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Original Article

Morphology of stomatopod larvae from National Parks: Sistema Arrecifal Veracruzano and Arrecife Puerto Morelos, Mexico

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Abstract

The present study provides information on the morphology of stomatopod larvae found in two different reef systems which are also considered national parks: the Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP). Zooplankton samples were collected at 26 stations of the SAVNP and four stations of the APMNP. Stomatopod larvae were identified and classified by their larval stage. We found representatives of three stomatopod superfamilies: the superfamily Gonodactyloidea Giesbrecht, 1910 was represented by *Neogonodactylus oerstedii* (Hansen, 1895), *Neogonodactylus wennerae* Manning and Heard, 1997, and Pseudosquillidae genus and species indeterminate; the superfamily Lysiosquilloidea Giesbrecht, 1910 was represented by Lysiosquilloidea genus and species indeterminate, *Lysiosquilla* sp., *Lysiosquilla scabricauda* (Lamarck, 1818) and *Nannosquilla adkisoni* Camp and Manning, 1982; the superfamily Squilloidea was represented by larvae of *Alima neptuni* (Linnaeus, 1768), *Squilla* spp., and *Squilla empusa* Say, 1818. We were able to identify and describe four stages of larval development for representatives of these superfamilies. This is the first study describing several stages of larval development of different species of the stomatopods from the Gulf of Mexico and Caribbean Sea.

Key words

Crustaceans, Stomatopoda, larval stages, zooplankton, coral reefs.

Introduction

The order Stomatopoda Latreille, 1817 consists of 481 species distributed in the tropical, subtropical and temperate regions of the world (Reaka *et al.*, 2009). During their development, stomatopods pass through different larval stages and could form part of both zooplankton and benthos (Ahyong *et al.*, 2014).

Four morphological types of stomatopod larvae are known: antizoea and pseudozoea are early larval stages, while erichthus and alima are late larval stages (Ahyong, 2004; Schram *et al.*, 2013). These forms do not necessarily have to be sequential. To date, three alternative sequences of larval development have been identified: antizoea/erichtus, pseudozoea/erichtus, and pseudozoea/alima (Ahyong *et al.*, 2014). The antizoea, the type in which the lysiosquilloids (and probably erythrosquilloids) hatch, is characterized by the presence of sessile eyes, antennules with a flagellum, five pairs of biramous thoracic appendages called maxillipeds (which are the most important differential characters among stomatopods), and the absence of appendages on the pleon. The carapace has a fixed spinous rostrum and covers most of the pleon except the last two or three pleomeres (Ahyong *et al.*, 2014). Squilloids, gonodactyloids, parasquilloids and some eurysquilloids hatch as pseudozoea. This larva is characterized by having pedunculated composite eyes, biflagellate antennules, two pairs of uniramous thoracic appendages (maxillipeds 1 and 2), and four (squilloids) or five pairs of biramous swimmers (pleopods). Both, antizoea and pseudozoea of gonodactyloids, parasquilloids and eurysquilloids develop into an erichthus larva type. This larva presents the second maxilliped as a rapacious claw, with some teeth in the occlusal margin of the dactyl; maxillipeds 3–5, pereopods and uropods are absent and present one or two intermediate denticles on the telson. Finally, squilloid pseudozoea develops into alima type larva, being unique for the squilloids. This larva differs from the erichthus by presenting a ventral spine on the antennular segment and four or more intermediate denticles on the telson (Ahyong *et al.*, 2014).

Of the approximately 500 species of stomatopods described so far, no more than 10% of the larval stages can be identified worldwide (Diaz, 1998; Haug *et al.*, 2016). Moreover, there are only a few studies where the complete larval development of stomatopod larvae has been described (Manning and Provenzano, 1963; Pyne, 1972; Provenzano and Manning, 1978; Greenwood and Williams, 1984; Hamano and Matsuura, 1987; Morgan and Goy, 1987). Likewise, partial larval series are known for a limited number of species (Gurney, 1946; Alikunhi, 1967; Michel, 1968; 1970; Michel and Manning, 1972; Shanbhogue, 1975; Rodrigues and Manning, 1992; Ahyong, 2002; Veena and Kaladharan, 2010; Feller, 2013; Antonio-Bueno, 2015). This lack of information is due in part to the complexity of the larval development of stomatopods, where the initial stages are propelagic and the late stages are planktic (pelagic) (Hamano and Matsuura, 1987). First, the female mantis shrimp will provide maternal care by using her maxillipeds to clean the eggs and circulate water around them; after hatching of the larvae, the female will continue protecting the newly hatched larvae and physiological adaptations make the early larval stages stay within the cave with the parental female, thus the first stages may be overlooked (Wortham-Neal, 2002). Maintaining an ovigerous female in captivity until hatching is by itself a difficult task, add to that the behavior of the parental female who will hide in a cave with the eggs first and later with the larvae and the task becomes almost impossible (Pyne, 1972). Besides changes on physiology, ethology and ecology of the larvae described above, the time of development is very large, from 35 days to nine months, depending on the species. No wonder why the most common way of describing stomatopod larvae is by collecting planktic stages, with the unintended consequences of describing only the later stages of development (Ahyong *et al.*, 2014).

Thus, the objective of this study was to provide additional information on the morphology of the planktonic larvae, at different stages of development, of some of the stomatopod species found in the southwestern Gulf of Mexico and the Mexican Caribbean, specifically on the Sistema Arrecifal Veracruzano and Arrecife Puerto Morelos.

Material and Methods

The Sistema Arrecifal Veracruzano (SAVNP) is a coral reef system located in the northwest sector of the Bay of Campeche, in the polygon delimited by 19°00'00" – 19°16'00"N and 95°45'00" – 96°12"00"W. It is formed by 23 coral reefs distributed in a northern group and a southern group, separated by the mouth of the Jamapa River (Granados *et al.*, 2007). The Arrecife Puerto Morelos National Park (APMNP) is part of the Mesoamerican Reef System which is in Puerto Morelos, Quintana Roo (20°54'16"N 86°49'39" W). The reef lagoon is connected to the open sea by two entrances. The bottom of the lagoon is covered with calcareous sand and stabilized by seaweed grasslands; patches of corals have colonized some areas becoming coral reef communities (Humann, 2002; Álvarez-Cadena *et al.*, 2007) (Fig. 1).

Field work on SAVNP: zooplankton samples were collected at 26 stations of the SAVNP. Trawls were made in the surface layer of the water column using conical plankton nets with a mesh light of 330 µm during five minutes, at a speed of three knots. The material was fixed in a 70% solution of ethanol and put in plastic containers previously labeled, and transferred to the Ecology Laboratory of the Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México (UNAM).

Field work in APMNP: two types of sampling were carried out: light traps were placed on three piers of the docking area of the Institute of Marine Sciences and Limnology during three nights, covering a 12 h cycle; these cycles were initiated at 18:00 h and stopped

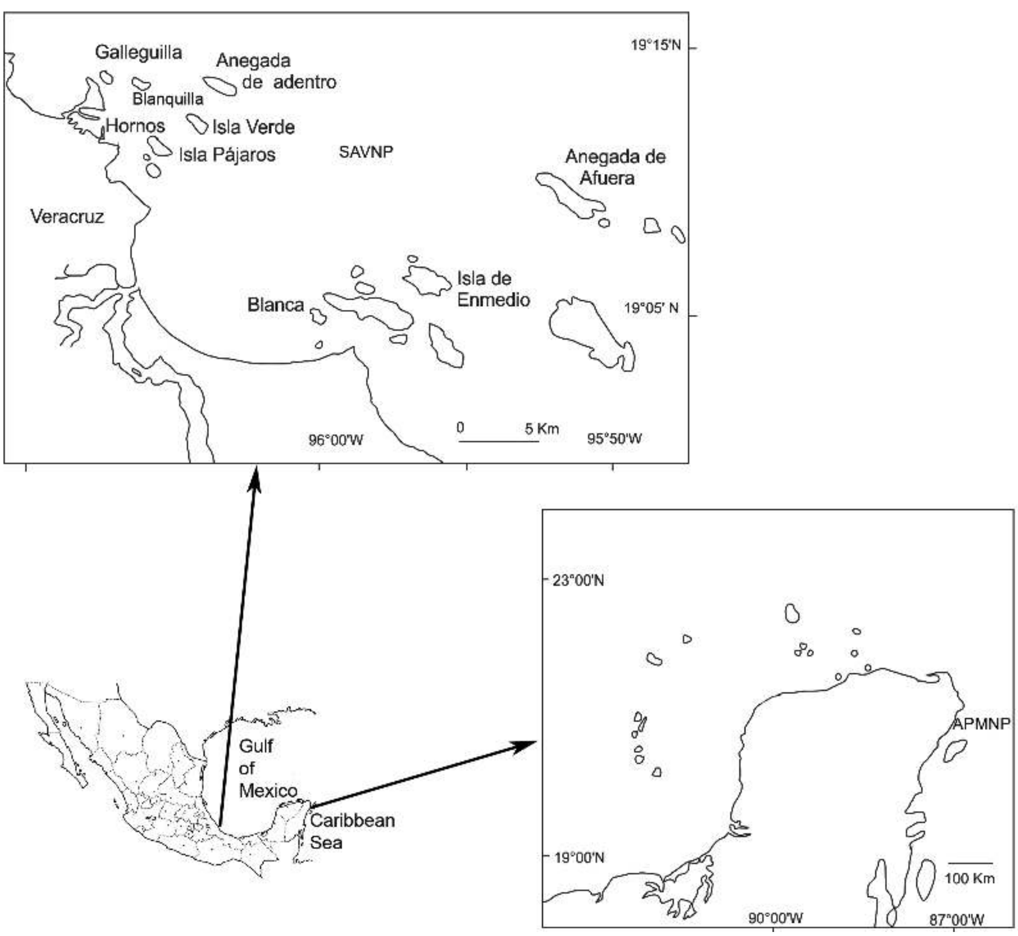

Figure 1. Location of sampling sites at the national parks Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP).

at 6:00 h of the next day on June 6, 7 and 8 on phase new moon. All traps had white light of 38 lumens. These traps were constructed with plastic boxes 0.4 m long, 0.25 m wide and 0.30 m high; a 40 mm diameter inlet holes were made in the upper part of each side of the box.

The contents were collected manually and concentrated in 500 ml plastic bottles at the end of the sampling period. The second sampling point was at the site called Rodman, where the sample was obtained in a coral stand at a depth of 20 m with SCUBA self-contained diving equipment. The substrate was placed in plastic bags for further review. All samples were preserved with 70% alcohol.

Samples were sorted out using a Motic SMZ-168 microscope at the Crustacean Laboratory. Identification of the larvae followed current literature [Manning (1969; 1995), Michel and Manning (1972); Rodrigues and Manning (1992); Ahyong *et al.* (2014); and Antonio-Bueno (2015), for larvae of stomatopods in general; Townsley (1953), for Lysiosquilloidea Giesbrecht, 1910, *Lysiosquilla* Dana, 1852 and Pseudosquillidae Manning, 1977; Manning (1962) and Fornshell (2012), for *Alima* Leach, 1817; Pyne (1972) and Diaz (1998) for *Squilla* Fabricius, 1787; Morgan and Provenzano (1979), for *Squilla empusa* Say, 1818; Morgan and Goy (1987), for *Neogonodactylus wennerae* Manning and Heard, 1997; Provenzano and Manning (1978), for *Neogonodactylus oerstedii* (Hansen, 1895); García-Calzada (2013), for *Nannosquilla adkisoni* Camp and Manning, 1982 and *Lysiosquilla scabricauda* (Lamarck, 1818)]. The larvae were deposited in the National Collection of Crustaceans (CNCR) of the Institute of Biology of the Universidad Nacional Autónoma de México (UNAM).

Measurements of larvae and abbreviations: carapace length (CL), carapace width (CW), dactyl length (DL), posterolateral spines length (PSL), propodus length (PL), rostral spine length (RSL), telson lateral spines length (TSL), telson length (TelL), telson submedian spines length (SSL), telson width (Telw), and total length (TL) (Fig. 2). We also counted the number of spines and denticles of the different structures. Images of the larvae were taken using a Leica DM750 microscope equipped with an Omax 14MP USB 3.0 digital camera.

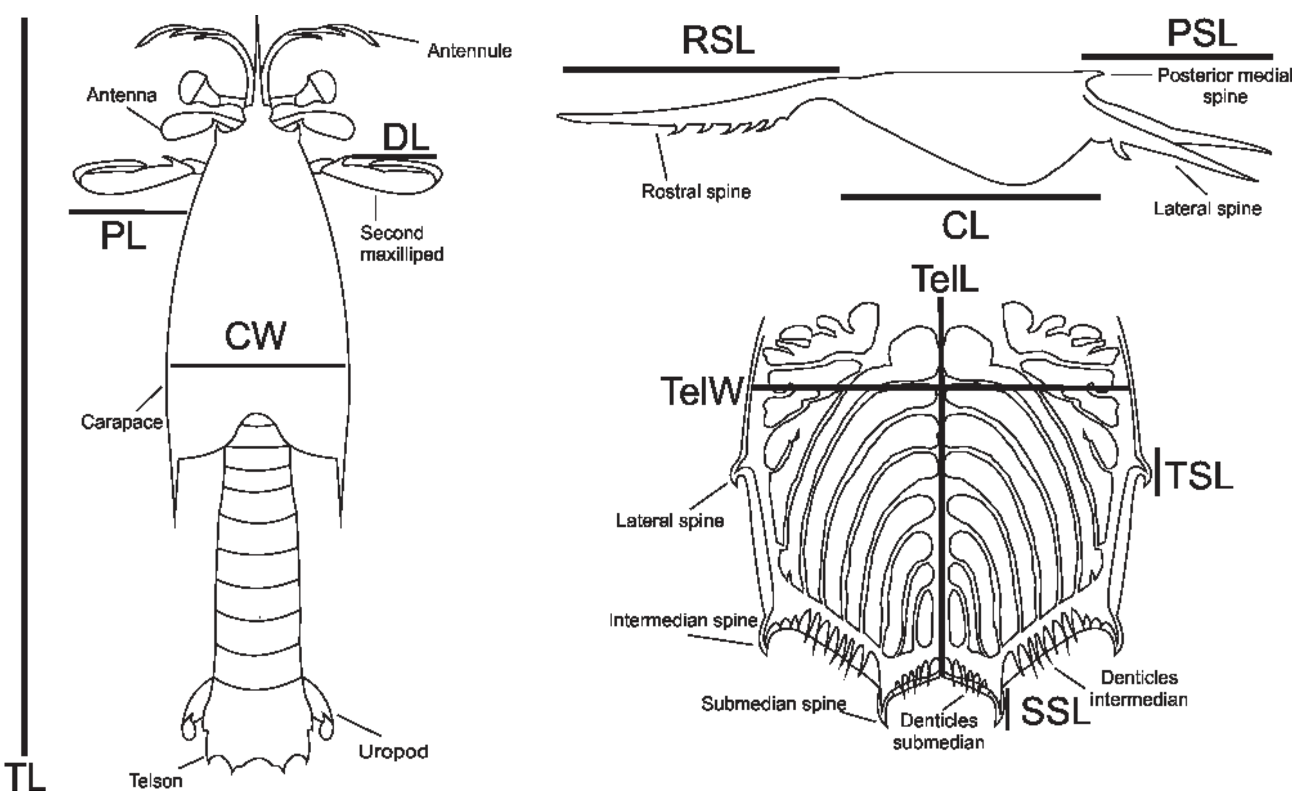

Figure 2. Stomatopod larvae. General morphology, structures and measurements. TL, total length; CL, carapace length; CW, carapace width; RSL, rostral spine length; PSL, posterolateral spines length; PL, propod length; DL, dactyl length; TelL, telson length; Telw, telson width; TSL, telson lateral spines length; SSL, telson submedian spines length.

Results

We collected 1759 stomatopod larvae belonging to three superfamilies, six families, seven genera and 10 species. The superfamily Gonodactyloidea Giesbrecht, 1910 was represented by *Neogonodactylus oerstedii*, *N. wennerae* and Pseudosquillidae genus and species indeterminate. The superfamily Lysiosquilloidea was represented by Lysiosquilloidea genus and species indeterminate, *Lysiosquilla* sp., *L. scabricauda*, and *Nannosquilla adkisoni*. Representatives of the superfamily Squilloidea Latreille, 1802 were also present as larvae of *Alima neptuni* (Linnaeus, 1768), *Squilla* spp., and *S. empusa*. Overall, we found larvae of nine stomatopod species at the SAVNP and of four at the APMNP. All morphological measurements are shown on Tab. 1 and Tab. 2.

Taxonomic account and larval description.

Superfamily Gonodactyloidea Giesbrecht, 1910

Family Gonodactylidae Giesbrecht, 1910

***Neogonodactylus oerstedii* (Hansen, 1895)**

Stage II: Pseudozoea (CNCR32467)
(Fig. 3A)

Description. Carapace lobate, short. Rostrum short, usually not surpassing peduncle of antennule (A1), with single posterior medial spine. Posterolateral spines short, extending to first or second pleonite, bearing thin proximal spine. Propodus of second maxilliped broadened, smooth, with mobile dactyl. Telson straight, bearing three pairs of articulated lateral spines, a pair of fixed posterolateral spines and 10–12 small denticles on either side of midline.

Habitat. Benthic, among coral rubbles.

Location. APMNP.

Stage III: Erichthus (CNCR32468)
(Fig. 3B)

Description. Carapace lobate, short. Rostrum small, reaching base of flagellum of A1, lacking ventral spines, posterolateral spines extend to second pleonite, bearing proximal small spine. Second maxilliped well developed, propodus broadened, smooth; mobile dactyl. Telson straight, bearing three pairs of fixed lateral spines and pair of posterolateral spines, bearing 10–12 denticles intercalated with small spines in between.

Habitat. Pelagic.

Location. SAVNP.

Stage IV: Erichthus (CNCR32469)
(Fig. 3C)

Description. Carapace longer than width, reaching first or second pleonite; bearing well-developed supraorbital spines. Rostrum relatively short, surpassing flagellum of A1, armed with 3–5 ventral spines. Posterolateral spines reaching fourth pleonite, bearing small proximal spine. First maxiliped with eight aesthetascs and strong seta on dactyl. Second maxilliped well developed, propodus with 14–16 denticles on inner margin; dactylus with distal portion of cutting edge as small saw. Telson straight, bearing three pairs of fixed lateral spines and pair of posterolateral spines, bearing 10–12 denticles on either side of midline.

Habitat. Pelagic.

Location. SAVNP.

Stage VI: Erichthus (CNCR32470)
(Fig. 3D)

Description. Carapace longer than width, extending to first pleonite, bearing well-developed supraorbital spines. Rostrum not exceeding flagellum of A1. Posterolateral spines reaching third pleonite, with small proximal spine. Propodus of second maxilliped armed with at least 10–13 small denticles, long sharp proximal spine, dactyl with basal bulge. Telson straight, bearing three pairs of fixed lateral spines and pair of strongly elongated lateral spines; bearing 22 denticles on each side of midline. Uropods fully developed.

Habitat. Pelagic.

Location. SAVNP.

Table 1. Stomatopod larvae collected at the national parks Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP) organized by species, larval stage, and type of larva. IN, indeterminate; X, presence; (-), absence. TL, total length; CL, carapace length; CW, carapace width; RSL, rostral spine length; posterolateral spines length (PSL).

Species	Type of larva	Stage	Number	SAVNP	APMNP	TL	RSL	CL	CW	PSL
Neogonodactylus wennerae	Erichtus	IV	56	X	-	4.08 ± 0.11	0.75 ± 0.09	1.49 ± 0.06	0.95 ± 0.03	0.53 ± 0.02
N. wennerae	Erichtus	VIII	4	X	-	7.75 ± 0.25	1.10 ± 0.11	2.26 ± 0.02	1.18 ± 0.32	1.07 ± 0.01
Neogonodactylus oerstedii	Pseudozoea	II	415	-	X	2.08 ± 0.11	0.17 ± 0.29	0.94 ± 0.06	0.55 ± 0.03	0.23 ± 0.02
N. oerstedii	Erichtus	III	719	X	-	2.25 ± 0.02	0.17 ± 0.01	0.96 ± 0.02	0.58 ± 0.02	0.27 ± 0.01
N. oerstedii	Erichtus	IV	503	X	-	4.06 ± 0.08	0.74 ± 0.09	1.59 ± 0.13	0.99 ± 0.08	0.63 ± 0.08
N. oerstedii	Erichtus	VI	5	X	-	6.04 ± 0.06	1.78 ± 0.09	2.22 ± 0.14	1.19 ± 0.053	1.05 ± 0.06
Pseudosquillidae genus and species indeterminate	Erichtus	IN	8	X	-	2.45 ± 0.05	0.27 ± 0.02	0.95 ± 0.02	0.51 ± 0.06	0.21 ± 0.02
Lysiosquilloidea genus and species indeterminate	Antizoea	IN	8	X	-	3.71 ± 0.06	0.51 ± 0.041	2.01 ± 0.06	1.11 ± 0.06	0.36 ± 0.02
Lysiosquilla sp.	Antizoea	IN	1	X	-	2.97	0.78	1.29	0.62	0.33
Lysiosquilla scabricauda	Erichtus	IN	1	X	-	26.11	3.6	11.8	6.5	0.3
Nannosquilla adkisoni	Erichtus	IN	2	-	X	17.75 ± 0.01	3.78 ± 0.07	10.16 ± 0.07	2.73 ± 0.04	6.8 ± 0.01
Alima neptuni	Alima	IV	8	X	-	8.41 ± 0.08	0.79 ± 0.06	2.61 ± 0.09	0.97 ± 0.09	0.37 ± 0.04
A. neptuni	Alima	IX	3	X	-	43.4 ± 0.04		16.5 ± 0.031	6.2 ± 0.06	2.1 ± 0.03
Squilla sp. 1	Alima	IX	4	X	X	27.48 ± 1.51	2.35 ± 0.50	42.65 ± 0.65	6.16 ± 0.01	2.26 ± 0.07
Squilla sp. 2	Alima	II	1	X	-	4.62	0.68	1.63	0.84	0.39
Squilla empusa	Alima	I	3	X	-	2.81 ± 0.07	0.31 ± 0.01	0.91 ± 0.03	0.61 ± 0.02	2.26 ± 0.07
S. empusa	Alima	II	5	X	-	4.73 ± 0.07	0.55 ± 0.05	1.71 ± 0.01	0.86 ± 0.05	0.43 ± 0.06
S. empusa	Alima	III	8	X	-	6.72 ± 0.05	1.35 ± 0.09	1.99 ± 0.04	1.28 ± 0.05	0.92 ± 0.06
S. empusa	Alima	IX	5	-	X	18.23 ± 0.07	3.63 ± 0.08	5.29 ± 0.09	3.49 ± 0.07	2.44 ± 0.09

Table 2. Stomatopod larvae collected at the national parks Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP) organized by species, larval stage, and type of larva. PL, propodus length; DL, dactylus length, TelL, telson length (TelL); Telw, telson width; TSL, telson lateral spines length; SSL, telson submedian spines length.

Species	Type of larva	Stage	PL	DL	TelL	TelW	TSL	SSL
Neogonodactylus wennerae	Erichtus	IV	1.44 ± 0.02	0.75 ± 0.03	0.75 ± 0.06	0.62 ± 0.03	0.06 ± 0.01	
N. wennerae	Erichtus	VIII	1.19 ± 0.01	1.16 ± 0.01	1.16 ± 0.01	1.16 ± 0.01	0.21±0.01	
Neogonodactylus oerstedii	Pseudozoea	II	0.44 ± 0.02	0.35 ± 0.03	0.5 ± 0.06	0.42 ± 0.03	0.06 ± 0.01	
N. oerstedii	Erichtus	III	0.49 ± 0.07	0.36 ± 0.06	0.56 ± 0.09	0.45 ± 0.08	0.06 ± 0.01	
N. oerstedii	Erichtus	IV	1.06 ± 0.11	0.73 ± 0.06	0.78 ± 0.04	0.68 ± 0.06	0.06 ± 0.01	
N. oerstedii	Erichtus	VI	1.16 ± 0.01	0.98 ± 0.05	0.96 ± 0.05	0.95 ± 0.05	0.15 ± 0.01	
Pseudosquillidae genus and species indeterminate	Erichtus	IN	0.62 ± 0.06	0.48 ± 0.02	0.46 ± 0.05	0.36 ± 0.08	0.03 ± 0.01	
Lysiosquilloidea genus and species indeterminate	Antizoea	IN			0.69 ± 0.05	0.92 ± 0.01	0.12 ± 0.01	
Lysiosquilla sp.	Antizoea	IN			0.64	0.62	0.19	
Lysiosquilla scabricauda	Erichtus	IN			2.27	5.9	0.09	
Nannosquilla adkisoni	Erichtus	IN	1.95 ± 0.02	1.55 ± 0.02	1.27 ± 0.01	2.12 ± 0.02	0.18 ± 0.02	0.17 ± 0.02
Alima neptuni	Alima	IV	1.99 ± 0.08	1.08 ± 0.03	0.98 ± 0.03	0.43 ± 0.03	0.11 ± 0.01	0.11 ± 0.01
A. neptuni	Alima	IX			8.7 ± 0.07	3.6 ± 0.032	0.43 ± 0.03	0.33 ± 0.01
Squilla sp. 1	Alima	IX	4.78 ± 0.18	3.05 ± 0.23	3.65 ± 0.07	3.15 ± 0.05	0.52 ± 0.03	0.41 ± 0.09
Squilla sp. 2	Alima	II	1.37	0.68	0.83	0.66	0.04	
Squilla empusa	Alima	I	0.77 ± 0.01	0.45 ± 0.07	0.45 ± 0.07	0.42 ± 0.02	0.07 ± 0.01	
S. empusa	Alima	II	1.21 ± 0.01	0.92 ± 0.05	0.81 ± 0.05	0.56 ± 0.06	0.08 ± 0.01	
S. empusa	Alima	III	1.56 ± 0.02	1.12 ± 0.06	1.09 ± 0.07	0.84 ± 0.05	0.11 ± 0.02	
S. empusa	Alima	IX	3.83 ± 0.01	2.66 ± 0.07	2.98 ± 0.05	2.98 ± 0.05	0.42 ± 0.05	0.26 ± 0.08

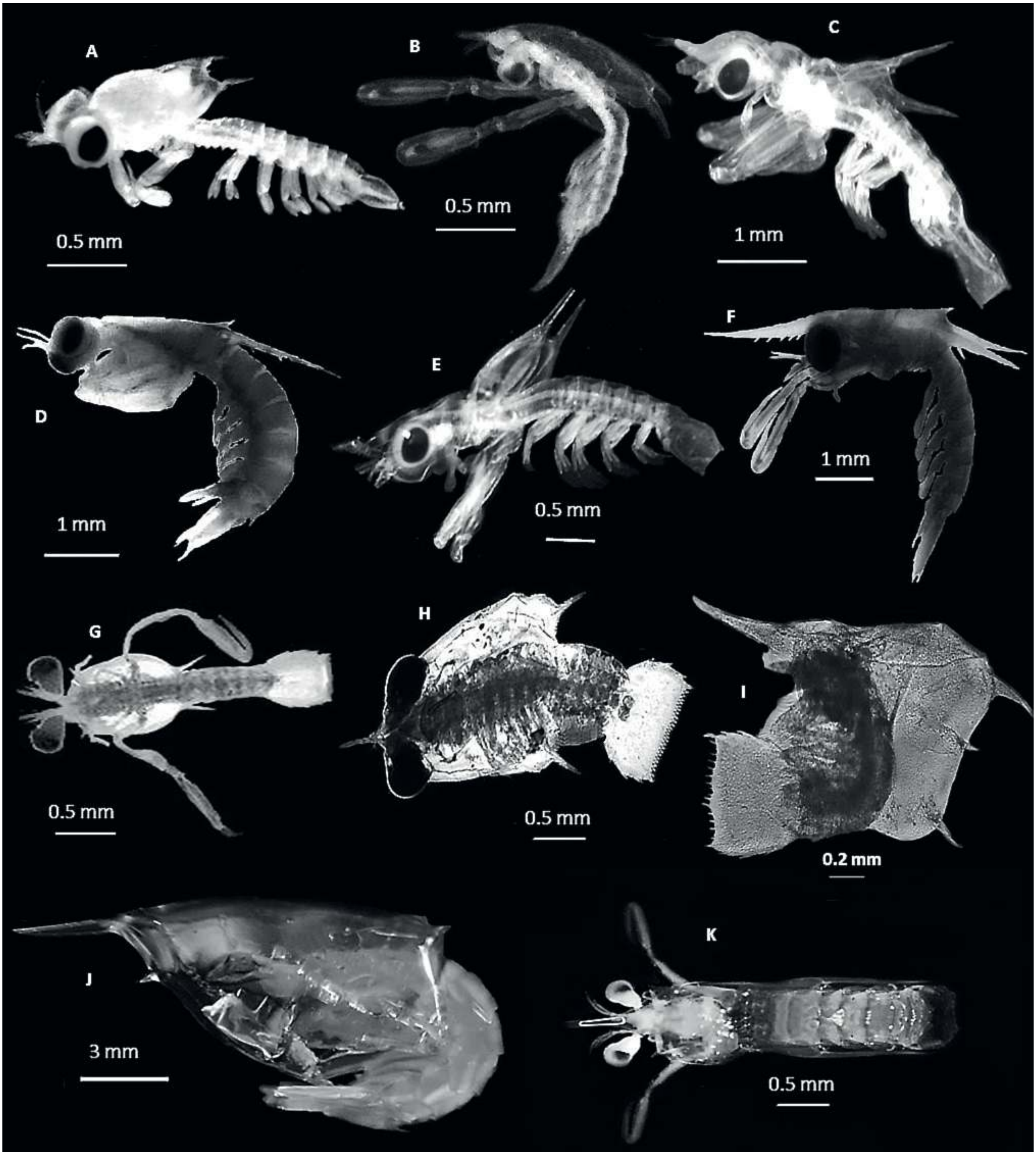

Figure 3. Stomatopod larvae collected at the national parks Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP). A, *Neogonodactylus oerstedii* (Hansen, 1895), stage II pseudozoea; B, *N. oerstedii*, stage III erichthus; C, *N. oerstedii*, stage IV erichthus; D, *N. oerstedii*, stage VI erichthus; E, *Neogonodactylus wennerae* Manning and Heard, 1997, stage IV erichthus; F, *N. wennerae*, stage VIII erichthus; G, Pseudosquillidae genus and species indeterminate, stage VI erichthus; H, Lysiosquilloidea genus and species indeterminate, antizoea; I, *Lysiosquilla* sp., antizoea; J, *Lysiosquilla scabricauda* (Lamarck, 1818), erichthus; K, *Nannosquilla adkisoni* Camp and Manning, 1982, erichthus.

Neogonodactylus wennerae Manning and Heard, 1997

Stage IV: Erichthus (CNCR32471)
(Fig. 3E)

Description. Carapace longer than width, extending to first or second pleonite; with well-developed posterolateral spines. Rostrum surpassing A1 flagellum, armed with 3–5 ventral spines. Posterolateral spines extend to fourth pleonite, bearing small proximal spine. First maxilliped dactyl with six aesthetascs, single strong seta. Second maxilliped well developed; propodus armed with three spines and 19–22 denticles; dactyl bearing 7–10 small setae. Telson straight, bearing three pairs of fixed lateral spines and pair of posterolateral spines; bearing 10–12 denticles on either side of midline.

Habitat. Pelagic.

Location. SAVNP.

Stage VIII: Erichthus (CNCR32472)
(Fig. 3F)

Description. Carapace longer than width, extending to first pleonite; with well-developed posterolateral spines. Rostrum reaching beyond flagellum of A1, armed with six ventral spines. Posterolateral spines extending to fourth pleonite, having small proximal spine. Second maxilliped well-developed; propodus with 28–30 denticles and well developed spines; dactyl bearing 9–10 short setae. Telson straight, bearing three pairs of fixed lateral spines and pair of strongly elongated posterolateral spines, bearing 22 denticles on each side of midline. Uropods well developed.

Habitat. Pelagic.

Location. SAVNP.

Family Pseudosquillidae Manning, 1977

Genus and species indeterminate

Stage (Indeterminate): Erichthus (CNCR32473)
(Fig. 3G)

Description. Carapace short, extending to fourth pleonite, slightly wider at base, bearing fine pairs of marginal spines, presenting pair of anterolateral spines. Rostrum relatively long reaching base of flagellum of A1, lacking ventral spines. Posterolateral spines reaching last pereonite, bearing well-developed proximal spine. Second maxilliped well developed, broadened propodus with 15–17 denticles and mobile dactyl. Telson straight, bearing three pairs of fixed lateral spines and pair of lateral spines; bearing seven denticles on either side of midline.

Habitat. Pelagic.

Location. SAVNP.

Superfamily Lysiosquilloidea Giesbrecht, 1910

Genus and species indeterminate

Stage (Indeterminate): Antizoea (CNCR32474)
(Fig. 3H)

Description. Carapace globular, not widening at base of posterolateral spines, slightly rectangular. Rostral spine as long as half length of carapace; lacking ventral spines. Posterolateral spines strong and slightly curved, middle spine present; pereopods well-developed. Second maxilliped not well differentiated. Telson straight bearing three spines on margin and well-developed lateral spine on each side, with 12 spines on each side of midline.

Habitat. Pelagic.

Location. SAVNP.

Lysiosquilla sp.

Stage (Indeterminate): Antizoea (CNCR32475)
(Fig. 3I)

Description. Carapace globular, widening at base of anterolateral spines, slightly triangular. Rostral spine as long as half length of carapace; lacking ventral spines, bearing strong and slightly curved posterolateral spines;

middle spine present. Pereopods well developed. Second maxilliped not well differentiated. Telson straight bearing three lateral spines; posterior margin bearing well-developed posterolateral spine on each side, with four short submedian spines, followed by long and two short spines on each side of midline; cleft present at midline.

Habitat. Pelagic.

Location. SAVNP.

Lysiosquilla scabricauda (Lamarck, 1818)

Stage (Indeterminate): Erichthus (CNCR32476) (Fig. 3J)

Description. Carapace extremely large, extending to third pleonite, rectangular, with very short anterolateral and posterolateral spines. Rostrum long, as long as half length of carapace; with three ventral spines, widened at base, triangular in shape. Pleon thick, last 2 pleomeres present spinules on posterolateral margin. Second maxilliped well developed; propodus with nearly 50 minute denticles; dactylus unarmed. Telson straight lacking well-differentiated median carina. Uropods well developed.

Habitat. Benthic, seagrass.

Location. Isla Sacrificios, SAVNP.

Family Nannosquillidae Manning, 1980

Nannosquilla adkisoni Camp and Manning, 1982

Stage (Indeterminate): Erichthus (CNCR32477) (Fig. 3K)

Description. Carapace longer than wide, with pair of small anterolateral spines. Rostrum half length of carapace, without ventral spines. Extremely long posterolateral spines reach beyond telson. Second maxilliped bearing 25–28 denticles; dactyl bearing six teeth. Spines of basal prolongation of uropod of same size. Telson straight with three movable spines on posterior margin, large lateral spines and eight denticles on each side of midline, with 2–9 spines between each pair of denticles. Uropods well developed, with spines on exopod.

Habitat. Benthic, among rubbles.

Location. APMNP.

Superfamily Squilloidea Latreille, 1802

Family Squillidae Latreille, 1802

Alima neptuni (Linnaeus, 1768)

Stage IV: Alima (CNCR32478) (Fig. 4A)

Description. Carapace three times longer than width, extending to middle of fourth pereonite, with pair of small anterolateral spines, bearing pair of posterolateral spines reaching base of sixth pereonite, presenting small spinule and small spine proximally; margin of carapace convex. Rostrum small, reaching half of A1. Second maxilliped with proximal spine; propodus eight times as long as wide, distal portion of upper margin pectinate with 28–29 denticles; dactylus bearing three teeth. Telson convex, twice as long as wide, bearing eight intermediate and 12 submedian denticles on either side of midline.

Habitat. Pelagic.

Location. SAVNP.

Stage IX: Alima (CNCR32479) (Fig. 4B)

Description. Carapace three times longer than wide, extending to sixth pereonite; bearing strong anterolateral spines that reach eighth pereonite; posterolateral spines much less pronounced than anterolateral ones; bearing small dorsal spine; margin of carapace strongly convex, armed with 12 spines. Antennules, maxillipeds and pleopods well developed. Second maxilliped with spine on basal portion, propodus eight times as long as wide, dorsodistal margin pectinate with 30–32 denticles; dactylus bearing six teeth. Telson convex, twice as long as wide, bearing intermediate, submedian and lateral spines, all with movable apexes, bearing

18 intermediate denticles between lateral spine and submedian, and 14 denticles between submedian spine and intermediate spine.

Habitat. Pelagic.

Location. SAVNP.

Squilla sp. 1

Stage IX: Alima (CNCR32480)
(Fig. 4C)

Description. Carapace three times longer than width, reaching sixth pereonite, concave margin with nine spines on each side, presenting pair of anterolateral spines, pair of short posterolateral spines extending to fifth pereonite, with small dorsal spine. Antennules, maxillipeds and pleopods well developed. Second maxilliped with spine on basal portion, propodus eight times as long as wide, distal portion of upper margin pectinate with 28–29 denticles; dactyl smooth. Telson concave, ornamented with defined medium carina, presents 10 intermediate denticles and 18 submedian spines on each side of midline.

Habitat. Pelagic

*Locatio*n. SAVNP and APMNP.

Squilla sp. 2

Stage II: Alima (CNCR32481)
(Fig. 4D)

Description. Carapace triangular, slightly convex, with three pairs of spines on posterolateral margin, presenting pair of anterolateral spines, pair of extremely long posterolateral spines reaching middle of telson, bearing proximal spine at base. Rostrum long, twice as long as A1, lacking ventral spines. Second maxilliped elongate; propodus with strong terminal tooth followed by seven denticles on inner margin; dactylus with distal portion of cutting edge as small saw. Telson concave, slightly longer than wide, with six intermediate denticles and nine submedian denticles on either side of midline.

Habitat. Pelagic.

Location. SAVNP.

Squilla empusa Say, 1818

Stage I: Alima (CNCR32482)
(Fig. 4E)

Description. Carapace slightly longer than broad, moderately globose; convex margin armed with four ventral spines on each side; with pair of anterolateral spines and dorsal medial spine. Rostrum extending slightly beyond flagellum of A1; lacking ventral spines. Posterolateral spines armed with ventral spine extending to fourth pleonite. Second maxilliped large; propodus with strong terminal tooth followed by 18 to 19 denticles on inner margin; dactylus with distal portion of cutting edge as small saw. Telson concave, bearing four pairs of intermediate and 15 submedian denticles covered with spinules.

Habitat. Pelagic.

Location. SAVNP.

Stage II: Alima (CNCR32483)
(Fig. 4F)

Description. Carapace longer than wide and moderately globose; convex margin armed with four ventral spines on each side; bearing pair of anterolateral spines and dorsal medial spine. Rostrum reaching beyond flagellum of A1; bearing four ventral spinules. Posterolateral spines armed ventrally with spine extending to base of telson. Second maxilliped elongate; propodus bearing proximal tooth followed by another large tooth and 19–20 denticles along inner margin; dactylus with distal portion of cutting edge as small saw. Telson concave, bearing four pairs of intermediate and 15 submedian denticles covered with spinules.

Habitat. Pelagic.

Location. SAVNP.

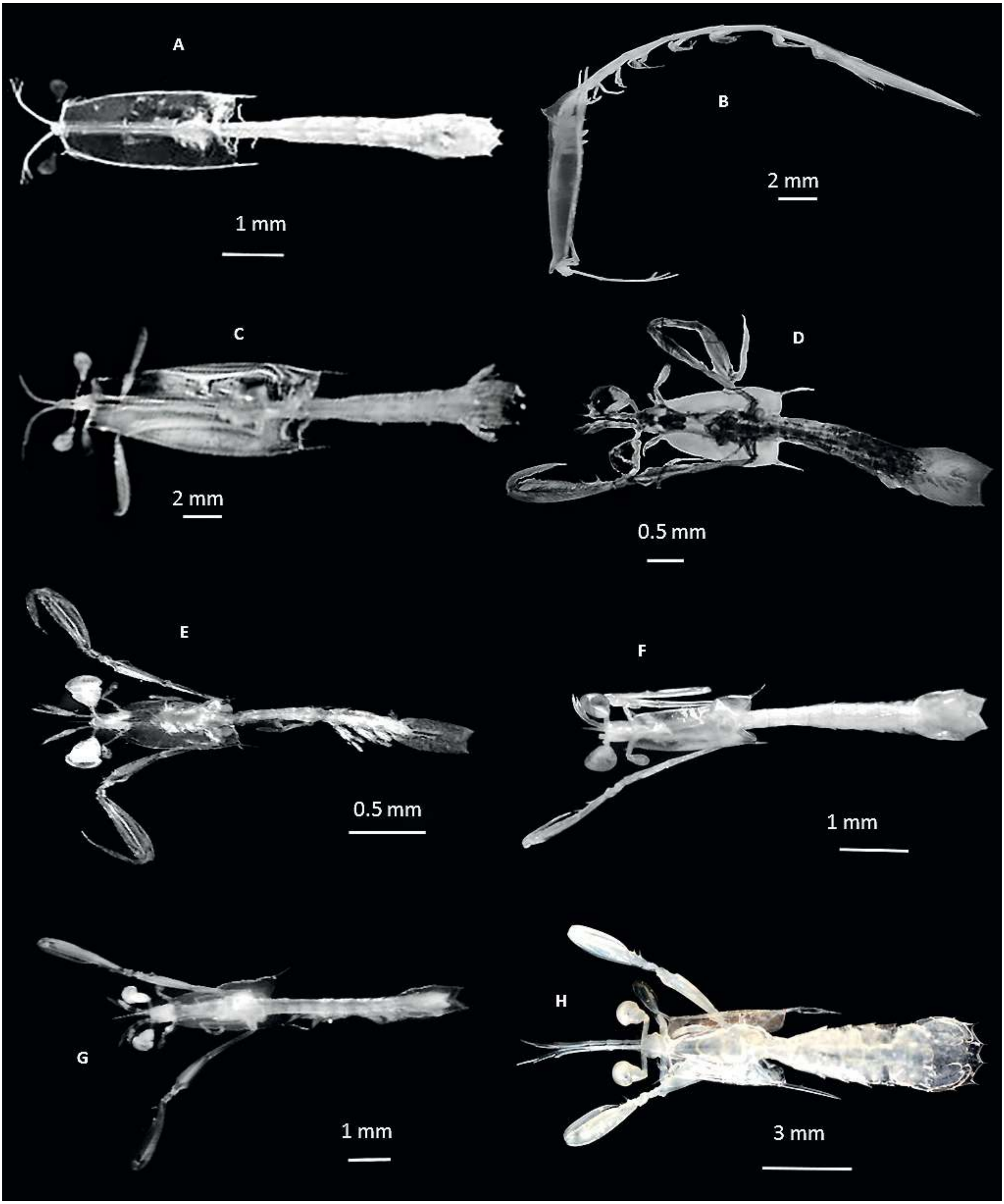

Figure 4. Stomatopod larvae collected at the national parks Sistema Arrecifal Veracruzano (SAVNP) and Arrecife Puerto Morelos (APMNP). A, *Alima neptuni* (Linnaeus, 1768), stage IV alima; B, *A. neptuni* stage IX alima; C, *Squilla* sp. 1, stage IX alima; D, *Squilla* sp. 2, stage II alima; E, *Squilla empusa* Say, 1818, stage I alima; F, *S. empusa*, stage II alima; G, *S. empusa*, stage III alima; H, S. *empusa*, stage IX alima.

Stage III: Alima (CNCR32484)
(Fig. 4G)

Description. Carapace longer than wide, trapezoid, convex margin armed with two anterior and three posterior ventral spinules on each side, with pair of anterolateral spines and one dorsal medial spine. Rostrum long, twice as long as A1; bearing more than four ventral spines. Posterolateral spines armed ventrally with spine extending to end of telson. Second maxilliped large; propodus bearing 24–26 denticles, basis bearing proximal spine well developed; dactylus with distal portion of cutting edge as small saw. Telson concave with 8–10 pairs of intermediate denticles and 15–27 submedian denticles covered with spinules.

Habitat: Pelagic.

Location. SAVNP.

Stage IX: Alima (CNCR32485)
(Fig. 4H)

Description. Carapace longer than wide, trapezoid, convex margin armed with two anterior and three posterior ventral spinules on each side, bearing pair of anterolateral spines and one dorsal medial spine. Rostrum long, twice as long as A1, presenting 2–6 ventral spines. Posterolateral spines armed with ventral spinule extending to posterior part of telson. Maxillipeds, pereopods, pleopods and uropods well developed. Second maxilliped elongate; propodus with 71–92 denticles; dactylus smooth. Telson concave, with 8–10 pairs of intermediate denticles and 26–34 submedian denticles covered with spinules.

Habitat. Benthic, among rubbles.

Location. APMNP.

Discussion

The most recent account of species of adult stomatopods in the Gulf of Mexico and Caribbean Sea lists 45 species contained in four superfamilies and 11 families (Reaka *et al.* 2009; García-Calzada, 2013). Only four complete larval development of the 45 species found in the area have been described in laboratory (Manning and Provenzano, 1963; Provenzano and Manning, 1978; Morgan and Provenzano, 1979; Morgan and Goy, 1987; Rodrigues and Manning, 1992). We found larval stages of nine of those species at the SAVNP and four at the APMNP. Although the number represents only a fifth of the total number of species reported for this area, it is remarkable since it is only the first study on the morphology of stomatopod larvae for the south of the Gulf of Mexico and the Caribbean Sea.

We were able to identify larvae of two of the seven species of *Neogonodactylus* Manning, 1995 present in the study area, *N. wennerae* and *N. oerstedii*, although we only found two and four stages of *N. wennerae* and *N. oerstedii*, respectively. The complete larval development has been described for both species from specimens cultured in laboratory conditions (Manning and Provenzano, 1963; Provenzano and Manning, 1978; Morgan and Goy, 1987). These two species present three propelagic and four pelagic stages (Morgan and Goy, 1987). From those we found a pseudozoea and five erichthus. To differentiate these two species in stage IV erichthus we used the number of aesthetascs on first maxilliped as a diacritic character; *N. wennerae* presents six aesthetascs, while *N. oerstedii* presents eight. These two species are a rare example of the complexity of the larval development of stomatopods. During their long larval development, which takes five weeks in laboratory conditions (Provenzano and Manning, 1978), their first three larval stages are propelagic and the other four are planktonic (Dingle 1969; Provenzano and Manning 1978). Distribution in the water column of these larval stages is not a mere accident; the propelagic larvae do not hunt, they are lecitotrophic.

In addition, they present two behaviors that make them unique among crustaceans, they are thigmokinetic and present negative phototaxis. Thus, they feed on embryonic material, hide from light and grab any solid that comes in contact with them (Dingle, 1969). The result is that they keep hiding under the protection of the mother (Dingle, 1969). Thus, our finding of one of these propelagic stages is remarkable since most of the time only the pelagic stages will be found. These pelagic stages change dramatically the morphology and habits of the larvae. For instance, they will become planktotrophic (will actively hunt), will be attracted to light (positive phototaxis) and their thigmokinesis will be reduced (Dingle, 1969).

On the other hand, we were able to identify the larvae of *A. neptuni* because of the size and morphological characters of both the carapace and telson. Larva of this species was described based on plankton samples (Manning, 1962, as *A. hyalina* Leach, 1817). There are two species of *Alima* distributed in the West Atlantic, *A. neptuni* and *Alima hildebrandi* (Schmitt, 1940). The former has been found in the Gulf of Mexico and Florida Keys, besides some other localities in the West Atlantic, while the latter is considered to be of amphi-Atlantic distribution, although never found within the Gulf of Mexico (Reaka *et al.*, 2009). In this study *A. neptuni* was represented by two larval stages.

The superfamily Lysiosquilloidea was represented by larvae of an unidentified genus and species of Lysiosquilloidea and an unidentified species of *Lysiosquilla*; both were found in the stage of antizoea (first phase of the larval development). Thus, the morphological characters used for identification were referred to Townsley (1953), who reported birramous thoracic appendages, where propodus of the four thoracic appendages are rounded, broader than long, and more than twice the fifth appendage. The telson is straight. In addition, we also identified one of the last larval stages of *L. scabricauda*. The larva can be traced back to the adult based on characters of the telson, the shape of the corneas and the edge of pereonites as reported by García-Calzada (2013). The most current literature recognizes two species of *Lysiosquilla* within the Gulf of Mexico and adjacent waters (Reaka *et al.*, 2009). These are *Lysiosquilla campechiensis* Manning, 1962 and *L. scabricauda*. We were able to recognize one larvae of *L. scabricauda*. However, we were unable to identify a second larval specimen of *Lysiosquilla* sp. Since there are two other species of this genus distributed in the study area, it may well be that the second larva belongs to one of those species, or even to *Lysiosquillina glabriuscula* (Lamarck, 1818) that is also distributed within the Gulf of Mexico. However, Giesbrecht (1910) has described nine pelagic stages for *Lysiosquilla* sp. but the adult form was not described. For the time being we cannot place our larva in any of those species of *Lysiosquilla* or *Lysiosquillina glabriuscula*. We wait either for a complete description of the larval development based on larvae reared on laboratory conditions or for a DNA analysis allowing the identification of our specimen.

The characters of Pseudosquillidae fit the description of other members of this genus (Brooks, 1886; Townsley, 1953). The telson is nearly rectangular, with eight denticles between submedian denticles and the eyes are not borne on long stalks as in alima of *Squilla*. The second maxilliped has the propodus finely pectinated along the upper margin and a dactylus with a single spine; the carapace is trispinous anteriorly, posteriorly bearing two long spines reaching the second pleonite. Considering the adult distribution and the observed characters, this individual may correspond to a specimen of *Pseudosquilla ciliata* (Fabricius, 1787) in its early larval stages. However, we could not place it based only on morphological characters and it remains as Pseudosquillidae. It is noteworthy that Townsley (1953) has described seven larval stages for this species.

Morgan and Provenzano (1979) reported that *S. empusa* undergoes nine pelagic stages before attaining the postlarval stage. Likewise, the authors mentioned that larvae of *S. empusa* may be identified by the spinules of the carapace and the intermediate denticles of the telson; stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles; the third to ninth stages are armed with six spinules on the lateral margin of the carapace; there are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed; the telson of the stages third to ninth have 8 to 10 intermediate denticles. The species *Squilla* sp. 2 shows all the characters of the larvae alima like the ornamentation on the telson, characteristic of the genus. However, it does not correspond with the description of *S. empusa*, due to the shape of the carapace. In *Squilla* sp. 2 the carapace is triangular, with three pairs of spines on lateral margin; in contrast, the carapace of *S. empusa* is longer than wide and moderately globose and the lateral margin is armed with four ventral spines on each side. Likewise, the larvae alima of *Squilla* sp. 1 in stage IX is larger and wider than *S. empusa* in the same stage. There are also differences in the ornamentation of the second maxilliped and telson. Thus, we are certain that these two larval stages, *Squilla* sp. 1 and *Squilla* sp. 2, fit the general morphology of *Squilla*. However, at this time we are unable to identify to species level these two specimens that could belong to any of the three species distributed in the area of study, *Squilla chydaea* Manning 1962, *Squilla edentata edentata* (Lunz, 1937) or *Squilla rugosa* Bigelow, 1893.

This study shows how it is possible to identify the larvae collected in zooplankton samples, even with only a few studies available describing a small number of stomatopod species. At the same time, it also shows that our knowledge about stomatopod larvae is scarce. It should be noted that if larval descriptions are scarce, the knowledge about their ecology is almost nonexistent. Some of the reasons for this lack of information are due to the complexity of the life history of these critters, as discussed above. Most of the observed characters agree with the original descriptions, which allowed the identification at specific level, although some differences were found. In others studies, it has been reported that there is an important variability in the intraspecific morphological characters of larvae reared under controlled conditions. Likewise, there is an important morphological variation of a species found in different regions (Criales and Anger, 1986; Pechenik, 1999; González-Gordillo and Rodríguez, 2000). The variety in the morphology of these larvae clearly shows extreme adaptations that we still do not fully understand.

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