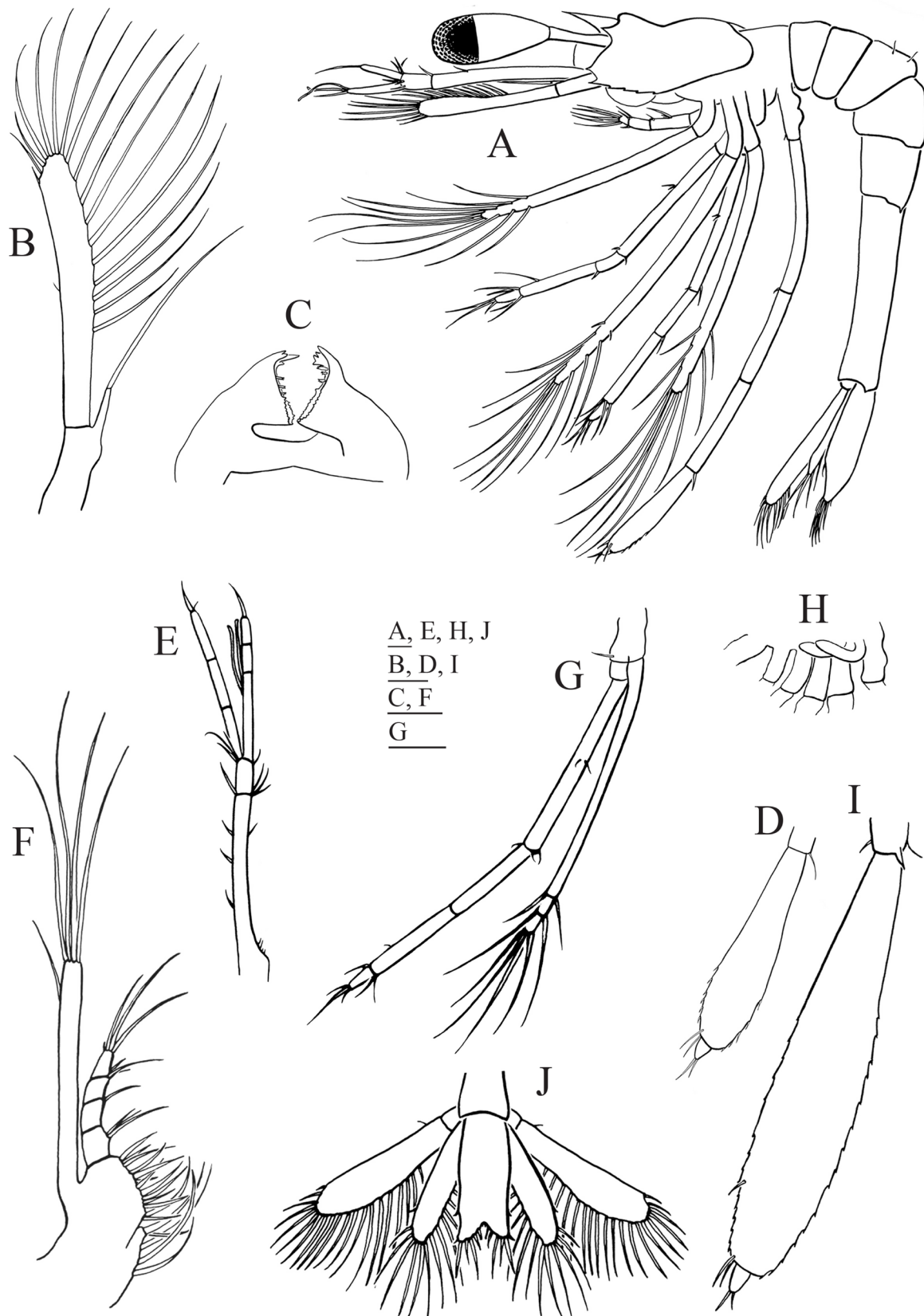


FIGURE 3. Fourth zoea: **A** complete larvae lateral view; **B** antenna; **C** mandibles; **D** detail of fifth's pereopod propodus and dactylus. Fifth zoea: **E** antennule; **F** first maxilliped; **G** second pereopod; **H** third pereopod; **I** detail of fifth's pereopod propodus and dactylus; **J** uropods and telson. Scale bars: 0.1mm.

Second maxilliped: exopod entire bearing 4 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Third maxilliped: unchanged besides size.

First pereopod: endopod: first article with 2+3 setae, second article with 1 plumodenticulate setae, third article with 1+4 plumodenticulate setae, fourth article with 2 simple and 1 plumodenticulate setae; otherwise unchanged besides size.

Second pereopod (Figure 3G): biramous, functional; coxopodite unarmed; basipodite with 1 simple setae; endopod: first article with 2+3 setae, second article without setae, third article with 4 plumodenticulate, fourth article with 2 simple and 1 plumodenticulate setae; exopod entire with 4 pairs of plumose setae on distal part.

Third pereopod (Figure 3H): biramous bud.

Fourth pereopods: absent

Fifth pereopod (Figure 3I): coxopodite with 1 simple setae; basis with 1 simple setae; first article with 2 setae; second article with 2 setae and a spine-like process; third article margins serrated with teeth on both sides and bearing 3 setae; otherwise unchanged besides size.

Pleon: 6 somites; 1 pair of small lateral spines on 6th somite and 2 pairs small posterior setae on 3rd somite.

Pleopods: absent

Uropod (Figure 3J): biramous, longer than telson; exopod with 22+1 plumose setae; endopod with 17 plumose setae.

Telson (Figure 3J): margins laterally parallel; posterior margin concave with a central invagination.

Sixth Zoea (Figure 4A–E)

Size: TL= 4.18±1.10 mm; CL= 1.01±0.63 mm; RL= 0.33±0.04 mm; N = 3

Carapace: 1 denticle along antero-ventral margin; otherwise unchanged besides size.

Antennule (Figure 4A): peduncle with 2 articles; proximal article with 4 small simple setae on stylocerite, 6 plumose setae along the inner margin, 1 simple setae and one row of plumose setae on outer posterior margin; distal article with a row of plumose setae on inner posterior margin; endopod with 6 articles, second and third articles with 1 aesthetasc each and, 1, 0, 2 setae in the distal articles, respectively; exopod with 4 articles with 3 aesthetascs in the second article and 1 plumose setae and 2 simple setae in the distal one.

Antenna: exopod entire, with 21 plumose setae on inner side, 1 spine plus a simple small setae; otherwise unchanged besides size.

Mandible (Figure 4B): asymmetrical, both mandibles bearing 4 incisors, 1 *lacinia mobilis* and 3 submarginal setae.

Maxillule: coxopodite with 11 cuspidate setae. Otherwise unchanged besides size.

Maxilla: coxopodite bilobed with 10 (4 serrulate and 6 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; basipodite bilobed, both bearing 4 (1 serrulate and 3 pappose) setae; endopod entire bearing 3 (2 serrulate and 1 simple) +2 serrulate +4 serrulate setae; exopod with 13 marginal plumose setae bearing lateral microtricha.

First maxilliped: coxopodite with 2+1+2 serrulate setae; basipodite with 14 (4 serrulate and 10 pappose) setae; endopod with 4 articles with 3,1,2,3 pappose setae; exopod entire with 1+3 plumose setae.

Second maxilliped: coxopodite unarmed; basipodite with 1+2+3 serrulate setae; exopod entire bearing 6 pairs of plumose setae on distal part. Otherwise unchanged.

Third maxilliped: coxopodite unarmed; basipodite with 3 serrulate setae along inner margin; endopod with 4 articles with 2+2 simple, 1 simple, 2+4 plumodenticulate, 2+1 (1 simple and 2 plumodenticulate) setae; exopod entire bearing 8 pairs of plumose setae on distal part.

First pereopod: biramous; coxopodite with 1 simple setae; basipodite with 1 simple setae; endopod: first article with 2+2 setae, second article with 3 plumodenticulate setae, third article with 3+4 plumodenticulate setae, fourth article with 2 simple and 1 plumodenticulate setae; exopod entire with 8 pairs of plumose setae on distal part.

Second pereopod: biramous; coxopodite without setae; basipodite with 2 simple setae; endopod: first article with 2+1 setae, second article with 2 plumodenticulate, third article with 4 plumodenticulate, fourth article with 2 simple and 1 plumodenticulate setae; exopod entire with 6 pairs of plumose setae on distal part.

Third pereopod (Figure 4C): biramous; coxa without setae; basipodite with 1 simple setae; endopod: first article with 2 simple setae, second article without setae, third article without setae, fourth article with 5 plumodenticulate setae, fifth article with 2 plumodenticulate setae; exopod entire with 3 pairs of plumose setae on distal part.

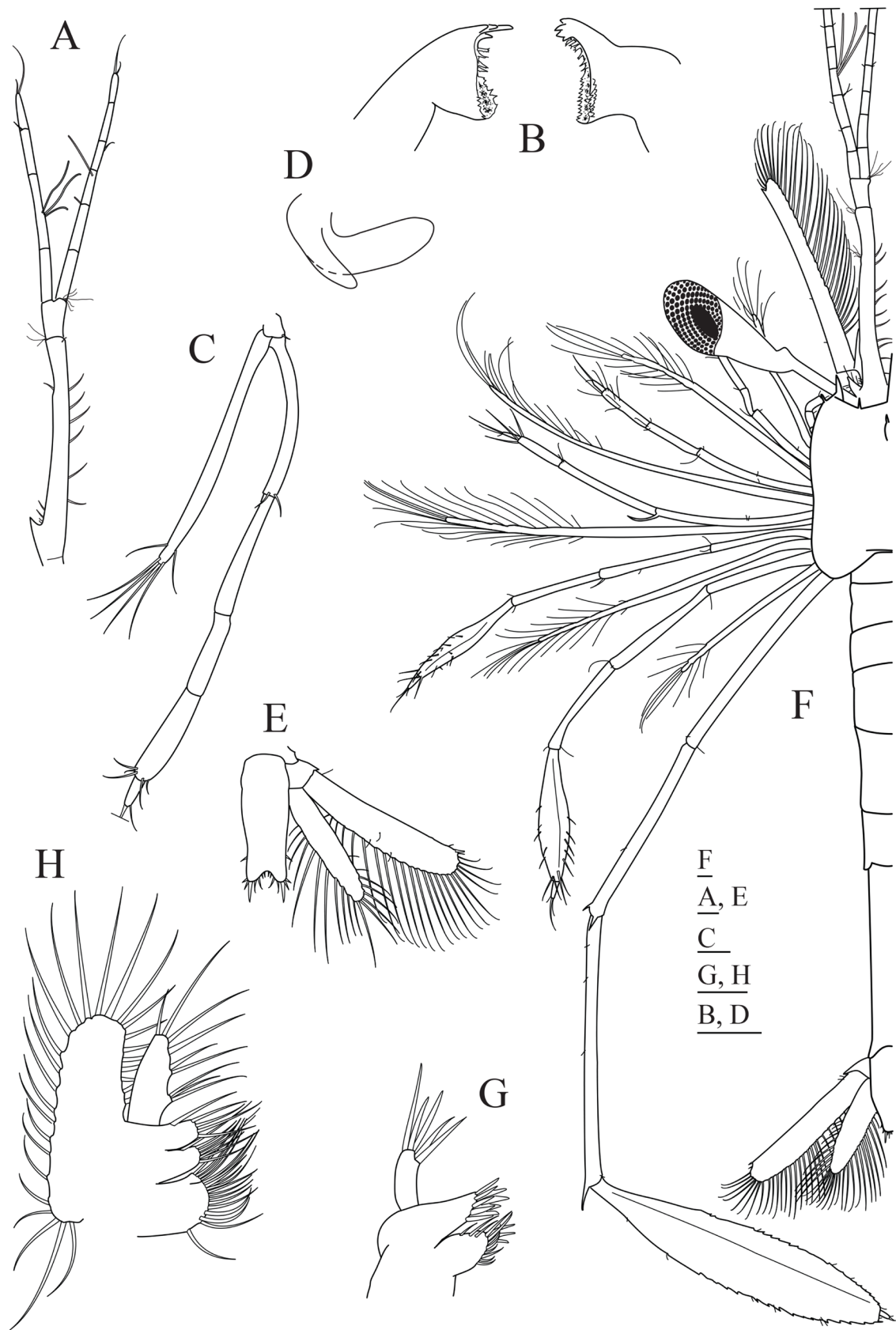


FIGURE 4. Sixth zoea: **A** antennule; **B** mandibles; **C** third pereiopod; **D** fourth pereiopod; **E** uropods and telson. Seventh zoea: **F** larvae dorsal view; **G** maxillule; **H** maxilla. Scale bars: 0.1mm.

Fourth pereopod (Figure 4D): biramous bud

Fifth pereopod: developed, uniramous. coxopodite without setae; basipodite bears 1 simple setae; endopod: first article without setae; second article with 1 setae and a spine-like process; third article with 1+2 setae and a spine-like process; fourth article paddle-like, margins 2/3 serrated with teeth on both sides and bearing 1+2+1 setae; fifth article small with 2 terminal setae.

Pleon: unchanged besides size.

Pleopods: absent

Uropods (Figure 4E): biramous, longer than telson, with 2 base spines; exopod with 2 simple setae +1 spine +24 plumose setae +3 simple setae; endopod with 3 simple setae +18 plumose setae.

Telson (Figure 4E): second pair of processes also in an anterolateral position; otherwise unchanged besides size.

Seventh Zoea (Figure 4F–H)

Size: TL= 5.46±0.40 mm; CL= 1.23±0.15 mm; RL= 0.56±0.06 mm; N = 10

Carapace (Figure 4F): rostrum with 1 spine in front of dorsal organ; antero-ventral margin without denticles; otherwise unchanged besides size.

Antennule (Figure 4F): peduncle with 2 articles; stylocerite with 5–7 small simple setae, proximal article with 3–4 setae on inner margin, 8–13 plumose setae along the inner margin of the article and 1 row of plumose setae on outer margin and posterior end; distal article with row of plumose setae terminally; endopod with 16–25 articles; exopod with 10–21 articles with 3 aesthetascs in the forth article and 1 plumose setae and 2 simple setae apically.

Antenna (Figure 4F): endopod reaching about a third of exopod, with 3 small setae apically; exopod with 23–30 plumose setae on inner side, 1 spine plus 1–3 simple small setae on the outer margin.

Mandible: both mandibles bearing 4 incisors, 1 *lacinia mobilis* and a molar process; right mandible with 2–6 submarginal setae and left with 3–5 submarginal setae.

Maxillule (Figure 4G): coxopodite with 14–15 cuspidate setae, basipodite with 9 cuspidate setae bearing lateral microtricha; endopod with 2 strong subterminal serrulate setae and 3 strong terminal serrulate setae.

Maxilla (Figure 4H): coxopodite bilobed with 14–15 (4 serrulate and 10 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; basipodite bilobed, bearing 6–7 (1 serrulate and 5 pappose) and 5–6 (1 serrulate and 4 pappose) setae; exopod with 19–30 marginal plumose setae bearing lateral microtricha; otherwise unchanged besides size.

First maxilliped: basipodite with 17–18 (8 serrulate and 10 pappose) setae; endopod with 4 articles with 3,1–2,2,4 pappose setae; exopod entire with 0–1 plumose setae on anterior outer margin and 1+4 plumose setae terminally; otherwise unchanged besides size.

Second maxilliped (Figure 4F): endopod with 3 articles with 2–3 (1–2 simple +1 plumodenticulate) +1 simple, 2–3 (1–2 simple +1 plumodenticulate), 0–1+5 (2–3 simple +3 plumodenticulate) setae; otherwise unchanged.

Third maxilliped (Figure 4F): endopod with 4 articles with 2+2 simple, 1 simple, 0–2 (0–1 simple +1 plumodenticulate) +2+4 plumodenticulate, 1–2 simple +2 plumodenticulate setae; otherwise unchanged besides size.

First pereopod (Figure 4F): coxopodite with 1–2 simple setae; basipodite with 0–3 simple setae; otherwise unchanged besides size.

Second pereopod (Figure 4F): basipodite with 2–3 simple setae; endopod: first article with 1–2+1–2 setae, second article with 2 plumodenticulate setae, third article with 4–5 plumodenticulate setae, fourth article with 2 simple and 1 plumodenticulate setae; exopod entire with 11–12 pairs of plumose setae on distal part; otherwise unchanged besides size.

Third pereopod (Figure 4F): basipodite with 2+0–1 simple setae; endopod: first article with 1–2 setae, second article with 1 simple setae and 1 spine-like process, third article with 1–3 setae, fourth article paddle-like bearing 11–18 sparsely plumodenticulate setae, fifth article small with 2 plumodenticulate and 1 simple terminal setae; exopod entire with 9–10 pairs of plumose setae on distal part; otherwise unchanged besides size.

Fourth pereopod (Figure 4F): biramous; coxopodite with 0–1 setae; basipodite with 1–2 simple setae; endopod: first article with 0–2 setae, second article with 1–2 setae, third article with 2–6 setae, fourth article enlarged, paddle-like, bearing 12–17 sparsely plumodenticulate setae, fifth article small with 2 simple and 1 simple terminal setae; exopod entire with 5–6 pairs of plumose setae.

Fifth pereopod (Figure 4F): coxopodite with 1 simple setae; basipodite bears 2 simple setae; first article with

0–2 setae; second article with 1–3 setae and a spine-like process; third article sparsely setose with 1–2 spine-like setae and a spine-like process; fourth article paddle-like, margins 2/3 serrated with teeth on both sides and bearing 5–15 sparsely plumodenticulate setae; fifth article small with 2 terminal setae.

Pleon (Figure 4F): unchanged besides size.

Pleopods: absent

Uropods (Figure 4F): longer than telson; protopod with edged margins dorsally; exopod with 27–33 plumose setae along inner and posterior margin, 2–3 simple setae on anterior and 1 spine posteriorly on outer margin; endopod with 24–34 plumose setae.

Telson (Figure 4F): margins slightly narrower posteriorly; otherwise unchanged besides size.

Eighth Zoea (Figure 5A–C)

Size: TL= 6.20±2.57 mm; CL= 1.67±0.15 mm; RL= 0.83±0.09 mm; N = 10

Carapace: unchanged besides size.

Antennule (Figure 5A): stylocerite with 8 small simple setae, proximal article now with 3 setae on inner margin, 11–15 plumose setae along the margin of the segment, one row of plumose setae on outer margin and posterior end, 0–3 simple setae and 1 row of plumose setae on outer margin and posterior end, 2–4 simple setae 1 row of plumose setae terminally; endopod with 24–26 articles; exopod with 18–26 articles with 2–3 aesthetascs in the third article and 3–4 aesthetascs in the fourth article and 1 plumose setae and 4–7 simple setae apically.

Antenna (Figure 5B): peduncle with 2 simple setae; endopod with 2 articles with 1–2 simple setae on the margin of the 2nd article and 5 small setae apically; exopod with 29–32 plumose setae on inner side, 1 spine plus 3–6 simple small setae.

Mandible (Figure 5C): right mandible with 6–8 submarginal setae and left with 4–5 submarginal setae; otherwise unchanged besides size.

Maxillule: coxopodite with 12–20 cuspidate setae, basipodite with 11–15 cuspidate setae bearing lateral microtricha; endopod with 2–3 strong subterminal serrulate setae and 3 strong terminal serrulate setae.

Maxilla: coxopodite bilobed with 15 (4 serrulate and 10 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; basipodite bilobed, both bearing 8 (1 serrulate and 7 pappose) setae; endopod entire bearing 3 (2 serrulate and 1 simple) +2 serrulate +4 serrulate setae; exopod with 28–34 marginal plumose setae bearing lateral microtricha.

First maxilliped: exopod with 1–4 plumose setae on anterior outer margin and 4–5 plumose setae terminally; otherwise unchanged besides size.

Second maxilliped: unchanged besides size.

Third maxilliped: unchanged besides size.

First pereopod: unchanged besides size.

Second pereopod: endopod: first article with 1–2+1–2 setae, second article with 1–4 setae and 2 plumodenticulate setae, third article with 4–5 plumodenticulate setae, fourth article with 2–3 simple and 1 plumodenticulate setae; exopod entire with 11–13 pairs of plumose setae on distal part; otherwise unchanged besides size.

Third pereopod: coxopodite with 1–2 simple setae; endopod: first article with 2–4 setae, second article with 0–2 setae and 1 spine-like process, third article with 2–4 setae, fourth article enlarged, paddle-like, bearing 16–22 sparsely plumodenticulate setae, fifth article small with 2 simple and 2–3 terminal plumodenticulate setae; exopod entire with 10–11 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Fourth pereopod: coxopodite with 1 setae; basipodite with 1–2 simple setae; endopod: first article with 1–4 setae, second article with 1–3 setae, third article with 3–6 plumodenticulate setae, fourth article margins 1/3 serrated bearing 13–24 sparsely plumodenticulate setae, fifth article small with 2–4 simple and 1 terminal setae; exopod entire with 6 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Fifth pereopod: developed, uniramous. Coxopodite with 0–1 simple setae; basipodite bears 1 simple setae; first article with 1–7 sparse setae; second article with 1–5 setae and 1 spine-like process; third article sparsely setose with 6 spine-like setae and 1 spine-like process; fourth article margins 2/3 serrated with teeth on both sides and bearing 14–31 sparsely plumodenticulate setae; fifth article small with 3–6 setae.

Pleon: 6 somites; possibly with 3 small simple dorsal setae on the 4th somite and 1–2 small dorsal setae on the 5th somite.

Pleopods: small buttons.

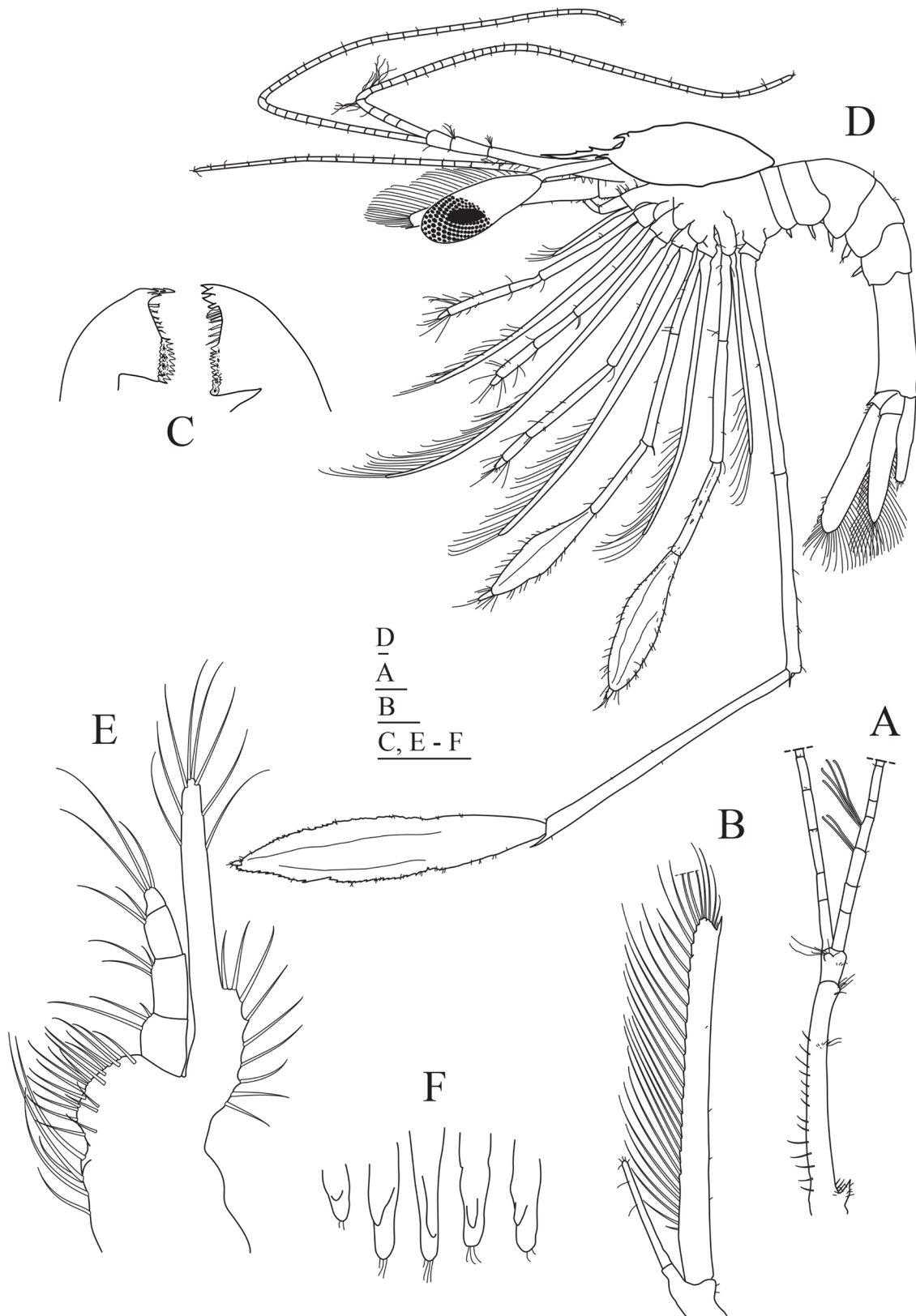


FIGURE 5. Eighth zoea: **A** antennule; **B** antenna; **C** mandibles. Ninth zoea: **D** larvae dorsal view; **E** first maxilliped; **F** pleopods. Scale bars: 0.1mm.

Uropods: exopod with 3–4 simple setae on anterior outer margin, 1–6 simple setae and 1 spine on posterior outer margin, followed by 32–40 plumose setae along posterior and inner margin; endopod with 33–38 plumose setae along margin. Otherwise unchanged besides size.

Telson: slightly narrower posteriorly. Otherwise unchanged besides size.

Ninth Zoea (Figure 5D–F)

Size: TL= 7.58±1.48 mm; CL= 2.26±2.57 mm; RL= 1.07 ±0.17 mm; N = 3

Carapace (Figure 5D): rostrum reaching about a third of antennular peduncle, one spine in front of the dorsal organ and 2 spines on the rostrum. Otherwise unchanged.

Antennule (Figure 5D): stylocerite with 7–10 small simple setae, proximal article with 2–3 setae on inner margin, 16–20 plumose setae along the margin of the article +1 row of plumose setae +1–2 simple setae +1 row of plumose setae, 1–4 simple setae +1 row of plumose setae; endopod with 35–38 articles; exopod with 40–45 articles with 0–1 aesthetascs in the third article, 3–5 aesthetascs in the fourth, 4–6 aesthetascs in the fifth, 2–5 aesthetascs in the sixth, 0–3 aesthetascs in the seventh and 4–5 simple setae apically.

Antenna (Figure 5D): endopod nearly twice the length of exopod, with 17–20 articles, each one with 0–3, except the terminal one with 3–5, simple setae; exopod entire, with 39–41 plumose setae on inner side, 1 spine plus 5–7 simple small setae.

Mandible: right mandible with 9–10 submarginal setae and left with 7 submarginal setae. Otherwise unchanged besides size.

Maxillule: coxopodite with 13–16 cuspidate setae, basipodite with 11–12 cuspidate setae; endopod with 3–4 strong subterminal serrulate setae and 3 strong terminal serrulate setae. Otherwise unchanged besides size.

Maxilla: coxopodite bilobed with 18 (4 serrulate and 14 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; endopod entire bearing 3 (2 serrulate and 1 simple) + 2–3 serrulate +4 serrulate setae; exopod with 48 marginal plumose setae. Otherwise unchanged besides size.

First maxilliped (Figure 5E): basipodite with 18–19 (8 serrulate and 10–11 pappose) setae; endopod with 4 articles with 2–3, 1–3, 2, 3–4 pappose setae; exopod showing the caridean lobe with 9–10 plumose setae along the margin and with 6–8 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Second maxilliped (Figure 5D): basipodite with 6–8 serrulate setae along inner margin; endopod with 3 articles with 2–3+1 (2 simple + 1–2 plumodenticulate), 2–4 plumodenticulate, 1+5 (3 simple and 3 plumodenticulate) setae; exopod entire bearing 5–6 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Third maxilliped (Figure 5D): coxopodite with 0–1 simple small setae; endopod with 4 articles, with 2+1 simple, 1 simple and 2 plumodenticulate, 16–24 plumodenticulate, 3–4 (1–2 simple and 2 plumodenticulate) setae; exopod entire bearing 11–13 pairs of plumose setae on distal part. Otherwise unchanged besides size.

First pereopod (Figure 5D): endopod: first article with 2–3 setae, second article with 2 plumodenticulate setae, third article with 1–2 simple and 8 plumodenticulate setae, fourth article with 5 simple and 1 plumodenticulate setae; exopod entire with 18 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Second pereopod (Figure 5D): coxopodite with 2–3 simple setae; endopod: first article with 4–5 setae, second article with 4 setae and 3 plumodenticulate setae, third article with 7–12 plumodenticulate setae, fourth article with 7 simple and 1 plumodenticulate setae; exopod entire with 23–25 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Third pereopod (Figure 5D): coxopodite with 2–4 simple setae; endopod: first article with 5–9 setae, second article with 1–6 setae and 1 spine-like process, third article with 4–6 setae, fourth article bearing 26–33 sparsely plumodenticulate setae, fifth article small with 4–5 simple and 1 terminal setae; exopod entire with 14–15 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Fourth pereopods (Figure 5D): coxopodite with 1–2 setae; basipodite with 3 simple setae along margin; endopod: first article with 5–6 setae, second article with 2–3 setae, third article with 10–15 plumodenticulate setae, fourth article bearing 34–40 sparsely plumodenticulate setae, fifth article small with 5 simple and 1 terminal setae; exopod entire with 10–11 pairs of plumose setae on distal part.

Fifth pereopod (Figure 5D): coxopodite with 1–3 simple setae; basipodite bears 1–3 simple setae; first article sparsely setose; second article with 4–7 spine-like setae and 1 spine-like process; third article sparsely setose with 11–16 spine-like setae and 1 spine-like process; fourth article bearing 21–27 sparsely plumodenticulate setae; Otherwise unchanged besides size.

Pleon (Figure 5D): with 0–4 small simple setae along dorsal margin on the 1st somite, 0–2 small simple setae along dorsal margin on the 3rd somite, 2–5 small simple setae along dorsal margin on the 4th somite, 1–2 small simple setae along dorsal margin and 0–1 simple setae on posterior ventral margin of the 5th somite and 6 small simple setae along ventral margin the 6th somite.

Pleopods (Figure 5D, 5F): bilobed, endopod bud-like with 2–4 simple apical setae as figured; exopod as bud.

Uropods (Figure 5D): exopod almost twice the length of telson with 6–10 simple setae on anterior outer margin, 6–8 simple setae and 1 spine on posterior outer margin, followed by 48–51 plumose setae along posterior and inner margin; endopod with 49–50 plumose setae along margin. Otherwise unchanged besides size.

Telson (Figure 5D): unchanged besides size.

Tenth Zoea (Figure 6A–U)

Size: TL= 11.61±1.62 mm; CL= 3.17±0.69 mm; RL= 1.95 ±0.49 mm; N = 6

Carapace (Figure 6A, 6B): one spine in front of the dorsal organ, 3–4 spines on the rostrum dorsal part and 0–1 ventrally. Otherwise unchanged.

Antennule (Figure 6A, 6C): peduncle with 2 articles; stylocerite with 12–17 small simple setae, proximal article with 4–6 setae on inner margin, 20–24 plumose setae along the margin of the article +1 row of plumose setae + 3 simple setae +1 row of plumose setae, 3–10 simple setae +1 row of plumose setae; endopod with 63–71 articles; exopod with 62–75 articles with 0–2 aesthetascs in the second article, 2–4 aesthetascs in the third article, 5–7 aesthetascs in the fourth, 6–7 aesthetascs in the fifth, 4–7 aesthetascs in the sixth, 3–7 aesthetascs in the seventh, 0–4 aesthetascs in the eighth, 0–3 aesthetascs in the ninth and 4–9 simple setae apically.

Antenna (Figure 6A, 6D): basipodite with 4+4–7 simple setae; endopod three times the length of scaphocerite, with 49–59 articles, each one with 0–4, except the terminal one with 3–4 simple setae; exopod entire with 48–54 plumose setae on inner side, 1 spine plus 10–13 simple small setae.

Mandible (Figure 6E): right mandible with 10–12 submarginal setae and left with 8–9 submarginal setae. Otherwise unchanged besides size.

Maxillule (Figure 6F): coxopodite with 18–21 cuspidate setae, basipodite with 19–21 cuspidate setae bearing lateral microtricha; endopod with 4–5 strong subterminal serrulate setae and 3 strong terminal serrulate setae.

Maxilla (Figure 6G): coxopodite with 20–21 (4 serrulate and 16–17 pappose) and 4 (1 serrulate and 3 pappose) setae, respectively; endopod entire bearing 3 (2 serrulate and 1 simple) +3–4+4 serrulate setae, and 0–1 small plumose setae on the ventral external side; exopod with 64–77 marginal plumose setae; microtricha as illustrated. Otherwise unchanged besides size.

First maxilliped (Figure 6H): coxopodite with 4–7 serrulate setae; basipodite with 20–22 (8–11 serrulate and 11–14 pappose) setae and 5–11 simple setae scattered around; endopod with 4 articles with 3–5, 4–6, 2, 4 pappose setae; exopod showing the caridean lobe with 15–18 plumose setae along the margin, entire, with 4 pairs of plumose setae on distal part; epipodite as bud.

Second maxilliped (Figure 6I): coxopodite with 0–1 simple setae; basipodite with 8 serrulate setae along inner margin and 1–3 simple setae along outer margin; endopod with 3 articles with 2 simple +2 plumodenticulate +3–4 simple, 1 simple +6 plumodenticulate, 4–5 simple +3 plumodenticulate setae; exopod entire bearing 5–6 pairs of plumose setae on distal part.

Third maxilliped (Figure 6J): coxopodite with 1–3 simple small setae; basipodite with 3–4 serrulate setae along inner margin; endopod with 4 articles with 3–6 simple, 1 simple and 3–5 plumodenticulate, 23–31 plumodenticulate, 5–6 (3–4 simple and 2 plumodenticulate) setae; exopod entire bearing 17–19 pairs of plumose setae on distal part.

First pereopod (Figure 6K): coxopodite with 0–3 simple setae; basipodite with 2–4 simple setae; endopod: first article with 7 setae, second article with 1–2 simple and 1+3 plumodenticulate setae, third article with 7 simple and 6 plumodenticulate setae and a forming chela about a 3rd of fourth article's size, fourth article with 10 simple and 1 plumodenticulate setae; exopod entire with 23–25 pairs of plumose setae on distal part.

Second pereopod (Figure 6L): basipodite with 1–4 simple setae; endopod: first article with 8–16 setae, second article with 8 setae and 6 plumodenticulate setae, third article with 7–9 plumodenticulate setae and a forming chela about a 3rd and a half of the fourth size bearing 6–8 simple setae, fourth article with 7–11 simple and 1 plumodenticulate setae. Otherwise unchanged besides size.

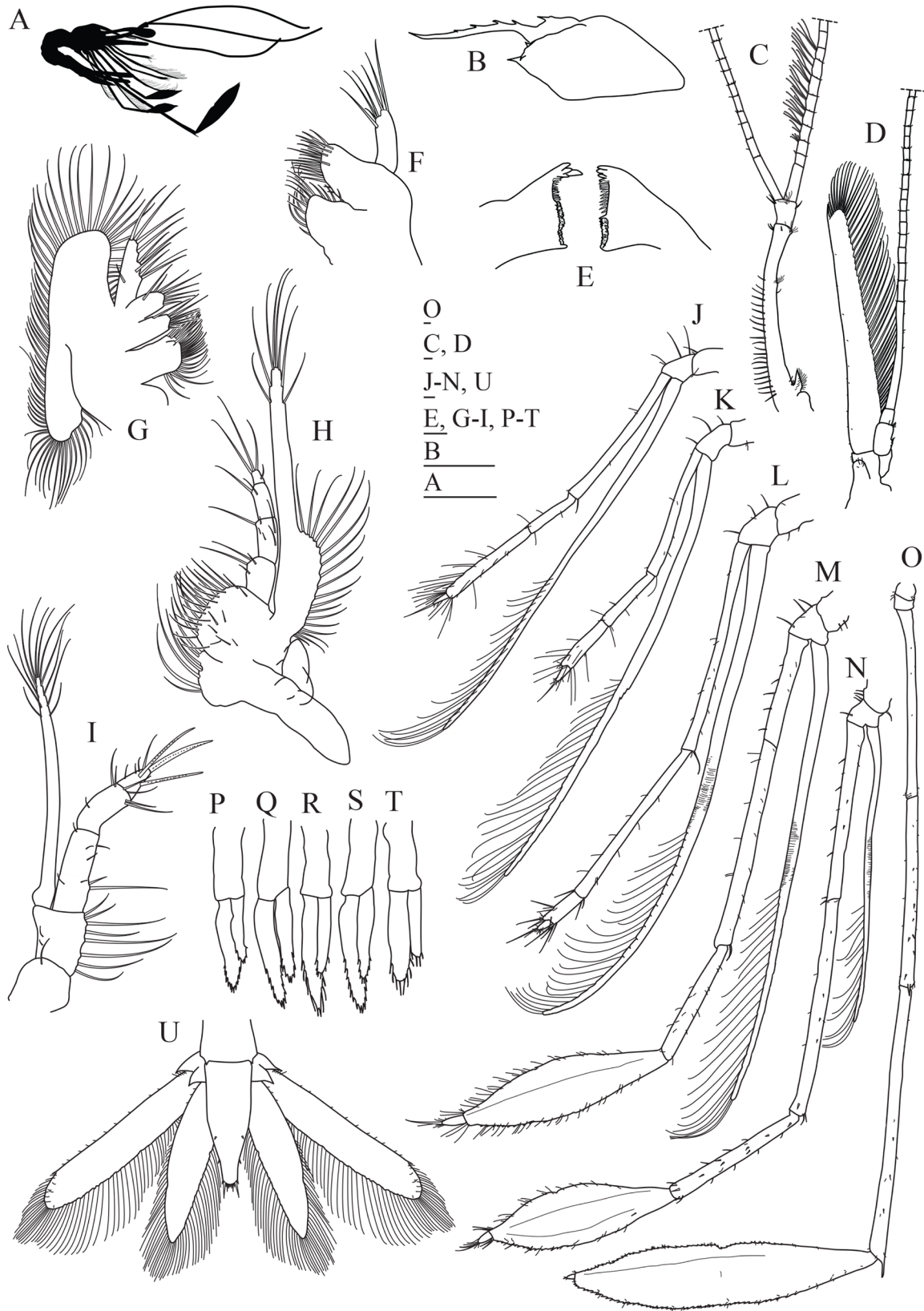


FIGURE 6. Tenth zoea: **A** complete larvae lateral view; **B** rostrum and carapace denticles; **C** antennule; **D** antenna; **E** mandibles; **F** maxillule; **G** maxilla; **H** first maxilliped; **I** second maxilliped; **J** third maxilliped; **K** first pereiopod; **L** second pereiopod; **M** third pereiopod; **N** fourth pereiopod; **O** fifth pereiopod; **P** first pleopod; **Q** second pleopod; **R** third pleopod; **S** fourth pleopod; **T** fifth pleopod; **U** telson and uropods. Scale bars: 0.1mm.

Third pereopod (Figure 6M): basipodite with 1–5 simple setae; endopod: first article with 7–9 setae, second article with 12–17 setae and 1 spine-like process, third article with 14–22 setae, fourth article bearing 57–74 sparsely plumodenticulate setae, fifth article small with 7–10 simple and 1 terminal setae; exopod entire with 20–23 pairs of plumose setae on distal part. Otherwise unchanged besides size.

Fourth pereopods (Figure 6N): coxopodite with 2–7 setae; basipodite with 1–3 setae along margin; endopod: first article sparsely setose with 8 setae, second article sparsely setose with 7 setae, third article sparsely setose with 18 plumodenticulate setae, fourth article margins 1/3 serrated bearing 20–61 sparsely plumodenticulate setae, fifth article small with 4–9 simple and 1 terminal setae; exopod entire with 13–16 pairs of plumose setae on distal part.

Fifth pereopod (Figure 6O): coxopodite with 2–3 simple setae; basipodite bears 2–4 simple setae; first article sparsely setose; second article sparsely setose with 4–7 spine-like setae and 1 spine-like process; third article sparsely setose with 3–6 spine-like setae and a spine-like process; fourth article margins 2/3 serrated with teeth on both sides and bearing 27–56 sparsely plumodenticulate setae; fifth article small with 5 simple terminal and 3 spine-like setae.

Pleon: with 3–5 small simple setae along ventral margin on the 1st somite, 2–6 small simple setae along ventral margin on the 3rd somite, 1–4 small simple setae along ventral margin on the 4th somite and 1–4 small simple setae along ventral margin on the 5th somite.

Pleopods (Figure 6P, 6Q, 6R, 6S, 6T): protopods without setae; endopods with 4–8 small spines and exopods with 8–16 small spines, as illustrated.

Uropods (Figure 6U): exopod with 3–7 simple setae on anterior outer margin, 8–16 simple setae and 1 spine on posterior outer margin, followed by 60–72 plumose setae along posterior and inner margin; endopod with 2–4 simple setae on anterior outer margin, 5–7 simple setae and 58–69 plumose setae along margin with lateral microtricha. Otherwise unchanged besides size.

Telson (Figure 6U): Unchanged besides size.

Decapodite (Figure 7A–U)

Size: TL= 26.19 mm; CL= 7.23 mm; RL= 4.38 mm; N = 1

Carapace (Figure 7A): carapace smooth, rostrum straight reaching over a half of antennular peduncle, with one spine in front of the dorsal organ, 6 spines on the dorsal part and 0–3 ventrally.

Antennule (Figure 7A, 7A', 7B): basal article of the antennular peduncle with stylocerite reaching over 1/4 of this article; peduncle with 3 articles; lateral antennular flagellum with aesthetascs extending from the 3rd article to 20th article.

Antenna (Figure 7A, 7A', 7C): basipodite with 4 simple setae; endopod nine times the length of scaphocerite, with 147 articles, each one with 0–1, except the terminal one with 8 simple setae; exopod entire, with 67 plumose setae on inner side, 1 spine plus 2 simple small setae.

Mandibles (Figure 7D): unequal, without palp; presenting incisor process, as figured.

Maxillule (Figure 7E): coxopodite with 36 cuspidate setae, basipodite with 51 cuspidate setae; endopod with 2 strong terminal serrulate setae and 5 setae along outer margin.

Maxilla (Figure 7F): coxopodite bearing 23 setae; basipodite bilobed, each bearing 25 setae and 29 setae respectively; endopod entire bearing 1 setae on inner side, 1 terminal setae and 1 setae along outer margin; scaphognathite well developed, very large and not very broad, with 115 plumose setae along the margin.

First maxilliped (Figure 7G): coxopodite with 8 serrulate setae; basipodite with 62 setae; endopod with 4 articles with (0,2,0,3) pappose setae; exopod showing the caridean lobe, not distinctly separated with 38 plumose setae along the margin, entire, with 10 pairs of plumose setae on distal part; epipodite bilobed.

Second maxilliped (Figure 7H): coxa with 7 simple setae and a large epipod laterally; basis with 10 setae along inner margin and 4 setae along outer margin; endopod stout, terminal article, distally elongated, with rows of long marginal and submarginal setae; ischium with 4 setae along inner margin and 6 simple setae along outer margin; merus with 3 setae; carpus short with 2 setae along the margin; propod with row of distributed setae; exopod entire bearing 13 pairs of plumose setae on distal part.

Third maxilliped (Figure 7I, 7I'): with long and slender endopod, distal article with 6 spines distributed terminally; exopod short, slender, reaching more than 2/3 of the two proximal endopod articles, with 2 terminal setae and 1 setae near the base.

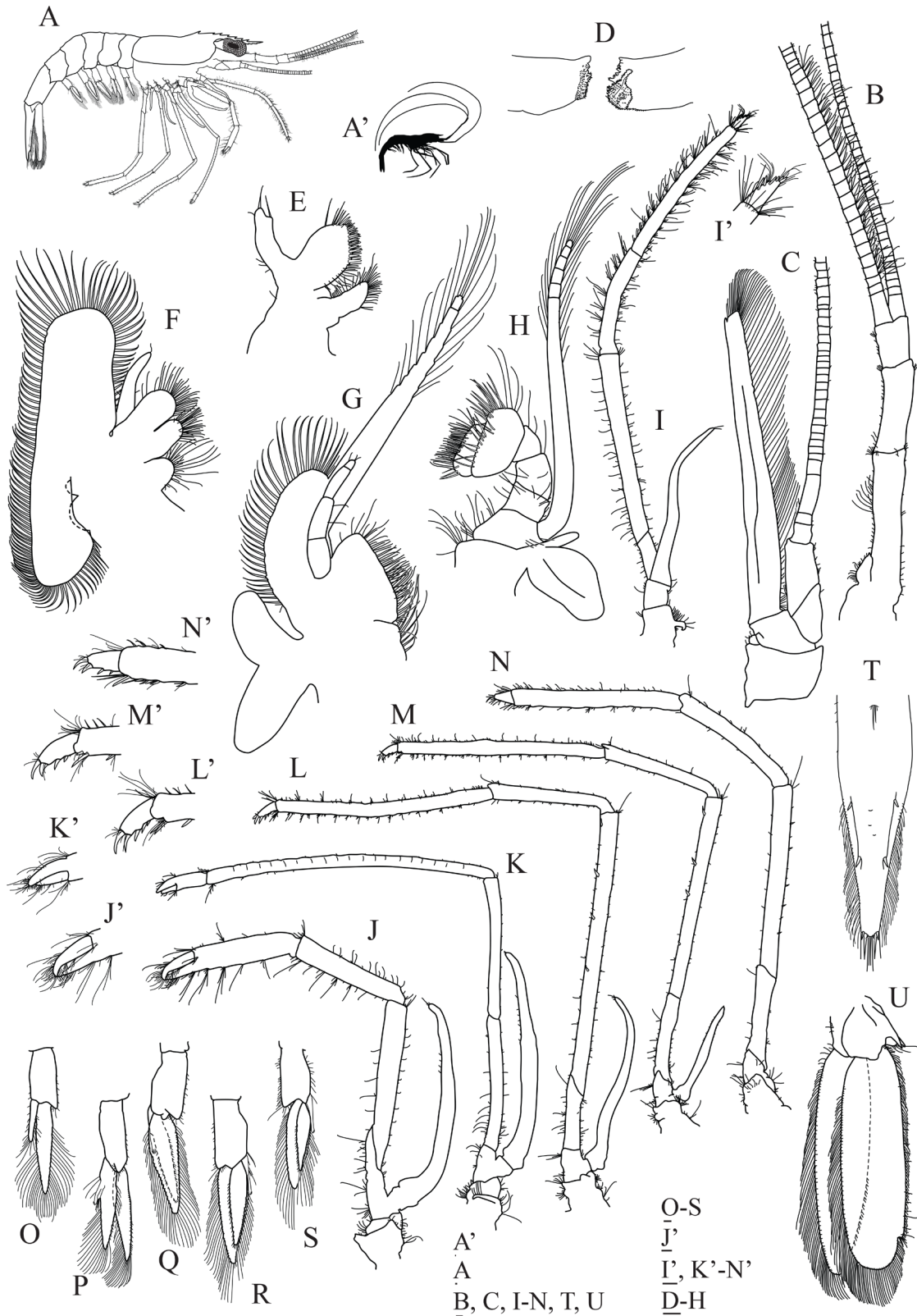


FIGURE 7. Decapodite: **A** specimen lateral view; **A'** complete specimen lateral view; **B** antennule; **C** antenna; **D** mandibles; **E** maxillule; **F** maxilla; **G** first maxilliped; **H** second maxilliped; **I** third maxilliped; **J** first pereiopod; **J'** first pereiopod, detail of chelae; **K** second pereiopod; **K'** second pereiopod, detail of chelae; **L** third pereiopod; **L'** third pereiopod, detail of chelae; **M** fourth pereiopod; **M'** fourth pereiopod, detail of chelae; **N** fifth pereiopod; **N'** fifth pereiopod, detail of chelae; **O** first pleopod; **P** second pleopod; **Q** third pleopod; **R** fourth pleopod; **S** fifth pleopod; **T** telson; **U** uropods. Scale bars: 0.1mm.

First pereiopod (Figure 7J, 7J'): all articles well differentiated and setose as figured; propodus with a simple chela, reaching beyond the end of scaphocerite; palm about 3.5 times as long as dactylus; carpus almost as long as merus; exopod entire with four setae on ventral posterior margin and four setae on distal part.

Second pereiopod (Figure 7K, 7K'): carpus twice as long as merus, with indistinct articulation; merus with equal length as ischium, both entire; exopod entire with eight setae on ventral posterior margin and two setae on distal part.

Third pereiopod (Figure 7L, 7L'): similar to fourth and fifth pereiopod, being the smallest in size; with unarmed ischium; merus with four stout ventrolateral spines, over twice as long as carpus; propodus slightly shorter than merus with setae along margins; dactylus about 1/10 length of propodus, biunguiculate, with three additional slender spines on flexor margin, terminal unguis longer than ventral unguis; exopod entire with four setae on distal part.

Fourth pereiopod (Figure 7M, 7M'): with four stout spines along ventrolateral margin of merus, which is almost two times as long as carpus; propodus slightly longer than merus with setae along margins; dactylus similar to third pereiopod, as figured; exopod entire with nine setae on ventral posterior margin, one on distal part and five on dorsal posterior margin.

Fifth pereiopod (Figure 7N, 7N'): merus with five stout spines along lateral margin; propodus slightly shorter than merus with spines and setae along margins; dactylus similar to third and fourth pereiopod, as figured.

Pleopods (Figure 7O, 7P, 7Q, 7R, 7S): endopod of first pleopod about half as long as exopod with 20 setae. Other pleopods with endopod slightly smaller than exopod, both with plumose setae on margins. *Appendix masculina* on second pleopod about half the size of *appendix interna*, with four setae on posterior end.

Uropods (Figure 7U): protopod with two lateral teeth with seven setae on margin; exopod sub equal to endopod length, both with plumose setae on margins.

Telson (Figure 7T): about 1.3 times as long as sixth pleomere; lateral margins of telson with many setae on distal half and 4 setae (2 long ones and 2 short ones) in the middle at proximal; dorsal surface with two pairs of spines, the first pair on 0.4 and second one on 0.8 of telson; posterior margins with a pair of short acute spines, two pairs of long acute ones, a pair of strong spines, a pair of short strong spines and a pair of long acute ones.

Discussion

Lysmata amboinensis larvae hatch with compound and sessile eyes that become stalked in the second stage, and with the first pereiopod as a small bud, which becomes biramous in the second stage and functional in the third zoeal stage. The fifth pereiopod appears as a bud in the second zoea, becoming developed with a paddle-like propodus with serrated margins in the fourth zoeal stage, and the second pereiopod appears in ZIV as biramous bud and becomes functional in ZV. The third pereiopod is present as biramous bud in ZV and becomes functional in ZVI, and so does the fourth pereiopod in ZVI and ZVII, respectively, both bearing paddle-like propodus similar to the fifth pereiopod but smaller.

In general, the present morphological description agrees with the one made by Wunsch (1996), with some minor differences observed such as the mandible description, as well as in the number of setae present in several appendages. Also, the rise of the pereiopods during the larval development stages agrees with present description, except for pereiopod 1 that was detected by us as a small bud in the first zoeal stage and pereiopod 5 in the second zoeal stage, while in Wunsch's study there are no records of pereiopods as small buds in these stages. They were only registered as biramous and uniramous buds in stage II and III, respectively (Wunsch 1996). There are also some slight differences regarding the articles of the endopod of the second and third maxillipeds, showing in the present study three and four articles each, respectively, instead of plus one on each of them as in Wunsch description (see Table I). The number of articles in the exopods of the maxillipeds and pereiopods is also quite different in both descriptions, which could perhaps be due to some natural variation amongst the species or could possibly be related to the difference in larviculture conditions.

However, it seems like Wunsch's larvae entered mark-time moult after ZVII (day 22), which led him to stop staging them but rather counting the days and moults. Additionally, after day 40, Wunsch (1996) records and observations were made based on only one specimen.

Through comparison with the results from the present study (see Table I), we consider that larvae aged day 40 described by Wunsch (1996) correspond to the ninth zoea stage, with larvae showing biramous pleopods with ru-

dimentary exopods and endopods with few setae, which therefore leads us to conclude that ZVIII does not seem to have been observed by Wunsch since there is no record of a larvae with the morphological characters of the present's study eighth zoeal stage. The equivalent to the present description's tenth zoeal stage seems to have been reached by day 80 on Wunsch's work, with both antenna and antennule presenting highly articulated flagella, both pereopods 1 and 2 showing a forming chela and with pleopods presenting a differentiated protopod, with endopods and exopods armed with setae, besides the general increase in the number of setae present in the other appendages.

Wunsch's larval cycle seems to have reached an additional stage, ZXI, on day 120 with larvae presenting more developed antennules, which increased in size, articles and number of setae in the flagella, and an increase in the number of setae in the maxillules coxopodite, maxillae basipodite and coxopodite, first maxilliped basipodite and pleopods and uropods, with first pleopod, showing an *appendix interna*. In the present description we have no record of this stage since larvae went directly from the tenth zoeal stage to decapodite. However, Kurata (1970) has also described an eleventh zoeal stage for *Lysmata wurdemanni* larval cycle. When comparing both eleventh and tenth zoeal stages the differences found are similar to the ones described by Wunsch (1996) in the case of *L. amboinensis*. Therefore we hypothesize that, depending on environmental/rearing conditions, some *Lysmata* species, the case of *L. amboinensis* and possibly of *L. wurdemanni*, could have the possibility to add a last zoeal stage to their larval series. This variation in the number of zoeal stages in development depending on rearing conditions has already been reported for decapods (e.g. Boyd & Johnson 1963) and particularly carideans species (e.g. Ramonell-Goyanes 1987).

By analysing the information available for the different *Lysmata* species (synthesised in Table 1) it is possible to see that, in general, all described larvae hatch with similar general morphological features: eyes sessile, carapace with a pterigostomian spine followed by 3 to 6 anterio-ventral marginal denticles, a slender and pointed rostrum, antennule with peduncle and exopod entire, antennal exopod with 5–6 articles bearing 9–12 plumose setae plus 1 simple one on apex, pleon 5th pleomere with a pair of dorso-lateral spines on posterior margin, a triangular shaped telson with 7+7 posterior processes, broader posteriorly and indented and without pleopods and uropods.

After the first zoeal stage, there is a range of variability on the larval development and, as such, there are few common traits amongst species. One of them is the eyes that when stalked, in second and older larval stages, are large with long peduncles, in a very characteristic shape (e.g. fig. 3A); the other is that for all species whose larvae have been described until now, the exopod of the antenna is articulated at hatching and will become not articulated by the fifth zoeal stage. One of the main differences between the larval series known to date is seen in the development of pereopods, where three types of development can occur. The first type can be observed in *L. amboinensis*, *L. wurdemanni*, *L. anchisteus* and possibly in *L. lipkei* (Table I) where pereopods arise sequentially in the following order P1, P5, P2, P3 and P4. For all the other *Lysmata* species, pereopods develop in four sequential moments, having a pair of them occurring simultaneously in one stage. That is, for *L. ensirostris* and *L. vittata* P1 emerges in the second zoea, P5 and P2 are both arising in the third zoea, with P3 and P4 developing in the following stages, while in the case of *L. moorei*, *L. galapagensis* and *L. seticaudata* both P1 and P5 arise in the first zoea, with P2, P3 and P4 developing in the following stages.

Considering the development of pleopods specifically, there seems to be four distinct moments for their development in *Lysmata*. Pleopods first come into view as small buds, then as biramous buds, followed by a stage having a protopod differentiated from the exopod and endopod, this third moment when the exopods and endopod presents several apical setae and a last one with a developed *appendix interna*. All *Lysmata* species larval cycle seem to skip one of these moments presenting only three of them, that is, in the case of *L. amboinensis* and *L. vittata* the first three (small buds, biramous buds, and protopod differentiated from exopod and endopod), or for *L. ensirostris* and *L. wurdemanni*, the last three moments (biramous buds, protopod differentiated from exopod and endopod, and pleopods with *appendix interna*). So far, *L. seticaudata* is the exception presenting all four developing moments in their larval cycle. Perhaps these variations could be another example of what Gore (1985) stated as the possibility of larvae to bypass one or more instars' as they proceed towards metamorphosis, an ability fairly common to species that undergo greatly extended larval development, as is the case for *Lysmata*. In general, *Lysmata* species have a long larval cycle with nine, ten or eleven zoeal stages, plus one decapodite stage.

Within genus *Lysmata*, larvae are very homogenous, with only a few morphological characters allowing the distinction between species, such as *L. galapagensis* unique anterior curved spine in the third pleomere, the presence of a cervical *carinae* present in the carapace of *L. moorei*, and the last three pereopods pairs with a paddle-like propodus with serrated margins in *L. amboinensis*. However, according to Wunsch's notes (1996) this feature is also seen in *L. debelius*.

TABLE 1. Comparison of selected morphological zoeal stages characters of *Lysmata* sp. Z—Zoea. Decap. —Decapodite. ZI, ZII, etc.—First zoea, second zoea, etc. Pl—Plumose seta. Si—Simple setae. NA—Not Available. ^a In ZV it wasn't yet; ^b In ZIV it had almost reached it.

Morphological feature	<i>L. amboinensis</i>	<i>L. amboinensis</i>	<i>L. ensirostris</i>	<i>L. vittata</i>	<i>L. galapagensis</i>
	Present study	Wunsch 1996	Bensam&Kartha 1967; Pillai 1974	Yang&Kim 1999	Bartilotti <i>et al.</i> 2012
ZI, Total length, mm	2.8–2.98	2.70–2.80	1.89–2.23	NA	2.46–2.89
ZI, carapace length, mm	0.9–1	NA	NA	0.33–0.37	0.92–1.00
ZIV, carapace length, mm	0.64–1	NA	1.01	0.44	1.61–2.15
ZVII, carapace length, mm	0.84–1.42	NA	1.40–1.41	0.62–0.68	4.08–4.32
Last Z, carapace length, mm	ZX: 2.81–4.35	ZXI: NA	ZIX: 3.5	ZIX: 0.784–0.832	-
First Zoea:					
Carapace: Pterigostomian spine	Present	Present	Present	Present	Present
Number of marginal denticles	3–5	3–4	3	3	4
Eyes sessile	Present	Present	Present	Present	Present
Antennule: peduncle and exopod	Entire	Entire	Entire	Entire	Entire
Antennal exopod: 5–6 articles	11Pl + 1Si	12Pl + 1Si	9Pl	10Pl + 1Si	11Pl + 1Si
Pair of dorsal spines on 5 th pleomere	Present	Present	Present	Present	Present
Pleopods	Absent	Absent	Absent	Absent	Absent
Uropods	Absent	Absent	Absent	Absent	Absent
Older Zoeas:					
Eyes stalked and pedunculate	ZII	ZII	ZII	ZII	ZII
Carapace without marginal denticles	ZVII	ZVII	ZV	ZIX	ZV
Carapace with cervical carinae	Absent	Absent	Absent	Absent	Absent
Rostrum first dorsal spine	ZVII	ZVI	ZIV	ZIII	ZII
Antennal exopod entire	ZIV	ZIV	ZV	ZIV	ZIV
First pereopod:					
Biramous bud	ZII (small bud: ZI)	ZII	ZII	ZII	ZI

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TABLE 1. (Continued)

Morphological feature	<i>L. amboinensis</i>	<i>L. amboinensis</i>	<i>L. ensirostris</i>	<i>L. vittata</i>	<i>L. galapagensis</i>
	Present study	Wunsch 1996	Bensam&Kartha 1967; Pillai 1974	Yang&Kim 1999	Bartilotti <i>et al.</i> 2012
	10 Z +1 decap. Indian Ocean, Indo-Pa- cific, South Pacific Ocean, Mozambique Channel	11 Z Indo-Pacific, Red Sea, Atlantic Ocean	9 Z+1 decap. Indo-Pacific	9 Z Indo-Pacific	7 Z E Pacific
Functional	ZIII	ZIII	ZIII	ZIII	ZII
Second pereiopod:					
Biramous bud	ZIV	ZIV	ZIII	ZIII	ZIII
Functional	ZV	ZV	ZIV	ZV	ZIV
Third pereiopod:					
Biramous bud	ZV	ZV	ZIV	ZIV (unir. rud)	ZV
Functional	ZVI	ZVI	ZV	ZVII	ZVI
Fourth pereiopod:					
Biramous bud	ZVI	ZVI	ZV	ZIV (unir. rud)	ZV
Functional	ZVII	ZVII	ZVI	ZVIII	ZVI
Fifth pereiopod:					
Uniramous bud	ZIII (small bud: ZII)	ZIII	ZIII	ZIII	ZI
Functional	ZIV	ZIV	ZIV	ZV	ZII
Pereiopods with paddled-like propodus	3rd, 4th and 5th	3rd, 4th and 5th	5 th	5 th	5 th
5 th pleomere without dorso-lat spines	ZVIII	ZIII	NA	ZV	NA
3 rd pleomere with curved spine	Absent	Absent	Absent	Absent	Present
Pleopods:					
Small buds	ZVIII	NA	-	ZV	ZVI
Biramous buds	ZIX	ZIX (day 40)	ZVII	ZVII	-
Differentiated protopod	ZX	ZX (day 80)	ZVIII	ZIX	ZVII
With <i>appendix interna</i>	-	ZXI (day 120)	ZIX	-	NA
Telson margins laterally parallel	ZV	ZV	ZV	ZVII	ZV

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TABLE 1. (Continued)

Morphological feature	<i>L. anchisteus</i>	<i>L. lipkei</i>	<i>L. moorei</i>	<i>L. wurdemanni</i>	<i>L. seticaudata</i>
	Knowlton & Alavi 1996 5 Z + Z IX SW Atlantic	Almeida <i>et al.</i> 2021 First 3 Z Western Atlantic	Bartilotti <i>et al.</i> 2012 4 Z + Last Z Caribbean Sea, SW Atlantic	Kurata 1970 11 Z+1 decap. SW Atlantic	Calado <i>et al.</i> 2004 9 Z+1 decap. NE Atlantic, Mediterranean Sea
ZI, Total length, mm	2.20–2.30	2.00–2.31	2.77–2.81	2.7	3.09–3.24
ZI, carapace length, mm	NA	0.31–0.40	0.92–0.96	0.87	0.98–1.03
ZIV, carapace length, mm	NA	NA	1.13–1.29	0.99	1.04–1.08
ZVII, carapace length, mm	NA	NA	NA	1.13	1.40–1.56
Last Z, carapace length, mm	ZIX: NA	NA	3.85–4.84 (ZIX?)	ZXI: 1.9–2.2	ZIX: 2.00–2.24
First Zoea:					
Carapace: Pterigostomian spine	NA	Present	Present	Present	Present
Number of marginal denticles	NA	4	4–5	NA	6
Eyes sessile	Present	Present	Present	Present	Present
Antennule: peduncle and exopod	Entire	Entire	Entire	Entire	Entire
Antennal exopod: 5–6 articles	12PI + 1Si	11PI + 1Si	11PI + 1Si	11PI + 1Si	11PI + 1Si
Pair of dorsal spines on 5 th pleomere	Present	Present	Present	Present	Present
Pleopods	Absent	Absent	Absent	Absent	Absent
Uropods	Absent	Absent	Absent	Absent	Absent
Older Zoetas:					
Eyes stalked and pedunculate	ZII	ZII	ZII	ZII	ZII
Carapace without marginal denticles	NA	NA	NA	NA	ZVII
Carapace with cervical carinae	Absent	NA	Present	Absent	Absent
Rostrum first dorsal spine	NA	NA	ZII	ZVI	ZIV
Antennal exopod entire	ZV	NA	ZIV	ZIV	ZIV
First pereiopod:					
Biramous bud	ZII	ZI	ZI	ZI	ZI
Functional	ZIV	ZIII	ZII	ZIII	ZII

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TABLE 1. (Continued)

	<i>L. anchisteus</i>	<i>L. lipkei</i>	<i>L. moorei</i>	<i>L. wurdemannii</i>	<i>L. seticaudata</i>
Morphological feature	<i>L. anchisteus</i> Knowlton & Alavi 1996 5 Z + Z IX SW Atlantic	<i>L. lipkei</i> Almeida <i>et al.</i> 2021 First 3 Z Western Atlantic	<i>L. moorei</i> Bartilotti <i>et al.</i> 2012 4 Z + Last Z Caribbean Sea, SW Atlantic	<i>L. wurdemannii</i> Kurata 1970 11 Z+1 decap. SW Atlantic	<i>L. seticaudata</i> Calado <i>et al.</i> 2004 9 Z+1 decap. NE Atlantic, Mediterranean Sea
Second pereopod:					
Biramous bud	ZV	ZIII	ZIII (ZII bir, very small)	ZIV	ZIII
Functional	NA	NA	ZIV	ZVI	ZIV
Third pereopod:					
Biramous bud	NA	NA	ZIV (bir, very small)	ZV	ZV
Functional	NA	NA	NA	ZVII	ZVI
Fourth pereopod:					
Biramous bud	NA	NA	NA	ZVI	ZV
Functional	NA	NA	NA	ZVIII	ZVI
Fifth pereopod:					
Uniramous bud	ZIV	ZII	ZI	ZII	ZI
Functional	NA	NA	ZII	ZIV	ZII
Pereopods with paddled-like propodus	5 th	NA	5 th	5 th	5 th
5 th pleomere without dorso-lat spines	NA	NA	NA	ZVII	ZIV
3 rd pleomere with curved spine	NA	NA	NA	Absent	Absent
Pleopods:					
Small buds	-	NA	NA	NA	ZVI
Biramous buds	ZIX (only PII)	NA	NA	ZIX	ZVII
Differentiated protopod	NA	NA	NA	ZX	ZVIII
With <i>appendix interna</i>	NA	NA	Last stage (ZIX?)	ZXI	ZIX
Telson margins laterally parallel	NA ^a	NA	NA ^b	ZIV	ZV

A situation often reported during the larviculture of *Lysmata* is the lost/ breakage of the long pereopods, specially the fifth pereopod that is particularly longer and with the propodus as an enlarged paddle leading to special requirements to be taken when rearing the species, such as the need for bigger tanks, and extra care on handling specimens (Calado *et al.* 2008b). This is probably one of the main drawbacks preventing knowledge on the morphology of the larvae of more *Lysmata* species. Further studies on the captive culture of *Lysmata* are needed, to optimize the aquaculture production of these species and minimize the potential environmental impacts associated with their capture. There is also undoubtedly a great need for further morphological larval studies in order to clearly identify the common morphological characters of genus *Lysmata* as whole, as well as analyse and detect possible patterns or morphological similarities during their larval development.

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