

Original Article

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Larval development of the Caribbean king crab *Maguimithrax spinosissimus* (Lamarck, 1818), the largest brachyuran in the western Atlantic (Crustacea: Decapoda: Majoidea)

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Abstract

The complete larval development of the spider crab *Maguimithrax spinosissimus* (Lamarck, 1818) is re-described and illustrated in detail from laboratory-reared material. The development consisted of the typical pattern reported for the Majoidea, two zoeal stages and one megalopa. The complete larval development from hatching to first crab lasted 5–6 days at temperatures that ranged between 24–28 °C. Both zoeal stages of *M. spinosissimus* exhibited moderate reduction in the number of setae in the maxilla and maxillipeds, from the first to the second zoeal stage, when compared with other closely related species. *Maguimithrax spinosissimus* can be easily distinguished from other species belonging to the closely related genus *Mithrax* by the (i) setation of the endopod of the maxillule, maxilla and second maxilliped in both zoeal stages; (ii) setation of the scaphognathite of the maxilla in the first zoeal stage; (iii) setation of the basis of maxilliped I in the second zoeal stage and megalopa; (iv) morphology of the antennule and antenna in the second zoeal stage; and (v) setation of the antennule, coxal endite of maxilla, and exopod of second maxilliped in the megalopa. All these characters support the recent generic status of *Maguimithrax* within the Mithracidae. Additional morphological details, not available previously, are provided. This study will provide support for conservation strategies in this species.

Introduction

Spider crabs that belong to the superfamily Majoidea (sensu Ng *et al.*, 2008) exhibit remarkable disparity in terms of body size, colouration, morphology and behaviour (Rathbun, 1925; Baeza *et al.*, 2010). Among them, the 'Channel clinging crab', 'Cangrejo de la Virgen', or 'Caribbean king crab' *Maguimithrax spinosissimus* (Lamarck, 1818) is one of the largest crabs in the world and the largest native crab in the tropical and subtropical western Atlantic, reaching a carapace length up to 180 mm and weighing more than 3 kg (Tunberg & Creswell, 1988, 1991; Baeza *et al.*, 2010, 2015). *Maguimithrax spinosissimus* exhibits a Caribbean-wide distribution, ranging from North Carolina in North America to the north-eastern coast of Venezuela in South America (Rathbun, 1925; Winfree & Weinstein, 1990; Tunberg & Creswell, 1991). The Caribbean king crab inhabits ledges and other structures in the shallow subtidal to depths approaching 200 m, remains cryptic during daylight hours, and emerges from shelter shortly after sunset to forage on macroalgae through the night (Winfree & Weinstein, 1990; Tunberg & Creswell, 1991; Wilber & Wilber, 1991). Recent studies of this species have focused on adult sexual dimorphism (Baeza *et al.*, 2012), female reproductive performance (Baeza *et al.*, 2015) and population genetics and connectivity (Márquez *et al.*, 2016; Hurtado-Alarcón *et al.*, 2017; Baeza *et al.*, 2019). The early life history of this species is less known.

Maguimithrax spinosissimus exhibits two zoea larval stages prior to megalopa stage (Brownell *et al.*, 1977; Tunberg & Creswell, 1988) as do all majoid crabs. However, *M. spinosissimus* is considered unusual among mithracids, due to a major reduction in the number of setae in the maxillae and maxillipeds, from the first to the second zoeal stage, as reported in its first larval description (Provenzano & Brownell, 1977). By contrast, other mithracids have both zoea with well-developed setae in maxillae and maxillipeds (e.g. Santana *et al.*, 2003; Rhyne *et al.*, 2006). This reduction in the number of setae could be explained by the putatively lecithotrophic strategy attributed to the larval stages of *M. spinosissimus* (Provenzano & Brownell, 1977; Porter *et al.*, 1986; Creswell *et al.*, 1989; Tunberg & Creswell, 1991). Similar reduction in setation and spines is observed in other brachyuran crabs with abbreviated



and/or direct development and lecithotrophic larvae (e.g. Taishaku & Konishi, 2001; Bolaños *et al.*, 2004, 2005; González-Gordillo *et al.*, 2010). Furthermore, a brief prezoal stage has been described in *M. spinosissimus* (Provenzano & Brownell, 1977; Tunberg & Creswell, 1988) as well as in the closely related *Mithrax pleuracanthus* (Goy *et al.*, 1981). The occurrence of a prezoal stage has been attributed to stress of either the gravid female or the developing embryos (Tunberg & Creswell, 1988).

The reduction in setation and spines during larval stages have led several authors to consider the need for a re-description of the larval stages of *M. spinosissimus* due to the uncommonly reported characteristics, the low quality of the illustrations, and the possibility of errors in the original description (Rice, 1980; Bolaños *et al.*, 1990; Santana *et al.*, 2003, 2004; Rhyné *et al.*, 2006). Detailed larval descriptions can be useful not only for taxonomic and phylogenetic studies, but are also relevant to inform fisheries management, aquaculture planning and conservation strategies (Santana *et al.*, 2016; Baeza *et al.*, 2019). Indeed, due to its body size and short larval period (~6 days from zoea I to megalopa), *M. spinosissimus* has an enormous potential for aquaculture. This crab is also currently caught incidentally for local consumption and targeted by artisanal fisheries along the greater Caribbean (Creswell, 2011; Hurtado-Alarcón *et al.*, 2017). Various previous studies have addressed essential information needed for its cultivation (e.g. Brownell *et al.*, 1977; Creswell *et al.*, 1989; Tunberg & Creswell, 1991; Creswell, 2011; Baeza *et al.*, 2015).

The purpose of this study is to re-describe and illustrate the complete larval development of *M. spinosissimus* and compare our results with the previous larval description by Provenzano & Brownell (1977). The larval morphology of *M. spinosissimus* is also compared with allied species within the family and the possible reasons for the dissimilarities observed between this description and that of Provenzano & Brownell (1977) are discussed.

Materials and methods

Seven ovigerous females of *Maguimithrax spinosissimus* were collected in January 1996, while free diving between 3–5 m depth from Laguna Central, south of Cayo Robusqui, Los Roques Archipelago, Venezuela. Females were transported to the laboratory and individually held in aquaria with average salinity of 36 psu, in a temperature-controlled room (26 ± 2 °C) until larval hatching. Larval rearing temperature was similar to that observed in the field, 23–31 °C (Brownell *et al.*, 1977).

Larval development and descriptions followed standard protocols (e.g. Pohle & Marques, 2000; Colavite *et al.*, 2014; Santana *et al.*, 2016), where 10 of the most active larvae from each of a total of 7 hatches were separated in groups and placed in jars filled with 200 ml of filtered seawater. The remaining larvae were kept in mass culture in 10 jars filled with 1 litre of filtered seawater for additional specimens to be used in morphological descriptions. Larvae were fed *ad libitum* with diatoms and *Artemia* nauplii. Seawater was changed and larvae were inspected and fed daily. All glass jars were washed in fresh water and air-dried before re-using the following day. A photoperiod of 12:12 light:dark was used for larval rearing.

At least 30 specimens from each stage (plus the exuviae) were fixed in 4% buffered formalin, and at least 10 specimens of each larval stage were carefully dissected. For morphological description, whole larva and dissected appendages were stained using methylene blue, acid fuchsin and/or chlorazol black. Polyvinyl lactophenol or Canada balsam were used as mounting media for slide preparations.

The description of setae generally follows that of Pohle & Telford (1981), but here we included only an analysis using light microscopy, using an Olympus BX 50 equipped with camera

Table 1. Dimensions (mm) of larval structures of *Maguimithrax spinosissimus* (Lamarck, 1818)

Stages	Total length	Carapace length	Carapace width
Zoea 1	3.53 ± 0.003 (3.30–3.80)	1.18 ± 0.14 (1.12–1.22)	–
Zoea 2	3.74 ± 0.14 (3.18–4.80)	1.23 ± 0.006 (1.13–1.33)	–
Megalopa	2.57 ± 0.06 (2.50–2.65)	1.24 ± 0.05 (1.18–1.30)	1.08 ± 0.07 (1.00–1.17)

Note: Values are given as the mean ± standard deviation, with range in parentheses.

lucida. Appendages are described from proximal to distal end. Measurements were taken from 10 specimens of each larval stage, being: total length (TL) the distance between the tip of rostrum and posterior end of telson furca; carapace length (CL) the distance from the anterior margin between the eyes and the carapace posterior-most margin in zoeal stages, and from the tip of rostrum to the posterior margin of carapace for the megalopa; carapace width (CW) taken at the level of its widest point in megalopa.

Larval stage samples and female crabs are available upon request and are deposited in the crustacean collection of the Grupo de Investigación en Carcinología de la Universidad de Oriente, Núcleo Nueva Esparta (GICUDONE), Isla Margarita, Venezuela, accession numbers GIC-935 and GIC-936. Research ethics approval was not needed to conduct this study.

Results

The complete larval development of *Maguimithrax spinosissimus* consists of two zoeal stages and one megalopa. In some cases, the first zoea was preceded by a non-swimming prezoal stage, that survived only for a few hours in the laboratory. Comparisons between specimens from different females show no major morphological differences. The duration from hatching to the first crab stage was 5–6 days at temperatures that ranged between 24–28 °C in the laboratory. Larval morphometrics are given in Table 1. Only morphological changes are described for the second zoea.

Maguimithrax spinosissimus (Lamarck, 1818) Figures 1–3

First zoea

Carapace (Figure 1A, B). Dorsal spine slightly curved posteriorly and distally. Rostral spine short, not reaching exopod of antenna, lateral spines absent. A pair of simple setae near dorsal organ and a pair of simple setae postero-lateral to dorsal spine. Ventral margin with long, densely plumose seta posterior to scaphognathite notch (anterior seta), with three smaller plumose setae. Eyes sessile. Small indistinct prominence frontally between dorsal spine and rostrum, bearing cuticular dorsal organ (sensu Martin & Laverack, 1992; Lerosey-Aubrill & Meyer, 2013). No yolk granules observed in the cephalothorax.

Antennule (Figure 1C). Uniramous, endopod (accessory flagellum) absent; exopod (primary flagellum) unsegmented, with four aesthetascs (two long, two short), and two very short simple setae distally.

Antenna (Figure 1D). Biramous. Protopod long, pointed, bearing two rows of spinules in distal third. Endopod bud reaching more than half of protopod. Exopod slightly longer than protopod, with a spinulated distal process bearing two serrulate setae (one long, one short) approximately one third of tip.

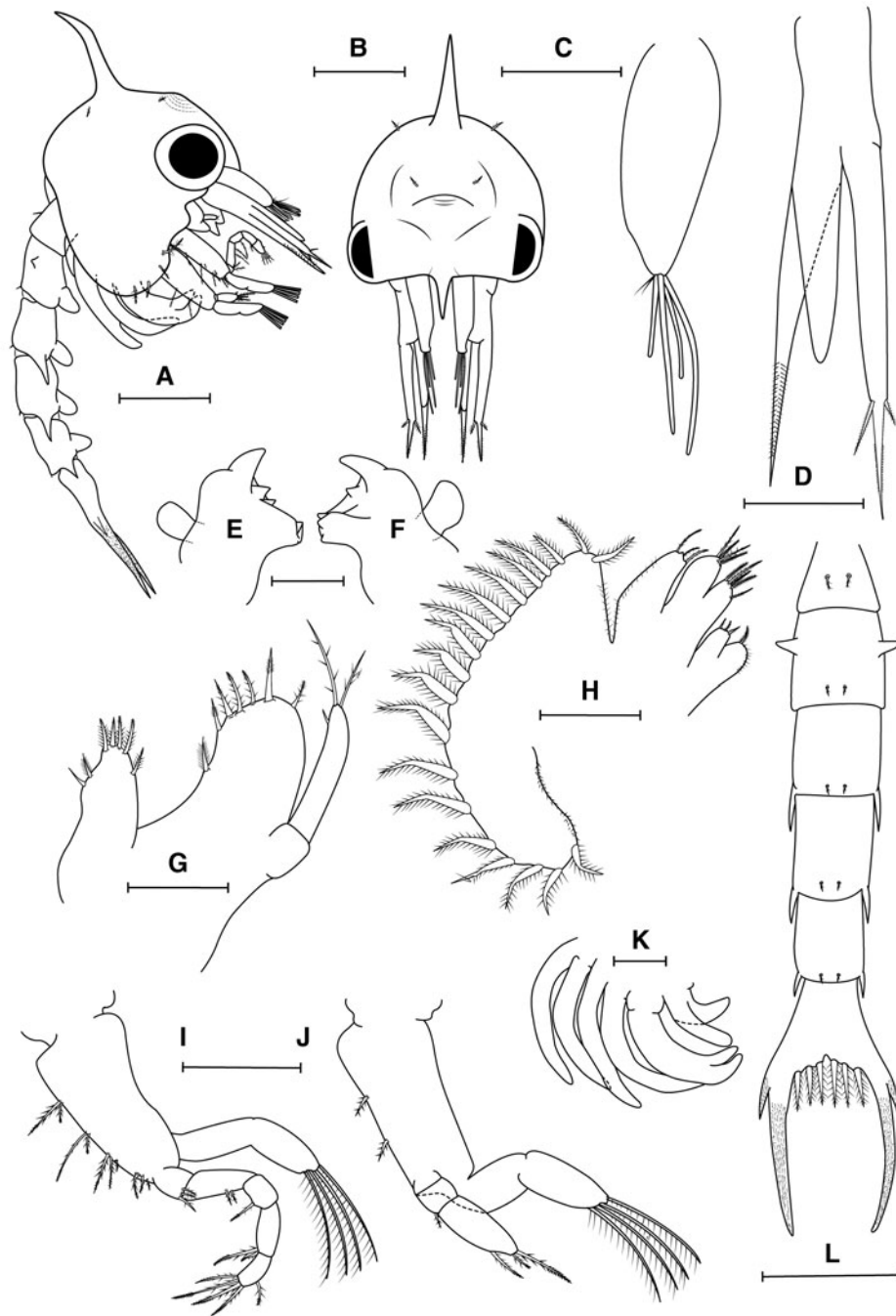


Fig. 1. *Maguimithrax spinosissimus* (Lamarck, 1818) first zoeal stage. (A) Lateral view; (B) frontal view; (C) antennule; (D) antenna; (E) right mandible; (F) left mandibles; (G) maxillule (H) maxilla; (I) maxilliped I; (J) maxilliped II; (K) maxilliped III and pereopods; (L) dorsal view of pleon and telson. Scale bars: A, B, H, K: 0.5 mm; C, D, I, J: 0.2 mm; E, F, G: 0.1 mm.

Mandible (Figure 1E, F). Asymmetrical, with medial toothed molar process and enlarged lateral incisor processes. Internal margin of incisor process of right mandible with one acute tooth, left mandible with two acute teeth. Palp bud prominent.

Maxillule (Figure 1G). Coxal endite with four terminal setae (three graded plumodenticulate, one plumodenticulate), three subterminal setae (two graded plumodenticulate, one simple). Basal endite with three terminal plumodenticulate cuspidate setae, three subterminal plumodenticulate setae and one plumose seta proximally. Endopod with two articles, proximal without setae, distal with one subapical short, simple seta, two apical plumodenticulate setae. Exopod absent.

Maxilla (Figure 1H). Coxal endite bilobed, proximal lobe with one plumodenticulate; distal lobe with three short setae (two

plumose, one plumodenticulate). Basal endite bilobed, proximal and distal lobes with five and 3–4 plumodenticulate setae, respectively. Endopod unsegmented, unilobed, with three plumodenticulate setae, a short apical protuberance present. Proximal lobe of coxal endite and endopod with microtrichia on lateral margin. Scaphognathite with 16–20 densely plumose setae on lateral margin, microtrichia on both margins.

First Maxilliped (Figure 1I). Coxa without seta; basis with 10 plumodenticulate setae arranged 2+2+3+3. Endopod with five articles, with 3,2,1,2,5 (distal segment with one subapical, four apical) plumodenticulate setae. Exopod incompletely 2-segmented, with four terminal plumose natatory setae.

Second Maxilliped (Figure 1J). Coxa without seta; basis with two plumodenticulate setae; endopod with three articles, with

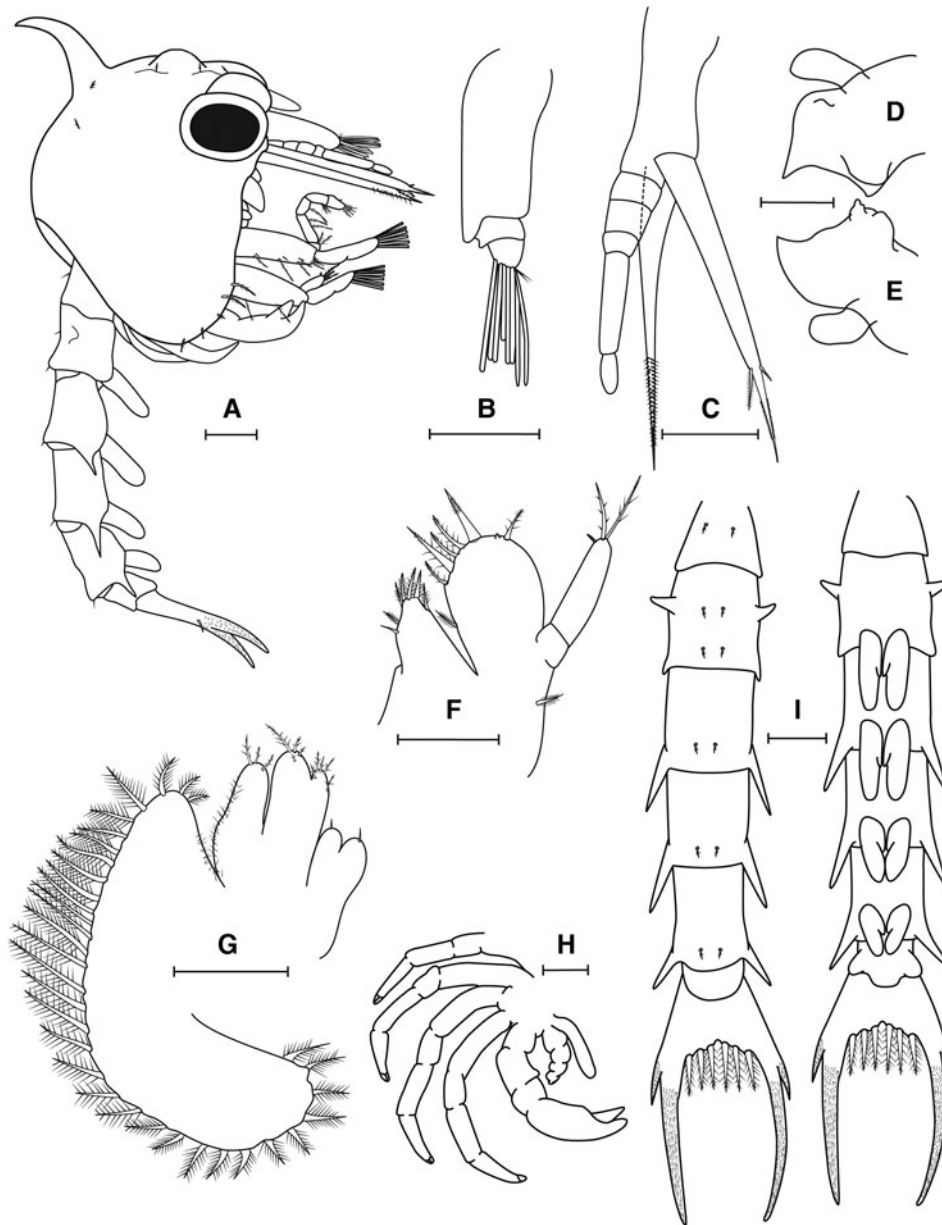


Fig. 2. *Maguimithrax spinosissimus* (Lamarck, 1818) second zoeal stage. (A) Lateral view; (B) antennule; (C) antenna; (D) right mandible; (E) left mandible; (F) maxillule; (G) maxilla; (H) maxilliped III and pereopods; (I) dorsal and ventral view of pleon. Scale bars: A, H, I: 0.5 mm; B, C: 0.2 mm; D, E, F, G: 0.1 mm.

0,1,3 (distal segment with one subapical; two apical, one long, one short) plumodenticulate setae; exopod incompletely 2-segmented with four terminal plumose natatory setae.

Third Maxilliped (Figure 1K). Present as a small bud, endopod and exopod distinguishable.

Pereopods (Figure 1A, K). Present as elongated buds, chela distinct, segmentation apparent in some pereopods.

Pleon (Figure 1A, L). Five pleonites. Pleonites I–V with a pair of plumodenticulate setae (pleonite I with longer middorsal pair, pleonite II–V with shorter posteromedial pair). Pleonite II with a pair of distinct dorsolateral processes. Posterolateral margin of pleonite II with blunt process, pleonites III–V with long acute spines. Pleopod buds uniramous on pleonites II–V, endopods absent.

Telson (Figure 1L). Bifurcated, small median notch. Three pairs of plumodenticulate setae on inner margin; each furcal shaft proximally bearing one distinct lateral spine, furcal shafts covered with rows of spinules to just below tips.

Second zoea

Carapace (Figure 2A). Eyes stalked. Five pairs of small plumodenticulate setae dorsally. Ventral margin with five setae (two densely anterior plumose, three shorter plumose). Protuberance bearing cuticular dorsal organ enlarged. No yolk granules observed in the cephalothorax.

Antennule (Figure 2B). Peduncle uniramous; endopod bud present, without setae; exopod with two annuli, proximal without setae, distal with eight long aesthetascs and two short simple setae.

Antenna (Figure 2C). Endopod with five articles, reaching more than two-thirds of endopod.

Mandible (Figure 2D, E). Palp bud enlarged.

Maxillule (Figure 2F). Exopodal seta pappose.

Maxilla (Figure 2G). Proximal and distal lobes of coxal endite with one short simple seta each. Basal endite with shorter setae. Endopod without short apical protuberance. Scaphognathite with 30–36 marginal plumose setae.

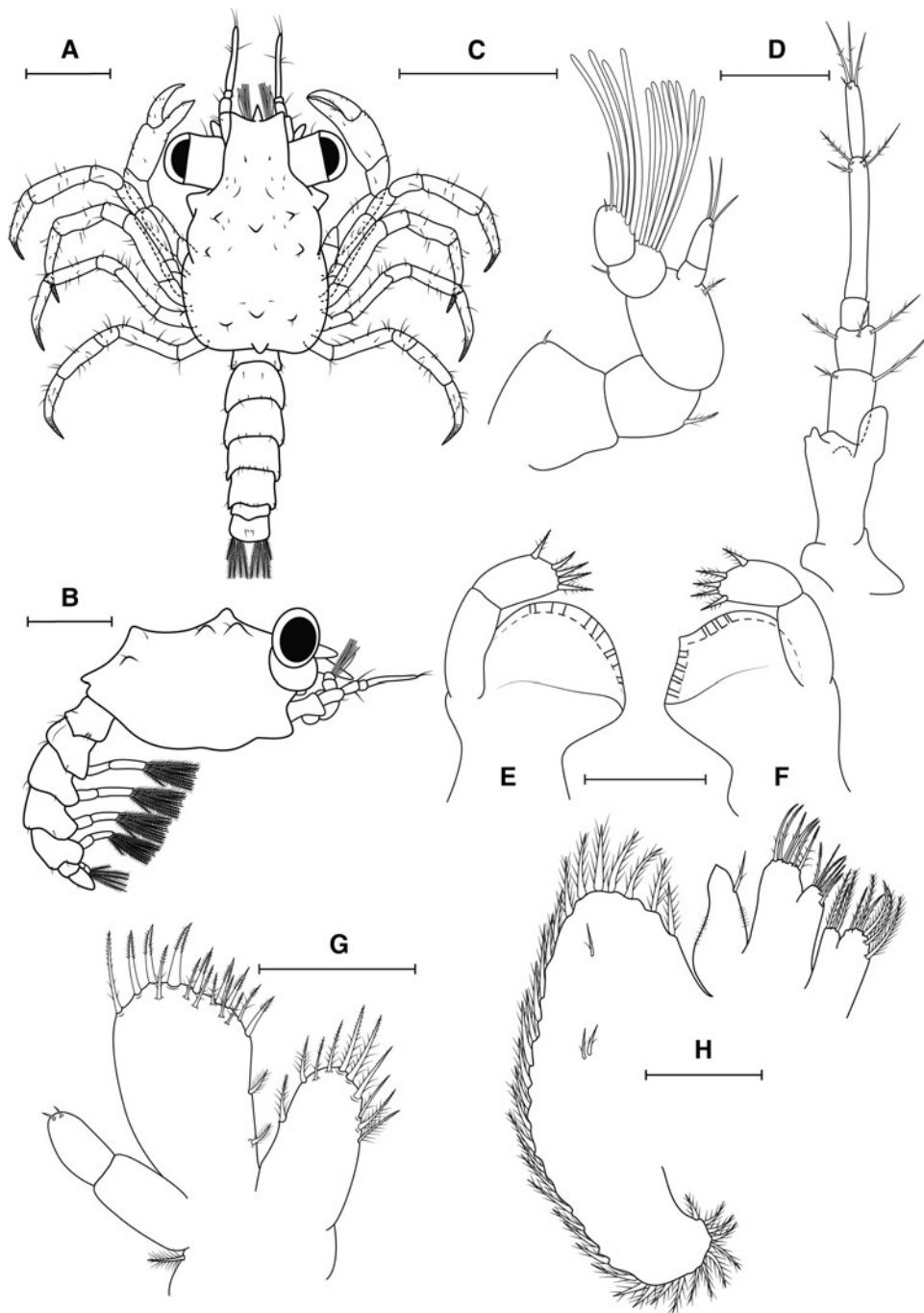


Fig. 3. *Maguimithrax spinosissimus* (Lamarck, 1818) megalopa stage. (A) Dorsal view; (B) lateral view; (C) antennule; (D) antenna; (E) left mandible; (F) right mandible; (G) maxillule; (H) maxilla. Scale bars: A, B: 0.5 mm; C, D: 0.2 mm; E–H: 0.1 mm.

First Maxilliped (Figure 2A). Exopod with 6 plumose natatory setae.

Second Maxilliped (Figure 2A). Exopod with 6 plumose natatory setae.

Third Maxilliped (Figure 2H). Endopod with five articles. Exopod long, unsegmented.

Pereiopods (Figure 2A, H). Longer, first with distinct chela. Segmentation apparent.

Pleon (Figure 2A, I). Six pleonites. Pleonite II with an extra pair of middorsal plumodenticulate setae. Pair of unsegmented, biramous pleopods on pleonites II–V (exopods long, endopods small). Sixth pleonite with uniramous uropod buds present.

Megalopa

Carapace (3A, B). Longer than wide, subrectangular. Rostral spine short, acute, slightly deflected ventrally. Hepatic region projected,

forming two knob-like lateral expansions, gastric region swollen with distinct protogastric and metagastric regions. Protogastric region bearing the dorsal organ medially. Branchial, cardiac and intestinal regions inconspicuously defined. Carapace surface covered mostly with simple setae as illustrated. No yolk granules observed in the cephalothorax.

Antennule (Figure 3C). Peduncle with three articles, proximal with very short simple seta; medial and distal segments with one plumodenticulate seta each. Accessory flagellum with 2 annuli, with three long simple setae (one subterminal and two terminal). Primary flagellum with 2 annuli, with 7 aesthetascs ventrally + one simple seta dorsally; 4–5 aesthetascs + two simple setae (one long subapical and one very short apical), respectively.

Antenna (Figure 3D). Articles proximally to distally with 0, 2, 3, 0, 4, 4 simple setae, respectively. Basal article with distinct exopod bud. Articles V and VI fused.

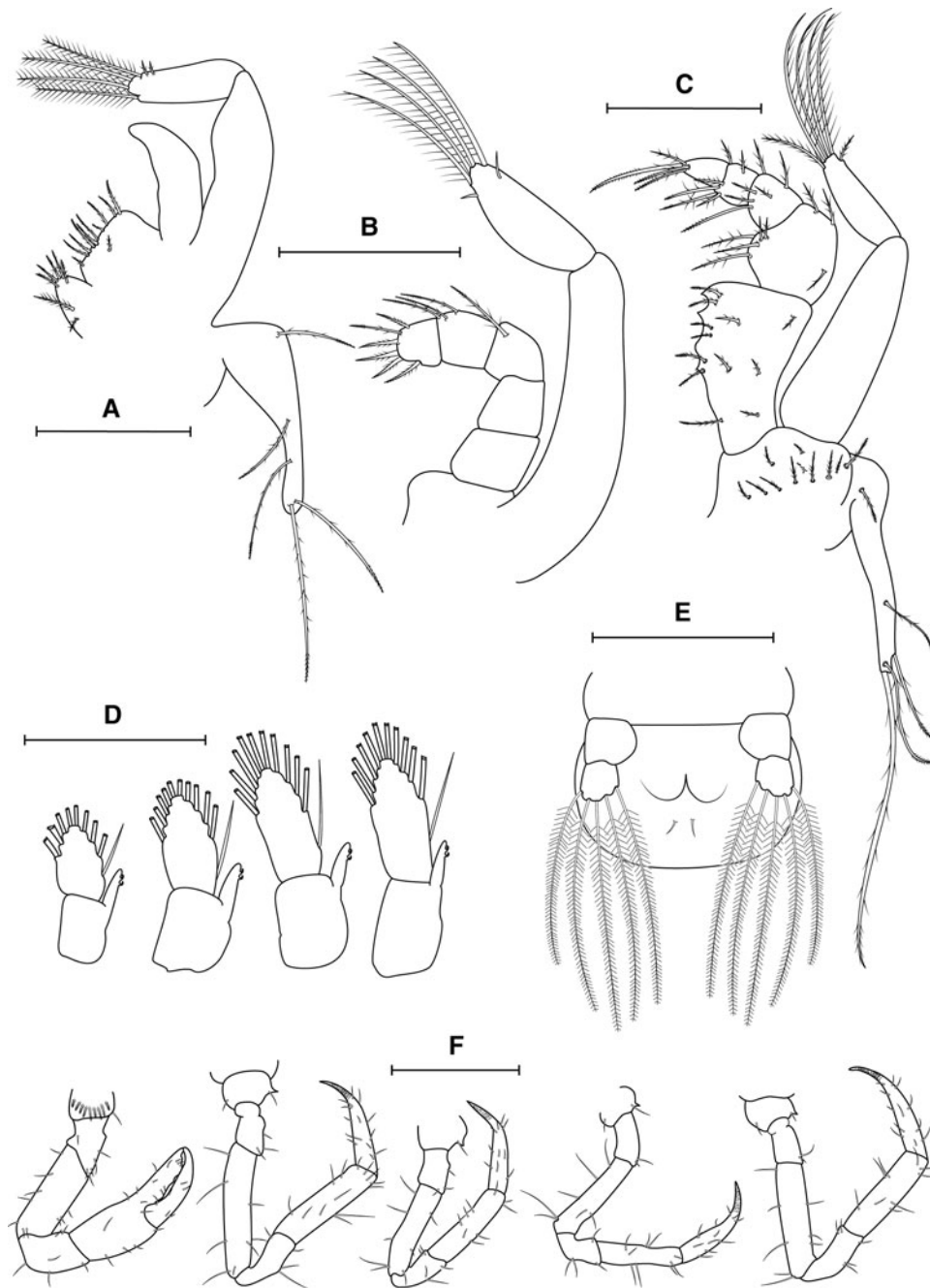


Fig. 4. *Maguimithrax spinosissimus* (Lamarck, 1818) megalopa stage. (A) maxilliped I; (B) maxilliped II; (C) maxilliped III; (D) pleopods; (E) telson; (F) pereopods; Scale bars: A–C: 0.5 mm; D, E: 0.3 mm, F: 0.5 mm.

Mandibles (Figure 3E, F). Asymmetrical, scoop-shaped process with cutting edge and small acute tooth in left mandible, right mandible without acute tooth. Palp with two articles, with five plumodenticulate setae on the distal segment.

Maxillule (Figure 3G). Coxal endite with 10 setae (six graded plumodenticulate, four plumodenticulate). Basial endite with 17 setae (seven terminal plumodenticulate cuspidate, eight subterminal plumodenticulate, two plumose setae on proximal margin). Endopod reduced, segmented, with two very short simple setae on distal segment. Exopod with a plumodenticulate seta.

Maxilla (Figure 3H). Coxal endite bilobed, proximal lobe with six setae (four plumose and two plumodenticulate), distal lobe with three setae (two plumose and one plumodenticulate). Basial endite bilobed with six plumodenticulate setae on each lobe. Endopod reduced, with microtrichia in both margins and one terminal plumodenticulate setae. Scaphognathite with

35–38 marginal plumose setae and three small plumodenticulate setae on blade.

First Maxilliped (Figure 4A). Coxa bearing seven setae (five plumodenticulate; two plumose, one long and one short). Basis endite with 11 plumodenticulate setae (eight long and three short) arranged as illustrated. Endopod unsegmented without setae. Exopod with two articles, proximal smooth, distal with six setae (four plumose and two short plumodenticulate). Epipod elongated with five long plumodenticulate setae (one proximal, two medial, two distal).

Second Maxilliped (Figure 4B). Coxa and basis not clearly differentiated. Endopod with five articles, proximally to distally with 0, 0, 1, 3, 6 plumodenticulate setae, respectively. Exopod with two articles, proximal without setae, distal with six setae (four plumose, two short simple setae). Epipod not present on examined specimens.

Table 2. Comparison of larval characters of the first zoea of *Maguimithrax spinosissimus* (Lamarck, 1818) and *Mithrax* Latreille, 1816

Species	Carapace	Antennule	Maxillule	Maxilla	Maxilliped I	Maxilliped II
<i>Mithrax hispidus</i> ¹	2s, 2 pl	2 + 2 ae	cox: 6 pld + 1 pl	cox: 4 pl + 1 pld, 3 pl + 1 pld		
	4 pl, 2 pld	1 s	bas: 6 pld + 1 pl	bas: 5 pld + 4 pld	bas: 10 pld	bas: 3 pld
			end: 7 pld	end: 5 pld	end: 3,2,1,2,5 pld	end: 0,1,5 pld
				sca: 13		
<i>Mithrax pleuracanthus</i> ²	4 s,	2 + 1 ae	cox: 7 pld	cox: 5 pld + 4 pld		
	6 pl	1 s	bas: 7 pld	bas: 5 pld + 4 pld	bas: 10 pld	bas: 3 s
			end: 7 pld	end: 5 pld	end: 3,2,1,2,5 pld	end: 0, 1 pld, 2 pld + 3 s
				sca: 13		
<i>Mithrax tortugae</i> ³	4 s,	2 + 2 ae,	cox: 5 pl + 2 s	cox: 5 pl + 4 pld		
	6 pl	1 s	bas: 6 pld + 1 pl	bas: 5 pld + 4 pld	bas: 6 pld + 4 s	bas: 3 s
			end: 1 s, 2 pl + 4 pld	end: 5 pld	end: 2 ss + 1 s, 2 ss,	end: 0, 1 pld, 5 s
				sca: 12	1 ss, 2 ss, 5 pld	
<i>Mithrax spinosissimus</i> ⁴	n/d	3 + 2 ae	cox: 5 s	cox: 1 s + 1 s		
			bas: 6 s	bas: 3 s + 3 s	bas: 0 ^a	bas: 0 ^a
			end: 2 s	end: 1 s	end: 0,1,1,2,4 s	end: 3 s ^a
				sca: 30		
<i>Maguimithrax spinosissimus</i> ⁵	4 s,	4 ae	cox: 6 pld + 1 s	cox: 1 pld + 2 pl + 1 pld		
	4 pl	2 s	bas: 6 pld + 1 s	bas: 5 pld + 3–4 pld	bas: 10 pld	bas: 2 pld
			end: 1 s + 2 pld	end: 3 pld	end: 3,2,1,2,5 pld	end: 0,1,3 pld
				sca: 19		

cox: coxal endite; bas: basis or basal endite; end: endopod; sca: scaphognathite; seg: segments; s: simple setae; ss: sparsely setose setae; pld: plumodenticulate setae; pl: plumose setae; pap: papose setae; ae: aesthetascs; n/d: not described; ?: number or setal type not specified.

^aObservation from figure. Data from: ¹ Santana *et al.* (2003); ² Goy *et al.* (1981); ³ Magalhães *et al.* (2017); ⁴ Provenzano & Brownell (1977); ⁵ Present study.

Third Maxilliped (Figure 4C). Coxa with 11 plumodenticulate setae. Basis fused to ischium with protuberances on mesial margin, indicative of crista dentata. Endopod with five articles, proximally to distally with 12, 5 + 3, 4 + 2, 4 + 2, 4 plumodenticulate setae. Exopod with two articles, proximal smooth, distal with 2 short subapical, 4 long plumose apical setae. Epipod with five long plumodenticulate setae (one proximal, 1 subterminal, 3 distal).

Pereiopods (Figure 4F). Cheliped and pereiopods with mostly simple setae as figured. Coxa of P2–5 with an acute spine on ventral margin. Dactyls of P2–5 with rows of spinules distally. Coxa of cheliped bearing 10 possible plumose setae in a semicircle shape.

Pleon (Figure 3A, B). Pleonites I–V with 6, 8, 6, 8, 6 simple setae arranged as illustrated. Pleonite VI without seta.

Pleopods (Figure 4D, E). Pleonites II–V with a pair of biramous pleopods. Exopod of pleopods I–IV with 11, 11, 11, 9 plumose natatory setae, respectively. Endopod with two cincinnuli each. Pleonites VI with a pair of uropods, uniramous, 2-segmented, with five natatory setae on distal segment.

Telson (Figure 4E). Rounded posteriorly, bearing a pair of simple setae on middorsal margin and a pair of simple setae on mid-ventral margin.

Discussion

We have described and illustrated in detail the complete larval development of *M. spinosissimus* using specimens collected

from Los Roques Archipelago, Venezuela, the same locality from which Provenzano & Brownell (1977) collected material for their study. In the following, we compare our results with (i) a previous larval description by Provenzano & Brownell (1977) and (ii) allied species within the family (see Windsor & Felder, 2014, 2017).

Dissimilarities between larval descriptions in *M. spinosissimus*

A comparison between our re-description and that of Provenzano & Brownell (1977) reveals major differences in larval morphology of *M. spinosissimus*, especially in zoeal stages, although the material was collected from the same region, but with a difference of nearly 20 years. The setal meristics strongly differ in almost all appendages, carapace and pleon in the zoeal stages (see Tables 2 and 3). Also, the segmentation of the endopod of the antenna is 5-segmented and in Provenzano & Brownell (1977: Figure 3) we can observe a 4-segmented endopod. The few similarities are in the basal endites of the maxillule and the coxal endites of the maxilla of the second zoea (Table 3). In the megalopa, similarities are only found in the basal endite, endopod and scaphognathite of the maxilla, the maxilliped II, the pleopods and the uropod (Table 4). Importantly, the setal types were poorly described and not illustrated for most appendages in Provenzano & Brownell (1977). Missing information on the carapace setation of the zoeal stages and the pleon setation for the zoeal stages and megalopa are here described for the first time.

Table 3. Comparison of larval characters of the second zoea of *Maguimithrax spinosissimus* (Lamarck, 1818) and *Mithrax* Latreille, 1816

Species	Carapace	Antennule	Maxillule	Maxilla	Maxilliped I	Maxilliped II
<i>Mithrax hispidus</i> ¹	10–12 s	8 ae	cox: 6 pld + 2 pl	cox: 4 pl + 1 pld, 3 pl + 1 pld		
	7–8 pl + pld	1 s	bas: 8 pld + 2 pl	bas: 4–5 pld + 5 pld	bas: 10 pld	
			end: 7 pld	end: 5 pld	end: 3,2,1,2,5 pld	end: 0,1,5 pld
			exo: 1 pap	sca: 24–25		
<i>Mithrax pleuracanthus</i> ²	10 s	7 ae	cox: 7 pld	cox: 5 pld + 5 pld		
	8 pl	1 s	bas: 11 pld	bas: 5 pld + 5 pld	bas: 10 pld	
			end: 7 pld	end: 5 pld	end: 3,2,1,2,5 pld	end: 0,1,1 s + 3 pld
			exo: 1 pld ? ^a	sca: 24		
<i>Mithrax tortugae</i> ³	6 s + 2 pl	7 ae,	cox: 5 pl + 3 s	cox: 5 pl + 4 pl		
	7 pl	1 s	bas: 7 pld + 2 pl	bas: 5 pld + 5 pld	bas: 6 pld + 4 s	
			end: 1 s + 6 pl	end: 5 pld	end: 2 ss + 1s, 2 ss,	end: 0, 1 pld, 5 s
			exo: ?	sca: 24	1 ss, 2 ss, 5 pld	
<i>Mithrax spinosissimus</i> ⁴	n/d	3 + 2 ae	cox: 6 s	cox: 1 + 1 s		
			bas: 7 s	bas: 2 + 2 s ^a	bas: 0 ^a	
			end: 2 s ? ^a	end: 2 s ^a	end: 1,1,1,1,4 s ^a	end: 2 s
			exo: 0 ^a	sca: 31		
<i>Maguimithrax spinosissimus</i> ⁵	5 pld	8 ae	cox: 6 pld + 1 s	cox: 1 s + 1 s		
	5 pl	2 s	bas: 6 pld + 1 s	bas: 5 pld + 3–4 pld	bas: 10 pld	
			end: 1 s + 2 pld	end: 3 pld	end: 2–3,2,1,2,5 pld	end: 0,1,3 pld
			exo: 1 pap	sca: 33		

cox: coxal endite; bas: basis or basal endite; end: endopod; exo: exopodite; sca: scaphognathite; seg: segments; s: simple setae; ss: sparsely setose setae; pld: plumodenticulate setae; pl: plumose setae; pap: papose setae; ae: aesthetascs; n/d: not described; ?: number or setal type not specified.

^aObservation from figure. Data from: ¹ Santana *et al.* (2003); ² Goy *et al.* (1981); ³ Magalhães *et al.* (2017); ⁴ Provenzano & Brownell (1977); ⁵ Present study.

Previous re-descriptions of larval development in other species of decapod crustaceans, including crabs, have revealed, in most cases, only minor differences between the first description and the latter (Gore, 1970; Santos & Paula, 2003; Calado *et al.*, 2004; Santana *et al.*, 2004). Major differences, as those observed here, may point to errors during dissection (e.g. broken setae), slide preparation (e.g. overlapping setae), or problems in the observation of larval traits due to the use of inadequate microscopes (e.g. Santana *et al.*, 2003), which we argue here explain the differences between our re-description and that of Provenzano & Brownell (1977). Furthermore, some of the detected differences suggest a problem in the identification of the second zoeal stages during larval rearing by Provenzano & Brownell (1977). For instance, the setation of the antennule, with no increment of setae from the first to the second zoea, and the similar number of setae on the scaphognathite of the maxilla of the first zoea described by Provenzano & Brownell (1977) might be explained if these authors mistakenly classified zoea I as zoea II larvae (and vice versa).

One of the main concerns raised by some authorities (Rice, 1980; Bolaños *et al.*, 1990; Santana *et al.*, 2003, 2004; Rhyne *et al.*, 2006) regarding the description provided by Provenzano & Brownell (1977) is the reduction in the number of setae in several appendages from the first to the second zoeal stage, a feature uncommon in the Brachyura, in general, and the Majoidea and Mithracidae, in particular (Clark, 2000). In Provenzano & Brownell (1977), the reduction in the number of setae occurred in the basis of the maxilla and in the endopod of the maxilliped I and II. In the present study, this reduction is not so pronounced,

and we observed a reduction in the number of setae only in the coxa of the maxilla and the basis of maxilliped I from zoea I to II (Tables 2 and 3). Nevertheless, the notion that setae represent a well conserved trait in the zoeal stages of crabs (Clark, 2000) is narrow and restraining. The stasis or reduction in the number of setae could be explained by facultative lecithotrophy attributed to the larvae of *Maguimithrax spinosissimus*, as observed in other brachyurans (e.g. Bolaños *et al.*, 2005; González-Gordillo *et al.*, 2010).

Maguimithrax spinosissimus is widely distributed throughout the tropical Atlantic (Rathbun, 1925; Williams, 1984; Wagner, 1990; Felder *et al.*, 2009; Creswell, 2011). Despite that, the connectivity among populations of *M. spinosissimus* seems to be very low, indicating the existence of an isolated or semi-isolated subpopulation in the south of the Caribbean (Baeza *et al.*, 2019). This could explain possible differences in larval morphology throughout its distribution but not within the same locality, as shown here. As for now, we suggest that the differences between the two descriptions are due to methodological problems (see above) in Provenzano & Brownell (1977). In this sense, to solve geographic morphological variation problems in the future, one possible approach is to sequence the DNA of the spent female crab (see Li *et al.*, 2019), which could also provide useful data for geographic comparisons. An alternative is to sequence the DNA barcode region of larvae collected at different geographic locations and examine their morphology, a methodology successfully applied to identify other marine organisms, such as fish and stomatopod larvae (Chu *et al.*, 2019; Wong *et al.*, 2021).

Table 4. Comparison of larval characters of the megalopa of *Maguimithrax spinosissimus* (Lamarck, 1818) and *Mithrax* Latreille, 1816

Species	Antennule	Antenna	Maxillule	Maxilla
<i>Mithrax hispidus</i> ¹	ped: 0,2,1 s	seg 1–7:	cox: 8 pld + 2 pl	cox: 7 pl + 1 pld, 2 pl + 1 pld
	end: 3 s	1,2,3,0,0,4,3 s	bas: 12–15 pld + 3 pl	bas: 5–6 pld + 6 pld
	exo: 8 ae, 5 ae		end: 2 pld	end: 0
<i>Mithrax pleuracanthus</i> ²	ped: 0,2,1 pld	seg 1–7:	cox: 10 pld	cox: 7 pl + 3 pl
	end: 3 pld	0,2,3,0,0,4,2 pld + 1 s	bas: 15 pld	bas: 6 pld + 6 pld
	exo: 8 ae + 1 pld, 5 ae		end: 2 pld	end: 2 s
<i>Mithrax tortugae</i> ³	ped: 0,2,1 s	seg 1–7:	cox: 8 pld + 2 pl	cox: 7 pld + 3 pld
	end: 3s	0,2,3,0,0,4,5 s	bas: 15 pld + 2 pl	bas: 6 pld + 6 pld
	exo: 8 ae + 1 s, 4 ae + 1 s		end: 0	end: 0
<i>Mithrax spinosissimus</i> ⁴	ped: 0,1,1 s ^a	seg 1–7:	cox: 8 ?	cox: 3–5 + 3–5 ?
	end: 2 s ^a	2,2,2,0,4,3 s? ^a	bas: 12–15 ?	bas: 5–6 + 5–6 ?
	exo: 5 ae, 4 ae + 1 s ^a		end: 0	end: 1 s? ^a
<i>Maguimithrax spinosissimus</i> ⁵	ped: 1 s, 1,1 pld	seg 1–7:	cox: 10 pld	cox: 4 pl + 2 pld + 2 pl + 1 pld
	end: 3 s	0,0,2,3,0,4,4 s	bas: 7 + 8 pld + 2 pl	bas: 6 + 6 pld
	exo: 1 s + 7 ae, 5 ae + 2 s		end: 2 s	end: 1 pld
			epi: 1 pld	sca: 36, 3 pld

cox: coxal endite; bas: basal endite; end: endopod; exo: exopod; epi: epipodite; sca: scaphognathite; ped: peduncle; seg: segments; s: simple setae; pld: plumodenticulate setae; pl: plumose setae; pap: papose setae; ae: aesthetascs;?: number or setal type not specified.

^aObservation from figure. Data from: ¹ Santana *et al.* (2003); ² Goy *et al.* (1981); ³ Magalhães *et al.* (2017); ⁴ Provenzano & Brownell (1977); ⁵ Present study.

Affinities of *M. spinosissimus* with other Mithracidae

A recent phylogenetic hypothesis, based on molecular data, proposed for the family Mithracidae positioned *Maguimithrax spinosissimus* as sister to a clade comprising *Mithrax hispidus* (Herbst, 1790), *Mithrax pleuracanthus* (Stimpson, 1871) and *Mithrax tortugae* (Rathbun, 1920) (Windsor & Felder, 2014). Thus, considering the phylogenetic position of *Maguimithrax*, herein we compare its larval development mostly with those available for species of *Mithrax* (Table 5).

Although Mithracidae comprise a well-supported monophyletic family, with most of the species in the clade having a remarkably uniform larval morphology (Yang, 1967; Wilson *et al.*, 1979; Santana *et al.*, 2003; Rhyné *et al.*, 2006), it is a consensus that larvae of *Maguimithrax spinosissimus* are unique when compared with other known species of the family. For example, as with the adults, the zoeal stages are distinctly larger than the other species, and the megalopa is bigger than most species, with the exception of *Mithrax pleuracanthus* which features a megalopa with approximately the same size as *Maguimithrax spinosissimus* (Table 6). However, the present re-description shows a larval morphology much more similar to *Mithrax* than previously thought due to the description of Provenzano & Brownell (1977). It is worthwhile to mention that *Mithrax pleuracanthus* presents considerable morphological differences to the other species of the genus. For instance, the setation of the antennule in the first zoea, maxillule in the second zoea and scaphognathite of the maxilla of the megalopa sets this species apart from the other *Mithrax* species. These characters need verification and perhaps re-description of the larvae of *Mithrax pleuracanthus* could clarify these discrepancies.

Maguimithrax and *Mithrax* share the following characters in the first zoeal stage: the setation of the carapace dorsally, aesthetascs of antennule (except *Mithrax pleuracanthus*), coxal and basal endites of maxillule, and basal endites of maxilla and first maxilliped (Tables 2–4). In the second zoea *Maguimithrax* and *Mithrax* share the following characters: the exopod of maxillule (except in *Mithrax tortugae*), and endopod of first maxilliped, and exopod of second maxilliped. The megalopa have a more heterogeneous morphology, with *Maguimithrax* and *Mithrax* having in common the setation of the coxal and basal endites of maxilla, pleopods and uropod. On the other hand, *Maguimithrax spinosissimus* can be easily distinguished from other Mithracidae by: (i) the setation of the endopod of maxillule, coxal endite and endopod of maxilla, and endopod of the maxilliped II in both zoeal stages; (ii) the scaphognathite of maxilla in the first zoeal stage; (iii) the basis of maxilliped I in the second zoeal stage and megalopa; (iv) the morphology of the antennule and antenna in the second zoeal stage presenting a segmentation similar to that observed in the megalopa, which can be a consequence of rapid facultative lecithotrophic larval development; (v) and the setation of the antennule, coxal endite of maxilla and exopod of maxilliped II in the megalopa (Tables 2–4). All these dissimilarities support the erection of the genus *Maguimithrax* sensu Klompmaker *et al.* (2015) to accommodate *Maguimithrax spinosissimus*.

In summary, we have re-described in detail the larval development of *Maguimithrax spinosissimus*. The short larval period here observed is in line with that reported by Provenzano & Brownell (1977) and supports the notion that this species has considerable potential for aquaculture in the region. Furthermore, due to its short larval development, various previous studies have suggested

Table 4. Continued

Species	Maxilliped I	Maxilliped II	Maxilliped III (endopodite setation)	Pleon (setation)	Pleopods and Uropod (P1–5)
<i>Mithrax hispidus</i> ¹	cox: 7–8 pld		11,8,5,5,4 pld ^a	PL1–6: 2,8,6,8,8,2 s;	P1–5: 11,11,10,9,5 pl
	bas: 10–11 pld			S1: 4 pl	
	end: 0	end: 0,1,2,5–6 pld			
	exo: 1 pap, 4 pl	exo: 0, 4 pl			
	epi: 4 pld ^a				
<i>Mithrax pleuracanthus</i> ²	cox: 3 pld		12,7,4,6,4 pld	PL1–6: 2,4,4,4,4,2 s	P1–5: 11,11,10,9,5 pl
	bas: 10 pld	end: 1,1,4,6 pld			
	end: 1 pld, 1 s	exo: 0, 4 pl			
	exo: 1 pld, 4 pl				
	epi: 4 s, 1 pld				
<i>Mithrax tortugae</i> ³	cox: 7 pld		7,5,5,4 pld	PL1–6: 6,8,8,8,8,2 pl	P1–5: 11,10,10,9,5 pl
	bas: 11 pld				
	end: 0	end: 0,1,3,6 pld			
	exo: 1 pl, 4 pl	exo: 0,4 pl			
	epi: 6 pld				
<i>Mithrax spinosissimus</i> ⁴	cox: 8 s? ^a		12,5,5,3,4 pld? ^a	n/d	P1–5: 11,11,11,9,5 pl? ^a
	bas: 8 s? ^a				
	end: 0	end: 0,1,3,6, s? ^a			
	exo: 0 ^a , 4–6 pl	exo: 0, 4–6 pl			
	epi: 4 s? ^a				
<i>Maguimithrax spinosissimus</i> ⁵	cox: 5 pld + 2 pl		12,8,6,6,4 pld	PL1–6: 6,8,6,8,6,0 s	P1–5: 11,11,11,9,5 pl
	bas: 11 pld				
	end: 0	end: 0,1,3,6 pld			
	exo: 4 pl + 2 pld	exo: 4 pl + 2 s			
	epi: 5 pld				

cox: coxa; bas: basis; end: endopod; exo: exopod; epi: epipod; sca: scaphognathite; ped: peduncle; seg: segments; PL: pleonites; P: pleopods; s: simple setae; pld: plumodenticulate setae; pl: plumose setae; pap: papose setae; ae: aesthetascs; n/d: not described; ?: number or setal type not specified.

^aObservation from figure. Data from: ¹ Santana et al. (2003); ² Goy et al. (1981); ³ Magalhães et al. (2017); ⁴ Provenzano & Brownell (1977); ⁵ Present study.

that *Maguimithrax spinosissimus* is either a lecithotrophic (e.g. Creswell et al., 1989; Baeza et al., 2019) or a facultative lecithotrophic species (e.g. Provenzano & Brownell, 1977; Porter et al., 1986; Tunberg & Creswell, 1991). Facultative lecithotrophy is not common but known to occur in some brachyuran crabs (Anger, 1995) and other decapod groups, and may be a physiological response to different temperature/food density combinations in natural habitats (Thessalou-Legaki et al., 1999). Here we fed all larval stages *ad libitum* (see Materials and methods section), but no assessment of food ingestion was made. However, strict lecithotrophic majoid species usually have a mass of yolk granules in the larval stages (e.g. Taishaku & Konishi, 2001), which is not the case for *M. spinosissimus*. Indeed, Tunberg & Creswell (1988) indicated that survival and size of the larvae of *M. spinosissimus* were greater when specimens were fed daily. Altogether, the information above suggests that rearing efforts need to provide nutrition to larvae so as to speed up development during the larval phase of *M. spinosissimus*. Partial lecithotrophy needs to be further explored in *M. spinosissimus* and, if confirmed, this trait will aid in the development of efficient culturing techniques in the species.

The complete larval development of *M. spinosissimus* provides support for conservation strategies of this species as well as coral

reefs. This crab achieves moderate to high abundance in the Florida Keys, USA and a wide distribution in the greater Caribbean Sea. Importantly, the structure of coral reef benthic communities, in particular those located in the Florida Keys, is changing quickly, turning from stony-coral-dominated communities into others in which soft corals, sponges and algae are among the main constituents (Norström et al., 2009; McMurray et al., 2015). As a herbivore, *Maguimithrax spinosissimus* has the potential to control algal growth in the field. Its larval re-description can help optimizing protocols for laboratory rearing, and the production of large quantities of juveniles could subsequently be used for 'seeding' this species to control the algal overgrowth of coral reefs that are already subject to major local disturbances and global climate change. Lastly, we have improved the battery of resources available for a reef-dwelling invertebrate inhabiting an already morphed seascape (coral reefs) that will likely continue to change given the increasing frequency and scale of contemporary disturbances (McMurray et al., 2015 and references therein). This new reef seascape dominated by a species-rich sponge and algal assemblage might become the dominant community state in the greater Caribbean (Norström et al., 2009; Bell et al., 2013; McMurray et al., 2015 and references therein). Together with major changes in coral reefs, for example, continuous

Table 5. Species of *Mithrax* Latreille, 1816 and *Maguimithrax spinosissimus* (Lamarck, 1818) with larval development described indicating source and stages described

Species	Authors	Stages described
<i>Mithrax hispidus</i> (Herbst, 1790)	Santana <i>et al.</i> (2003)	ZI; ZII; M
<i>Mithrax pleuracanthus</i> Stimpson, 1871	Goy <i>et al.</i> (1981)	ZI; ZII; M
<i>Mithrax tortugae</i> Rathbun, 1920	Magalhães <i>et al.</i> (2017)	ZI; ZII; M
<i>Maguimithrax spinosissimus</i> (Lamarck, 1818) as <i>Mithrax spinosissimus</i>	Provenzano & Brownell (1977)	PZ; ZI; ZII; M; CI
<i>Maguimithrax spinosissimus</i> (Lamarck, 1818)	Present study	ZI; ZII; M

PZ: prezoaea; ZI: zoea I; ZII: zoea II; M: megalopa; CI: first crab.

Table 6. Comparison of carapace length of larval stages of *Maguimithrax spinosissimus* (Lamarck, 1818) and *Mithrax* Latreille, 1816 species

Carapace length	ZI	ZII	Megalopa
<i>Mithrax hispidus</i> ¹	0.92 ± 0.04 (0.86–1.0)	1.07 ± 0.04 (1.02–1.12)	1.10 ± 0.18 (0.87–1.37)
<i>Mithrax pleuracanthus</i> ²	0.96 (0.93–0.98)	1.10 (0.99–1.20)	1.40 (1.30–1.50)
<i>Mithrax tortugae</i> ³	0.83 ± 0.02	0.94 ^a	1.08 ^a
<i>Maguimithrax spinosissimus</i> ⁴	1.10 (1.0–1.20)	1.15 (1.10–1.20)	1.30 (1.20–1.50)
<i>Maguimithrax spinosissimus</i> ⁵	1.18 ± 0.14 (1.12–1.22)	1.23 ± 0.06 (1.12–1.22)	1.24 ± 0.05 (1.18–1.30)

Note: Values are given as the mean ± standard deviation, with range in parentheses.

^aStandard deviation and range not described. Data from: ¹ Santana *et al.* (2003); ² Goy *et al.* (1981); ³ Magalhães *et al.* (2017); ⁴ Provenzano & Brownell (1977); ⁵ Present study.

decrease in coral cover in several localities across the Caribbean as has been well documented in recent years (McMurray *et al.*, 2015 and references therein), we expect the behaviour of these coral-dwelling species to change concomitantly while they acclimatize (in the short term) and adapt to these morphing seascapes. Ultimately, the development of the present and other resources are also of utmost importance as they will improve the understanding of the biology of *M. spinosissimus* and its responses to local, regional and global anthropogenic disturbance for a species inhabiting an environment already facing considerable environmental threats.

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References

Anger K (1995) Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. II. Facultative lecithotrophy of larval stages. *Marine Ecology Progress Series* **117**, 75–81.

- Baeza JA, Bolaños JA, Fuentes S, Hernández JE, Lira C and Lopez R (2010) Molecular phylogeny of enigmatic Caribbean spider crabs from the *Mithrax*–*Mithraculus* species complex (Brachyura: Majidae: Mithracinae): ecological diversity and a formal test of genera monophyly. *Journal of the Marine Biological Association of the United Kingdom* **90**, 851–858.
- Baeza JA, Anderson JR, Spadero AJ and Behringer DC (2012) Sexual dimorphism, allometry, and size at first maturity of the Caribbean king crab *Mithrax spinosissimus*, in the Florida Keys. *Journal of Shellfish Research* **31**, 909–916.
- Baeza JA, Simpson L, Ambrosio LJ, Guéron R, Mora N and Owen D (2015) Reproductive investment in a phyletic giant, the Caribbean king crab *Damithrax spinosissimus*: exploring egg production costs in large brooding marine invertebrates. *Journal of Shellfish Research* **34**, 1049–1056.
- Baeza JA, Holstein D, Umaña-Castro R and Mejía-Ortiz LM (2019) Population genetics and biophysical modeling inform metapopulation connectivity of the Caribbean king crab *Maguimithrax spinosissimus*. *Marine Ecology Progress Series* **610**, 83–97.
- Bell JJ, Davy SK, Jones T, Taylor MW and Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* **19**, 2613–2624.
- Bolaños J, Lares L and Hernández JE (1990) Desarrollo larval de *Mithrax caribbaeus* Rathbun, 1920 (Crustacea: Decapoda: Majidae) realizado en condiciones de laboratorio. *Boletín del Instituto Oceanográfico de Venezuela* **29**, 67–89.
- Bolaños J, Cuesta JA, Hernández G, Hernández J and Felder DL (2004) Abbreviated larval development of *Tunicotheres moseri* (Rathbun, 1918) (Decapoda, Pinnotheridae), a rare case of parental care in brachyuran crabs. *Scientia Marina* **68**, 373–384.
- Bolaños J, Rivero W, Hernández J, Magán I, Hernández G, Cuesta JA and Felder DL (2005) Abbreviated larval development of the pea crab *Orthotheres barbatus* (Decapoda: Brachyura: Pinnotheridae) described from laboratory-reared material, with notes on larval characters of the Pinnotherinae. *Journal of Crustacean Biology* **25**, 500–506.
- Brownell WN, Provenzano AJ and Martínez M (1977) Culture of the West Indian spider crab (*Mithrax spinosissimus*) at Los Roques, Venezuela. In *Proceedings of the Annual Meeting – World Mariculture Society*. Oxford: Blackwell Publishing, pp. 157–168.
- Calado R, Bartilotti C, Narciso L and dos Santos A (2004) Redescription of the larval stages of *Lysmata seticaudata* (Risso, 1816) (Crustacea, Decapoda, Hippolytidae) reared under laboratory conditions. *Journal of Plankton Research* **26**, 737–752.
- Chu C, Loh KH, Ng CC, Ooi AL, Konishi Y, Huang SP and Chong VC (2019) Using DNA barcodes to aid the identification of larval fishes in tropical estuarine waters (Malacca Straits, Malaysia). *Zoological Studies* **58**, 30.
- Clark PF (2000) Interpreting patterns in chaetotaxy and segmentation associated with abbreviated brachyuran zoeal development. *Invertebrate Reproduction & Development* **38**, 171–181.
- Colavite J, Santana W and Pohle G (2014) Larval development of the spider crab *Menaethius monoceros* (Latreille, 1825) (Crustacea: Decapoda: Brachyura: Epialtidae). *Journal of Natural History* **48**, 2273–2292.
- Creswell RL (2011) The cultivation of marine invertebrates indigenous to the Wider Caribbean Region: established culture techniques and research needs for crustaceans. *Fisheries and Aquaculture Proceedings* **19**, 105–117.
- Creswell RL, Tunberg B and Winfree R (1989) Mariculture of the Caribbean king crab *Mithrax spinosissimus* (Lamarck, 1818) in the Caribbean Region:

- progress and constraints. *Proceedings of the Thirty-Ninth Annual Gulf and Caribbean Fisheries Institute* **39**, 469–476.
- Felder DL, Álvarez F, Goy JW and Lemaitre R (2009) Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea. In Felder DL and Camp DK (eds), *Gulf of Mexico – Origins, Waters, and Biota. Volume 1. Biodiversity*. College Station, TX: Texas A&M Press, pp. 1019–1104.
- González-Gordillo JJ, Anger K and Schubart CD (2010) Morphology of the larval and first juvenile stages of two Jamaican endemic crab species with abbreviated development, *Sesarma windsor* and *Metopaulius depressus* (Decapoda: Brachyura: Sesarmidae). *Journal of Crustacean Biology* **30**, 101–121.
- Gore RH (1970) *Petrolisthes armatus*: a redescription of larval development under laboratory conditions (Decapoda, Porcellanidae 1). *Crustaceana* **18**, 75–89.
- Goy JW, Bookhout CG and Costlow Jr JD (1981) Larval development of the spider crab *Mithrax pleuracanthus* Stimpson reared in the laboratory (Decapoda: Brachyura: Majidae). *Journal of Crustacean Biology* **1**, 51–62.
- Herbst JFW (1790) *Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Volume 1*. Berlin and Stralsund.
- Hurtado-Alarcón JC, Campos NH, Bermúdez Tobón A and Márquez EJ (2017) Phylogeographic patterns in *Maguimithrax spinosissimus* (Decapoda: Mithracidae) from Colombian Caribbean. *New Zealand Journal of Marine and Freshwater Research* **52**, 118–137.
- Klompmaaker AA, Portell RW, Klier AT, Prueter V and Tucker AL (2015) Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracidae. *PeerJ* **3**, e1301.
- Lamarck JBPA (1818) *Histoire naturelle des animaux sans vertèbres présentant les caractères généraux et particuliers de ces animaux, leur distribution, leur classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels, de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie. Volume 5*. Paris: Deterville and Verdier Libraire. <https://doi.org/10.5962/bhl.title.12712>.
- Latreille PA (1816) Nouveau dictionnaire d'histoire naturelle. *Par une Société de Naturalistes et d'Agriculteurs Paris* **6**, 565–566.
- Lerosey-Aubril R and Meyer R (2013) The sensory dorsal organs of crustaceans. *Biological Reviews of the Cambridge Philosophical Society* **88**, 406–426.
- Li JJ, Shih YJ, Ho PH and Jiang GC (2019) Description of the first zoea of the cavernicolous crab *Karstama boholano* (Ng, 2002) (Crustacea: Decapoda: Sesarmidae) from Taiwan, with notes on ecology. *Zoological Studies* **58**, 36.
- Magalhães T, Souza-Carvalho ED, Biagi R, Cuesta JA and Mantelatto FL (2017) Larval stages of the crab *Mithrax tortugae* (Brachyura: Mithracidae) with comparisons between all species of *Mithrax*. *Marine Biology Research* **13**, 1108–1117.
- Márquez EJ, Hurtado-Alarcón JC, Isaza JP, Alzate JF and Campos NH (2016) Mitochondrial genome of the Caribbean king crab *Damithrax spinosissimus* (Lamarck, 1818) (Decapoda: Majidae). *Mitochondrial DNA* **27**, 1724–1725.
- Martin JW and Laverack MS (1992) On the distribution of the crustacean dorsal organ. *Acta Zoologica* **73**, 357–368.
- McMurray SE, Finelli CM and Pawlik JR (2015) Population dynamics of giant barrel sponges on Florida coral reefs. *Journal of Experimental Marine Biology and Ecology* **473**, 43–50.
- Ng PK, Guinot D and Davie PJ (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology* **17**, 1–286.
- Norström AV, Nyström M, Lokrantz J and Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* **376**, 295–306.
- Pohle G and Marques F (2000) Larval stages of *Paradasygius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae. *Proceedings of the Biological Society of Washington* **113**, 739–760.
- Pohle G and Telford M (1981) Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). *Bulletin of Marine Science* **31**, 736–752.
- Porter KL, Iglehart JM, Craig M and Adey WH (1986) Section III. Mariculture techniques for *Mithrax spinosissimus* including broodstock larval and post-larval rearing and growout techniques. In Adey WH and Farrier DF (eds), *The Biology, Ecology and Mariculture of Mithrax spinosissimus, Utilizing Cultured Algal Turfs*. Los Angeles, CA: Mariculture Institute, pp. 1–17.
- Provenzano AJ and Brownell WN (1977) Larval and early post-larval stages of the West Indian spider crab, *Mithrax spinosissimus* (Lamarck, 1818) (Decapoda: Majidae). *Proceedings of the Biological Society of Washington* **90**, 735–752.
- Rathbun MJ (1920) New species of spider crabs from the Straits of Florida and Caribbean Sea. *Proceedings of the Biological Society of Washington* **33**, 23–24.
- Rathbun MJ (1925) The spider crabs of America. *Bulletin of the United States National Museum* **129**, 1–613.
- Rhynie AL, Fujita Y and Calado R (2006) Larval development and first crab of *Mithraculus sculptus* (Decapoda: Brachyura: Majoidea: Mithracidae) described from laboratory-reared material. *Journal of the Marine Biological Association of the United Kingdom* **86**, 1133–1147.
- Rice AL (1980) Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* **35**, 271–424.
- Santana W, Pohle G and Marques FPL (2003) Zoeal stages and megalopa of *Mithrax hispidus* (Herbst, 1790) (Decapoda: Brachyura: Majoidea: Mithracidae): a reappraisal of larval characters from laboratory cultured material and a review of larvae of the *Mithrax–Mithraculus* species complex. *Invertebrate Reproduction & Development* **44**, 17–32.
- Santana W, Marques F and Pohle G (2004) Larval stages of *Stenocionops furcatus* (Olivier, 1791) (Decapoda: Brachyura: Majoidea) and a reappraisal of larval morphological characters for Mithracidae. *Journal of Plankton Research* **26**, 859–874.
- Santana W, Colavite J, Bolaños J, Hernández JE and Canepa M (2016) Morphology of the larval stages of *Pitho aculeata* (Gibbes, 1850) (Crustacea, Brachyura, Majoidea) and its implications on the taxonomic position of the genus. *Marine Biology Research* **12**, 854–863.
- Santos AD and Paula J (2003) Redescription of the larval stages of *Upobebia pusilla* (Petagna, 1792) (Thalassinidea, Upogebiidae) from laboratory-reared material. *Invertebrate Reproduction & Development* **43**, 83–90.
- Stimpson W (1871) Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L.F. de Pourtales, Assist. U.S. Coast Survey. *Bulletin of the Museum of Comparative Zoology, Harvard College* **2**, 109–160.
- Taishaku H and Konishi K (2001) Lecithotrophic larval development of the spider crab *Goniopugettia sagamiensis* (Decapoda, Brachyura, Majidae) collected from the continental shelf break. *Journal of Crustacean Biology* **21**, 748–759.
- Thessalou-Legaki M, Peppas A and Zacharaki M (1999) Facultative lecithotrophy during larval development of the burrowing shrimp *Callinassa tyrrenha* (Decapoda: Callinassidae). *Marine Biology* **133**, 635–642.
- Tunberg BG and Creswell RL (1988) Early growth and mortality of the Caribbean king crab *Mithrax spinosissimus* reared in the laboratory. *Marine Biology* **98**, 337–343.
- Tunberg BG and Creswell RL (1991) Development, growth and survival in the juvenile Caribbean king crab *Mithrax spinosissimus* (Lamarck) reared in laboratory. *Journal of Crustacean Biology* **11**, 138–149.
- Wagner HP (1990) The Genera *Mithrax* Latreille, 1818 and *Mithraculus* White, 1847 (Crustacea: Brachyura: Majidae) in the Western Atlantic Ocean. *Zoologische Verhandlungen* **264**, 1–65.
- Wilber DH and Wilber TP (1991) Environmental influences on the growth and survival of West Indian spider crabs *Mithrax spinosissimus* (Lamarck) in culture. *Journal of Experimental Marine Biology and Ecology* **146**, 27–38.
- Williams AB (1984) *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Washington, DC: Smithsonian Institution Press.
- Wilson KA, Scotto LE and Gore RH (1979) Studies on decapod Crustacea from the Indian River region of Florida. XIII. Larval development under laboratory conditions of the spider crab *Mithrax forceps* (A. Milne Edwards, 1875) (Brachyura: Majidae). *Proceedings of the Biological Society of Washington* **92**, 307–327.

- Windsor AM and Felder DL** (2014) Molecular phylogenetics and taxonomic reanalysis of the family *Mithracidae* MacLeay (Decapoda: Brachyura: Majoidea). *Invertebrate Systematics* **28**, 145–173.
- Windsor AM and Felder DL** (2017) Corrigendum to: Molecular phylogenetics and taxonomic reanalysis of the family *Mithracidae* MacLeay (Decapoda: Brachyura: Majoidea). *Invertebrate Systematics* **31**, 232.
- Winfree RA and Weinstein S** (1990) Food habits of the Caribbean King crab *Mithrax spinosissimus* (Lamarck). *Proceedings of the Gulf Caribbean Fisheries Institute* **39**, 458–464.
- Wong KJH, Tsao Y-F, Tsai P-C, Hsieh W-P, Li H-R, Machida RJ and Chan BKK** (2021) To the light side: molecular diversity and morphology of stomatopod larvae and juveniles (Crustacea: Malacostraca: Stomatopoda) from crustose coralline algal reefs in Taiwan. *Marine Biodiversity* **51**. <https://doi.org/10.1007/s12526-020-01150-z>.
- Yang WT** (1967) A study of zoeal, megalopal, and early crab stages of some *Oxyrhynchus* crabs (Crustacea: Decapoda). PhD thesis, University of Miami, Coral Gables, FL.