Intraspecific variation in megalopae of *Clibanarius antillensis* (Anomura, Diogenidae) among western Atlantic populations

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ABSTRACT

The objective of this study was to describe the morphology of *Clibanarius antillensis* Stimpson, 1859 megalopae collected in the vicinity of Isla Sacrificios, Mexico, and compare it to previous descriptions originated from Brazilian and Panamanian specimens raised in laboratory conditions. We found four meristic differences between the Brazilian and the Panamanian and Mexican populations with the Brazilian population: the outer flagellum of antennule in the Panamanian and Mexican populations has more aesthetascs on the second, third, and fourth segments of the outer flagellum (0, 6, 5, 3, 0) than the Brazilian population (0, 4, 4, 2, 0); the maxilla has more setae on the scaphognathite in the Brazilian specimens (70) than in the Mexican and Panamanian specimens (49-62); the crista dentata of the third maxilliped is formed by only three denticles in the Brazilian specimens, while 4 or 6 denticles form the same structure in the Panamanian and Mexican populations; there are fewer number of setae on the endopod of the uropod in the Brazilian population. The differences may be explained by intraspecific variation.

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KEY WORDS

Crustacea, Anomura, interspecific variation, megalopa stage, taxonomy.

INTRODUCTION

The genus *Clibanarius* Dana 1852 is represented by 60 species worldwide (Lemaitre and McLaughlin, 2018); four of these species can be found in the Gulf of Mexico, *Clibanarius antillensis* Stimpson, 1859, *C. sclopetarius* Herbst 1796, *C. tricolor* (Gibbes, 1850), and *C. vittatus* (Bosc, 1802) (Felder *et al.*, 2009). These four species have also been reported in Veracruz (Álvarez *et al.*, 2011). Recent plankton studies performed in the Parque Nacional Sistema Arrecifal Veracruzano (PNSAV), on the southwestern Gulf of Mexico, have found megalopae of eight species of hermit crabs of the family Diogenidae: *Calcinus tibicen* (Herbst, 1791), *Clibanarius antillensis*, *C. sclopetarius*, *C. vittatus*, *Dardanus insignis* (de Saussure, 1858), *Paguristes sericeus* A. Milne Edwards, 1880, *P. spinipes* A. Milne-Edwards, 1880, and *Petrochirus diogenes* (Linnaeus, 1758) (Cházaro-Olvera *et al.*, 2013).

Bartilotti *et al.* (2008) described the complete larval development of two species of *Clibanarius*. While doing so, the authors reviewed morphological larval characters among species of the genus. In general, larval development within the genus is very homogenous, consisting of four or five zoeal stages and one megalopa. However, morphometry of the larval stages varies within the genus and species can be identified based on specific larval characters (Siddiqui *et al.*, 1991; 1993; Bartilotti *et al.*, 2008). Although morphology of larval characters are believed to be species-specific, some morphological variations have been found among larval developmental stages described under laboratory conditions of *C. antillensis* from Brazil (Brossi-Garcia and Hebling, 1983) and Panama (Siddiqui *et al.*, 1991); these morphological variations are believed to be the result of geographic differences and/or differing laboratory conditions (Siddiqui *et al.*, 1991; Bartilotti *et al.*, 2008).

The distribution of the hermit crab *C. antillensis* extends throughout the western Atlantic including Bermuda, Eastern Florida, Gulf of Mexico, Caribbean Sea, and Brazil (Felder *et al.*, 2009). Within-species larval variations in decapod crustaceans are not uncommon in the marine environment. In particular, latitudinal variations have been explained by increased seasonality and unpredictability of primary productivity: a macro-ecological gradient is formed, and it modifies the number of larval instars or the morphology in the same stage of development in some marine crustaceans (Anger, 2001; Oliphant *et al.*, 2013). The objective of this study was to compare the morphology of the megalopa of *C. antillensis* collected at the PNSAV to those reared in laboratory conditions from both Brazilian and Panamanian populations.

MATERIAL AND METHODS

The PNSAV 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 northern and southern groups, which are separated by the mouth of the Jamapa River (Granados *et al.*, 2007) (Fig. 1).

Megalopae were collected using light traps placed off the northwest of Isla Sacrificios for three consecutive nights, on June 2015. These collecting cycles were initiated at 21:00h and stopped at 01:00h on the next day during the new moon phase. The temperature recorded was almost invariable (28 to 29 °C), and salinity was 35 psu. All traps were constructed with plastic boxes that were 0.4 m long, 0.25 m wide and 0.30 m high, with 40 mm diameter inlet holes in the upper part of each side of the box; the box contained a white light of 38 lumens (Fig. 2). Trap contents were collected manually and placed in 500 ml plastic bottles at the end of the sampling period. All samples were preserved in 70% ethanol.

Samples were sorted by using a Motic SMZ-168 microscope at the Crustacean Laboratory, FES Iztacala, UNAM. Identification of the larvae followed current literature (Lang and Young, 1977; Brossi-Garcia, 1987; Sidiqui *et al.*, 1991; Bartilotti *et al.*, 2008; Cházaro-Olvera *et al.*, 2013). After closer inspection, identification of the megalopae of *C. antillensis* followed two publications (Brossi-Garcia and Hebling, 1983; Siddiqui *et al.*, 1991). We obtained morphometric and meristic features of 96 specimens. Measurements of the carapace length, carapace width, total length and number of segments, setae and spines of the carapace, antennule, antenna, mandible, maxillule, maxilla, maxilliped 1, maxilliped 2, maxilliped 3, chelipeds, walking legs, fourth and fifth pereopods, pleon, pleopods, telson and uropods were taken. We also counted the number of spines and denticles of the different structures. The descriptions of these morphological characters were made following

Figure 1. Sampling station northwest off Sacrificios Island (*), Sistema Arrecifal Veracruzano.
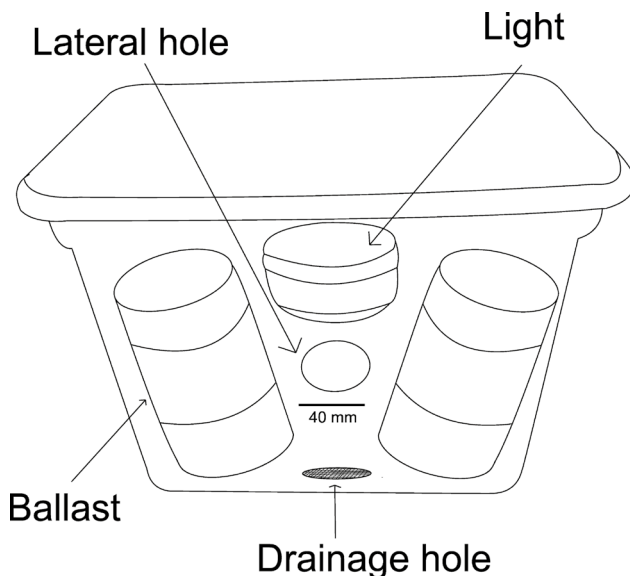

Figure 2. Light traps for collecting megalopae of *Clibanarius*.

Clark *et al.* (1998), while setal classification followed that proposed by Garm (2004). Images of the larvae were taken using a Leica DM750 microscope equipped with an Omax 14MP USB 3.0 digital camera. The illustrations were made with the Corel Draw V.12 program.

RESULTS

We found 2,795 larvae of the genus *Clibanarius*: 968 of these were identified as *C. antillensis*, 656 as *C. sclopetarius*, and 1171 as *C. vittatus* (Tab. 1). We were able to differentiate the species *C. antillensis* from *C. sclopetarius* and *C. vittatus* considering the total length, number of aestethascs in the external flagellum of the antennule, number of segments of the antenna, number of segments of the palp of the mandible and the number of plumose marginal setae in the endopod and exopod of uropods (Tab. 2).

Table 1. Abundance of *Clibanarius* species in the sampling area.

Species	Sampling time					Total
	21:00	**22:00**	**23:00**	**00:00**	**01:00**	
Clibanarius antillensis	216	443	291	13	5	968
Clibanarius sclopetarius	327	211	86	25	7	656
Clibanarius vittatus	542	364	242	16	7	1171
Total	1085	1018	619	54	19	2795

Table 2. Comparison of relevant megalopae features of *Clibanarius antillensis*, collected from a Mexican population to those obtained in laboratory conditions from Brazilian (Bra) (Brossi-Garcia and Hebling, 1983) and Panamanian (Pan) populations (Siddiqui *et al.*, 1991). The same features are compared to *C. sclopetarius* and *C. vittatus* collected in the same area ([1], Brossi-Garcia, 1987; [2], Lang and Young, 1977; * obtained from the figure).

Feature	*C. antillensis* (Bra)	*C. antillensis* (Pan)	*C. antillensis* (Mex)	*C. sclopetarius*[1]	*C. vittatus*[2]
Total length (mm): antennule	2.50-2.60*	2.70-2.90	2.00-2.30	3.40-3.50*	3.20-4.10
Outer flagellum five segments/aesthetascs	0, 4, 4, 2, 0	0, 6, 5, 3, 0	0, 6, 5, 3, 0	0, 6, 5, 2, 0	0, 4, 4, 3, 0
Antenna flagellum: segments	10	10	10	10	11
Mandible: segments	2	2	2	3	3
Maxilla: scaphognathite setae	70	49-55	50-55	52	60
Second maxilliped: exopod setae	9	7-8	8	7	6-8
Third maxilliped: crista dentata denticles	3	5-6	4-6	4-5	-
Uropod: endopod setae/scales	9-10/4	11-14/5-7	11-14/5-7	8-10/5-6	11-14/5-7
Uropod: exopod setae/scales	19-20/8-10	19-21/8-12	19-21/8-12	11-14/5-6	12-20/6-7

We found intrapopulation variation for seven characters of the megalopa of *C. antillensis*, size (2.0–2.3mm TL), number of setae on the scaphognathite of maxilla (50–55), number of denticles of crista dentata (4–6), and number of setae on the protopod (0–4), endopod (11–14), and exopod (19–21) of uropods (Tab. 2). When comparing the same characters to other populations of *C. antillensis*, we also found inter-population differences, which are described below in the remarks section.

Clibanarius antillensis Stimpson, 1859

Megalopa

Size (Fig. 2A). Carapace length = 0.9–1.1 mm; carapace width = 0.7-0.81 mm; total length = 2.0–2.3 mm; n = 96.

Carapace (Fig. 3A). Longer than broad, with few scattered setae; rostrum triangular; ocular peduncles bulbous, reaching half of distal segment of antennular peduncle.

Antennule (Fig. 3B). Biramous. Peduncle 3-segmented; basal segment with 6 simple setae, 1 strong seta at ventrodistal angle; penultimate segment with 3 subterminal setae, 2 simple terminal setae; basal segment with 2 subterminal, 4 short terminal setae. Endopod 3-segmented, with 1, 4, 6 (3 subterminal, 3 terminal) setae, respectively. Exopod with 5 segments, aesthetascs as 0, 6, 5, 3, 0, last segment with 3 subterminal and 1 long terminal setae.

Antenna (Fig. 3C). Basal segment not delineated. Second segment with angular process ending on tip, third segment with 5 simple marginal setae. Flagellum with 10 segments, with setae from proximal to distal segment: 0, 3, 4, 5, 4, 5, 5, 6, 5, 9 (6 subterminal and 3 terminal). Exopod reduced, with 5 plumose marginal setae.

Mandible (Fig. 3D). Reduced, simple; palp 2-segmented, 9 marginal serrate setae.

Maxillule (Fig. 3E). Coxal endite with 17 serrate setae. Basal endite with 3 plumose intermediate, 12 cuspidate, 7 serrate setae. Endopod with well-developed internal lobe, with 1 simple long terminal seta, external lobe recurved.

Maxilla (Fig. 3F). Coxal endite with 2 plumose subterminal, 4 terminal setae. Basal endite with 10 plumose setae at distal lobe and 5 at proximal lobe. Endopod narrow, significantly twisted, not lobed, without setae. Scaphognathite elongate, proximal free lobe of protopod, with 55 to 60 plumose marginal setae.

Maxilliped 1 (Fig. 3G). Coxal endite with 5 cuspidate, 10 plumose submarginal setae. Basal endite with 5 cuspidate, 11 marginal plumose setae. Endopod 1-segmented and narrow. Exopod 1-segmented, with 9 plumose marginal setae.

Maxilliped 2 (Fig. 3H). Endopod 4-segmented, with 1 or 2, 2, 7, 5 or 6 plumose setae. Exopod 2-segmented, 8 or 9 plumose terminal setae, 1 or 2 plumose setae on inner margin.

Maxilliped 3 (Fig. 3I). Endopod 5-segmented; crista dentata on proximal segment with 4 to 6 denticles, 2 subterminal, 5 simple terminal setae, second segment with 2 simple subterminal setae, 2 simple terminal setae, third segment with 11 subterminal setae, 5 terminal setae, 5 marginal setae, fourth segment with 13 plumose setae and fifth segment with 7 plumose setae. Exopod 2-segmented, with 1 simple marginal seta, 8 plumose terminal setae.

First pereiopod (chelipeds) (Fig. 3J). Chelae equal, with segments smooth; coxa with 3 simple setae; basis with 6 simple setae; ischium with 5 simple setae; merus, longest segment, with 8 simple setae; carpus with 6
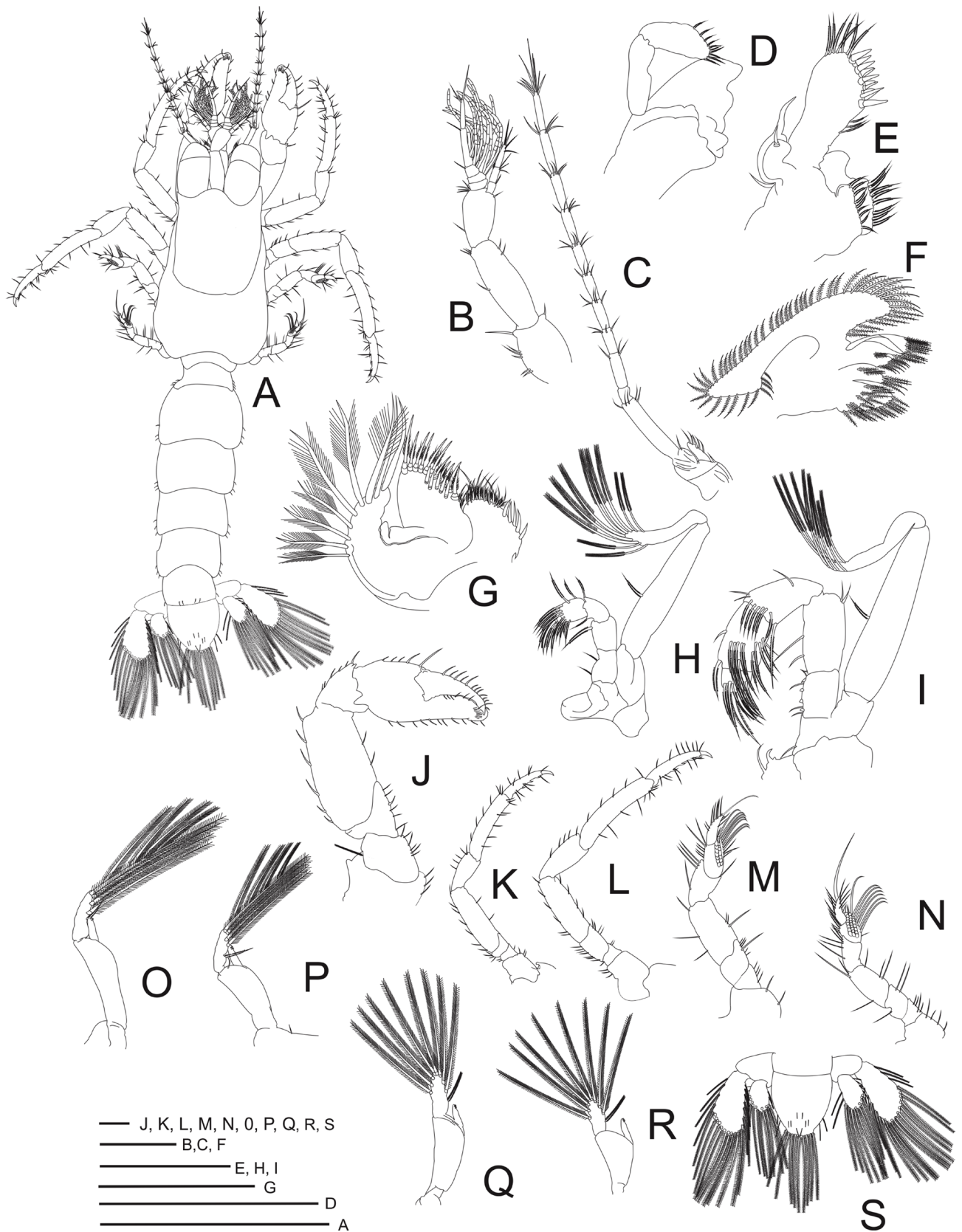
Figure 3. *Clibanarius antillensis*. Megalopa: A, dorsal view; B, antennula; C, antenna; D, mandible; E, maxillula; F, maxilla; G, maxilliped 1; H, maxilliped 2; I, maxilliped 3; J, cheliped; K, second pereiopod; L, third pereiopod; M, fourth pereopod; N, fifth pereopod; O-R, pleopods of abdominal somites; S, telson and uropods. Scale bars: A = 1.0 mm, B-S = 0.1 mm.

simple setae; propodus with 16 simple setae, distal upper extremity corneous; dactyl length about half palm including the propodal prolongation, with 16 simple setae and distal extremity corneous.

Second pereiopod (Fig. 3K). Coxa with 2 simple setae; basis smaller with 3 simple setae; ischium with 4 simple setae; merus, longest segment, with 9 simple setae; carpus less than half the ischium length, with 5 simple setae; propodus longer than carpus, with 15 simple setae and; dactylus very stout, apically curved with corneous tip, with 11 simple setae and 3 spines.

Third pereiopod (Fig. 3L). Coxa with 3 simple setae; basis with 3 simple setae; ischium with 11 simple setae; merus longer than ischium and with 10 simple setae; carpus with 5 simple setae; propodus longer than carpus, with 14 simple setae and 3 stout cuspidate seta; dactylus very stout, apically curved and corneous, with 16 simple setae and 4 spines.

Fourth pereiopod (Fig. 3M). Coxa with 2 simple setae; basis with 4 simple setae; ischium with 4 simple setae; merus with 6 simple setae; carpus with 5 simple setae; propodus, with 5 simple setae and 17 pseudochaetae scales forming protopodal plate; dactyl with 1 long papposerrate seta, 7–9 simple setae and 3 teeth on distal extremity.

Fifth pereiopod (Fig. 3N). Coxa with 4 simple setae; basis with 4 simple setae; ischium with 3 simple setae; merus with 6 simple setae; carpus with 5 simple setae; propodus, with 6–7 long papposerrate, 10–11 simple setae and 23 pseudochaetae scales; dactyl with 7 simple setae, 1 long papposerrate distal and 5 pseudochaetae scales.

Pleon (Fig. 3A). Pleonites 2–5 with rounded posterolateral angles, lateral margins with 3 simple short setae; pleonite 6 with 4 simple setae at posterior dorsal margin and 2 simple setae at posterolateral angles.

Pleopods (Figs. 3O–R). Pleopod developed on pleonites 2–5, decreasing in size distally. Endopod unsegmented, with pair of hooks at apical margin. Exopods 2-segmented with 9 plumose setae.

Uropods (Fig. 3S). Segment protopodal with 0–3 simple setae. Endopod with 1 or 2 simple setae on dorsal surface, 11–14 plumose marginal setae and 5–7 corneal scales; Exopods with 0–4 short plumose setae on dorsal surface, 19–21 plumose marginal setae and 8–12 corneous scales.

Telson (Fig. 3S). Shape rounded posterior margin, with 9 posterior plumose marginal setae, 2 pairs of submarginal short plumose setae, 4 pairs of short simple setae on dorsal surface.

Remarks. We found four meristic differences among the Brazilian (Brossi-Garcia and Hebling, 1983) the Panamanian (Siddiqui et al., 1991) and Mexican populations (Tab. 1). The antennule in the Panamanian and Mexican populations had more aesthetascs on the second, third and fourth segments (0. 6, 5, 3, 0) with respect to the Brazilian population (0, 4, 4, 2, 0). There were fewer plumose setae on the scaphognathite in the Panamanian and Mexican populations (49–55) with respect to the Brazilian population (70 plumose setae). In the second maxilliped, the difference was of 1 seta, whereas in maxilliped 3, there were 1–3 fewer denticles in the Brazilian population on the crista dentata. The exopod of the uropod had fewer (10) marginal plumose setae in the Brazilian population.

DISCUSSION

We identified hundreds of larvae of *C. antillensis*, *C. sclopetarius*, and *C. vittatus* and the observed key characters of the megalopa of *C. sclopetarius* and *C. vittatus* corresponded to those observed in the literature (Lang and Young, 1977; Brossi-Garcia, 1987). Thus there was no doubt concerning the identity of the megalopae of *C. antillensis* collected; such variations in morphology of the megalopae must be explained.

We found that the Panamanian and Mexican populations were morphologically more similar in the number of aesthetascs on the antennule, setae on the scaphognathite, second maxilliped, number of denticles on the crista dentate and number of setae on the exopod of the uropod.

There are two potential explanations for such differences: either these differences are the result of intraspecific variations, probably following a latitudinal gradient or there are two cryptic taxa, currently unrecognized: one distributed mainly in Brazil and another distributed in the Caribbean, Mexico and the USA.

In the first option, McLaughlin and Gore (1988) showed that it is highly probable that considerable developmental differences can occur between geographically separated populations. The differences during larval development relate to the changes in environmental conditions, such as the mixture of water masses, food deficiency or changes in temperature

and salinity. This flexibility is an evolutionary and ecological strategy which enhances survival and allows the distribution of the larvae to be extended (Welch and Epifanio, 1995; Hartnoll, 2001; Thatje and Bacardit, 2000; Negreiros-Fransozo *et al.*, 2008). In this respect, Tirmizi and Siddiqui (1980), McLaughlin and Gore (1988) and Siddiqui *et al.* (1991) found differences in the setation and spination of *Pagurus kulkarnii* Sankolli, 1962, *Pagurus hirsutiusculus* (Dana, 1851) and *C. antilliensis.* Furthermore, the morphological variability increases in the later larval or decapodid stages. For example, in *Crangon crangon* (Linnaeus, 1758), in the first decapodid stage, at least two forms can be distinguished, differing primarily in the developmental state of the antennae, the maxillipeds, the pereiopods, and the pleopods (Linck, 1995). Brossi-Garcia and Hebling (1983) found more setae on the scaphognathite of the maxilla of the Brazilian population; this could be explained by the availability of food affecting the life cycle of many benthic marine invertebrates, with significant implications for their survival, growth and metamorphosis (Calado and Leal, 2015; Pechenik and Tyrell, 2015). It has been found that the morphology of the feeding structures is more developed in the megalopa and juveniles, and the mouthparts present an increasing number of setae compared to previous developmental stages, which indicates that these stages are more able to capture food and they are capable of processing solid food available in their benthonic environment (Abrunhosa *et al.*, 2006). The ability to process small food particles increases because of the increment in the size of the foregut and the number of setae on the mouthparts (Abrunhosa and Melo, 2008). The phytoplankton is most abundant in high latitudes and in upwelling zones along the equator and near coastlines. However, phytoplankton is scarce in the subtropical regions, where nutrient levels are low and drop off in the summer (NASA, 2018).

For the second potential explanation, we were considering genetically comparing different populations of *C. antillensis* since it has been shown that cryptic species do occur among species of this genus. Furthermore, Negri *et al.* (2014) found morphological and genetic differences strong enough to resurrect *C. symmetricus* (Randall, 1840). This species was reported for many years under the name *C. vittatus* because of their close morphological similarities. The authors defined the genetic divergences between *C. vittatus* and *C. symmetricus,* identifying that the latter species may occur more broadly in the Caribbean, the Antilles, or the southern Gulf of Mexico. Similar to *C. vittatus*, *C. antillensis* has a broad range in the western Atlantic, from the southeastern coast of the United States, and from Bermuda to Brazil (Felder *et al.*, 2009), although the distribution is not continuous, so differences might be found. While the present study was in review, we were not aware that Nishikawa (2017) already preformed a robust and representative sampling with two molecular markers (16S and COI) and found no genetic structure among different western Atlantic populations of *C. antillensis*, including populations from Mexico, Panama and Brazil. Thus it appears that differences observed in the megalopa stage among geographically separated populations are the result of interpopulation variation.

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No potential conflict of interest was reported by the authors.

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