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ORIGINAL ARTICLE

Observations of life history traits of *Typton carneus* Holthuis, 1951 (Caridea, Palaemonidae): a poorly known sponge-dwelling shrimp

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ABSTRACT

The objective of this study was to investigate some life history traits of the palaemonid shrimp *Typton carneus* collected from a reef in northeastern Brazil. Samples of the sponges *Amphimedon compressa*, *A. viridis*, *Desmapsamma anchorata*, *Dysidea etheria*, *Haliclona implexiformis* and *Tedania ignis* were analyzed and shrimps were removed from them. A total of 41 individuals were found in *Te. ignis*, three in *H. implexiformis* and one in *D. etheria*; the latter two sponges are new records of sponge hosts for *Ty. carneus*. Of the specimens associated with *Te. ignis*, 24 were males, 10 ovigerous females, six non-ovigerous females and one juvenile male. Fecundity varied between 19 to 56 eggs (37 ± 14) per female, and the mean egg volume was 0.033 ± 0.010 mm^3. Eleven heterosexual pairs were obtained. Characteristics of the pairs suggest a monogamous mating system for the studied population, such as: the absence of sexual dimorphism in weaponry and body size and presence of paired non-brooding and brooding females carrying eggs in different development stages; and a sex ratio that does not differ from the expected 1:1. However, the lack of size-assortative pairing as well as the low proportion of pairs, compared to solitary individuals, have been observed in polygamous mating systems.

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Caridean shrimps, heterosexual pairing, Porifera, symbiosis, *Tedania ignis*.

INTRODUCTION

A wide range of caridean shrimps, those of the families Alpheidae Rafinesque, 1815, Anchistioididae Borradaile, 1915, Hippolytidae C.S. Bate, 1888, Lysmatidae Dana, 1852 and Palaemonidae Rafinesque, 1815, for example, have been reported in association with sponges (Bruce, 1976; Ďuriš *et al.*, 2011). However, for most species, the exact type of association is still unknown (Hultgren, 2014). Shrimps associated with other invertebrates exhibit specialized morphological characteristics; however, their adaptive value still needs to be better understood (Bauer, 2004; Ďuriš *et al.*, 2011). For example, palaemonid shrimps of the genus *Onychocaris* Nobili, 1904 and *Typton* Costa, 1844 have a vermiform body, a relatively short cephalothorax and an elongated pleon, which presumes adaptations to life in tubular sponge channels (Bruce, 1976). The interior architecture of many sponges, with a large network of channels of different diameters, provides a suitable habitat, not only for these shrimps, but for several other groups as well (Ďuriš *et al.*, 2011).

Species of *Typton* are usually smaller than 10 mm and are characterized by a laterally compressed rostrum with no teeth, mandible without palp, strongly asymmetrical second pair of pereopods and second pair of pleopods without *appendix masculina,* among other morphological features (Holthuis, 1951; Vieira *et al.*, 2012). These shrimps are known as sponge symbionts, where they are found alone or in heterosexual pairs (Ďuriš *et al.*, 2011). Overlapping generations, with juveniles remaining, at least initially, in the natal sponge, have been observed in some sponge-dwelling shrimps (Duffy, 2003). However, cases in which larvae are released into the water column, where they remain for days or weeks before settling into the benthos, have also been recorded (Duffy, 2003). When embryonic development is abbreviated or direct, larger eggs and high yolk amounts are expected (Bauer, 1991; Wehrtmann and Albornoz, 2002). If *Typton* shrimps experience such development, they are expected to have large embryos.

The genus currently includes 20 species distributed worldwide (De Grave and Fransen, 2011; Almeida *et al.*, 2014; Ayón-Parente *et al.*, 2015; Neves, 2020), of which seven have been recorded in Brazil: *Typton carneus* Holthuis, 1951, *Typton distinctus* Chace, 1972, *Typton fapespae* Almeida, Anker and Mantelatto, 2014, *Typton gnathophylloides*, Holthuis, 1951, *Typton prionurus* Holthuis, 1951, *Typton tortugae* McClendon, 1911 and *Typton vulcanus* Holthuis, 1951 (Coelho *et al.*, 2006; Vieira *et al.*, 2012; Almeida *et al.*, 2014; Pachelle *et al.*, 2015; 2016; Soledade *et al.*, 2017).

Typton carneus is distributed in the western Atlantic in western Florida, Bahamas, Barbuda, Cuba (Los Arroyos), Mexico (Bahia de la Ascensión), Haiti (Tortuga), Panama, Tobago, and Brazil (Fernando de Noronha, Ceará, Paraíba, and Pernambuco States), from 0 – 73 m depth (Holthuis, 1951; Chace, 1972; Coelho *et al.*, 2006; Román-Contreras and Martínez-Mayén, 2010; Vieira *et al.*, 2012; Pachelle *et al.*, 2016; De Grave and Anker, 2017). However, information about its biological aspects, such as interactions with its hosts and reproduction, is still wanting, and data is mostly limited to occurrences and associations with sponges (Holthuis, 1951; Chace, 1972; Ramos-Porto and Coelho, 1998; Vieira *et al.*, 2012; Pachelle *et al.*, 2016; De Grave and Anker, 2017). So far, the only specific study about this shrimp species analyzed its stomach contents, suggesting a possible parasitic habit on their sponge hosts (Ďuriš *et al.*, 2011). The objective of the present study was to address certain aspects of the life history of *Ty. carneus,* such as association with sponge hosts, breeding biology and heterosexual pairing (pairing frequency, sexual dimorphism between paired males and females, presence of size-assortative pairing) in a reef area in northeastern Brazil.

MATERIAL AND METHODS

Three specimens of the sponges *Amphimedon compressa* Duchassaing and Michelotti, 1864, *Amphimedon viridis* Duchassaing and Michelotti, 1864, *Desmapsamma anchorata* Carter, 1882, *Dysidea etheria* Laubenfels, 1936, *Haliclona implexiformis* Hechtel, 1965 and *Tedania ignis* Duchassaing and Michelotti, 1864 were collected monthly from reefs off Praia de Pontas de Pedra, Goiana Municipality, Pernambuco, northeastern Brazil (07°37'00"S 34°48'51"W) (Fig. 1) from September 2014 to February 2016. Collections were carried out during periods of spring low tide, totaling 54 specimens analyzed for each species. The sponges were collected by free diving in the shallow subtidal zone at a maximum depth of one meter. The sponge specimens were sampled with a minimum distance of five meters between each sponge and were removed from the substrate with knives and spatulas. Afterwards, each specimen was separately packed in a plastic bag and preserved in 70 % ethanol. Size, volume and weight of the living sponge specimens were not recorded. In the laboratory, shrimps were removed from the sponge channels with tweezers and preserved in 70 % ethanol after entire host fragmentation. Individuals retrieved from the same channel were considered paired. Voucher specimens were deposited in the crustacean collection at the Museu de Oceanografia Professor Petrônio Alves Coelho of the Universidade Federal de Pernambuco, Recife, Brazil (MOUFPE 19327 - 19416).

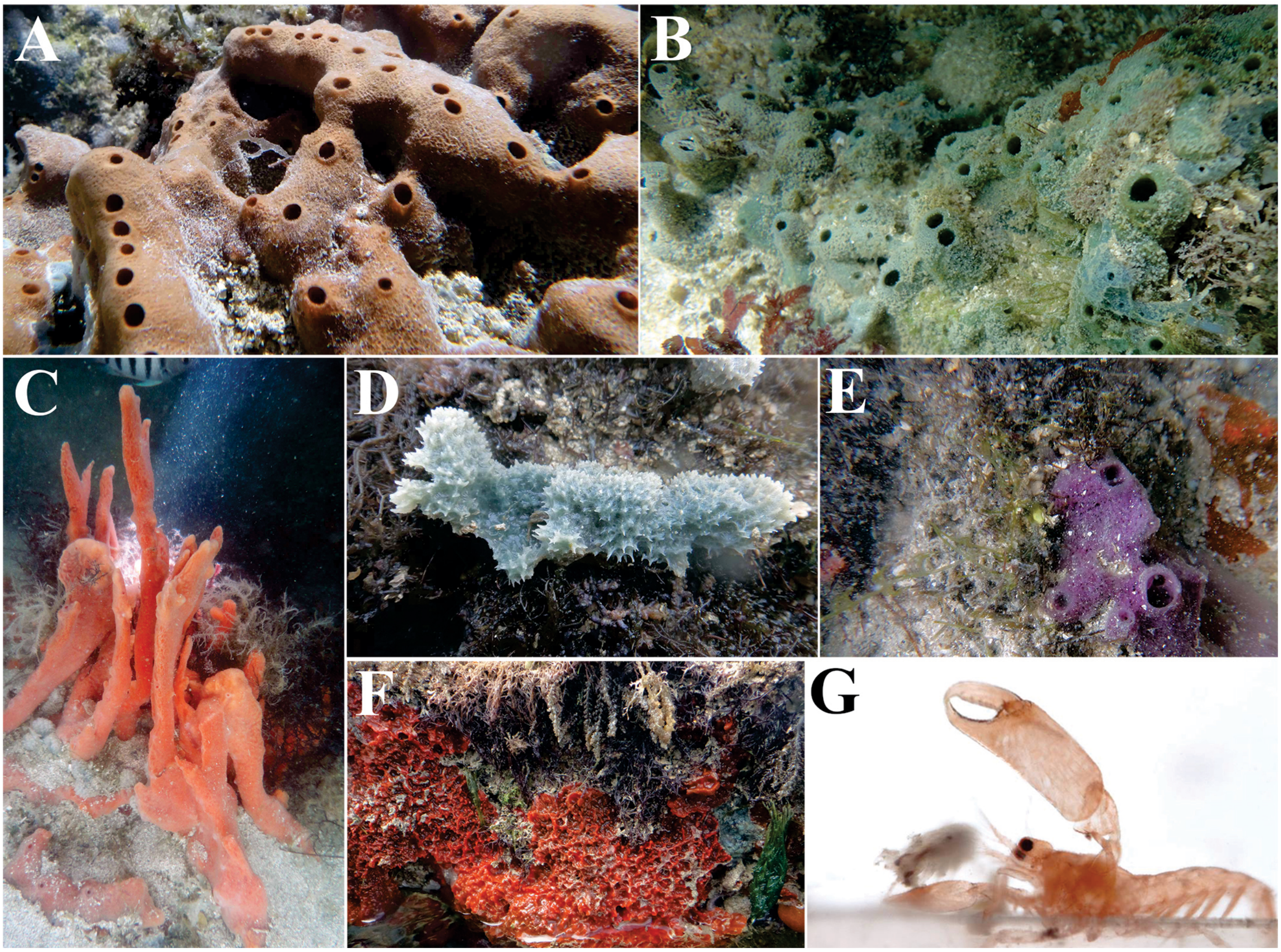

Figure 1. (**A–F**) Sponges sampled from Ponta de Pedras, Pernambuco, northeastern Brazil. **A**, *Amphimedon compressa* Duchassaing and Michelotti, 1864; **B**, *Amphimedon viridis* Duchassaing and Michelotti, 1864; **C**, *Desmapsamma anchorata* Carter, 1882; **D**, *Dysidea etheria* Laubenfels, 1936; **E**, *Haliclona implexiformis* Hechtel, 1965; **F**, *Tedania ignis* Duchassaing and Michelotti, 1864; **G**, Living individual of *Typton carneus* Holthuis, 1951 just retrieved from its sponge host, lateral view (Photographs: **A–F**, T.E.R. Cavalcanti; **G**, F. Barletta).

Shrimp were identified using identification keys (*e.g.*, Chace, 1972; Abele and Kim, 1986) and by consulting the original species descriptions (Holthuis, 1951). Sex of caridean shrimps is mostly determined by the presence (males) or absence (females) of the *appendix masculina* on the endopod of the second pleopod (Bauer, 2004). However, as such a structure is absent in males of *Typton*, we analyzed characters such as the presence/absence (females/males) of eggs underneath the pleon and the height of the pleura of the pleonal segments (lower in males than in females) for sex recognition. Individuals with a CL larger than the smallest ovigerous female were considered adults. Due to the small number (four) of shrimps found in the other sponge species, the breeding biology and heterosexual pairing analyzes were conducted based on those sampled in *Te. ignis* only.

Subsequently, each individual was photographed under a stereomicroscope with an image capture system (Leica EZ4). The same procedure was adopted for the eggs, which were removed from the pleon of the ovigerous females with brushes, and egg development stages were classified according to Mossolin *et al.* (2006): initial (I – embryos with no visible eyes; yolk occupying more than 75 % of the embryonic volume), intermediate (II – embryos with small, elongated eyes; yolk occupying 50–75 % of the embryo volume) and final (III - embryos with well-developed eyes; yolk occupying 25–50 % of the embryo volume). The longest (d1) and shortest (d2) egg diameter were measured in the ImageJ software (1.45s) (Schneider *et al.*, 2012) to calculate the volume using the formula: $v = 1/6 \times \pi \times (d1)^2 \times d2$ (Bauer, 1991) (Fig. 2). Only females carrying eggs in stage I were used (n = 5), (1.09–2.16 mm in CL) due to the low number of females with eggs in stage III. Mean egg volume was measured from the same five ovigerous females, all of which carried well-preserved eggs.

Afterwards, the following body parts were measured using ImageJ software: carapace length (CL) (from the tip of the rostrum to the posterior margin of the carapace) and the length and width of propodus of the second pair of pereopods (major and minor chelae). All data were tested for normality, non-parametric tests were used whenever possible and the significance level of 5 % was adopted for all statistical analyses. Differences in mean CL and other body parts (length and width of propodus of the second pair of pereopods) between the sexes were verified by an analysis of covariance (ANCOVA) with Kruskal-Wallis test *a posteriori*. The CL was used as the independent variable in all analyzes. The presence of CL correlations between paired males and females (*i.e.*, size-assortative pairing) was calculated by the Spearman correlation coefficient. A Chi-Square test with Equal Expected Proportions with a Yates Correction *a posteriori* was used to determine whether the sex ratio followed the expected ratio of 1:1. Statistical analyzes were performed in the Paleontological Statistic program (Past), version 2.17c and in the BioEstat, version 5.3.

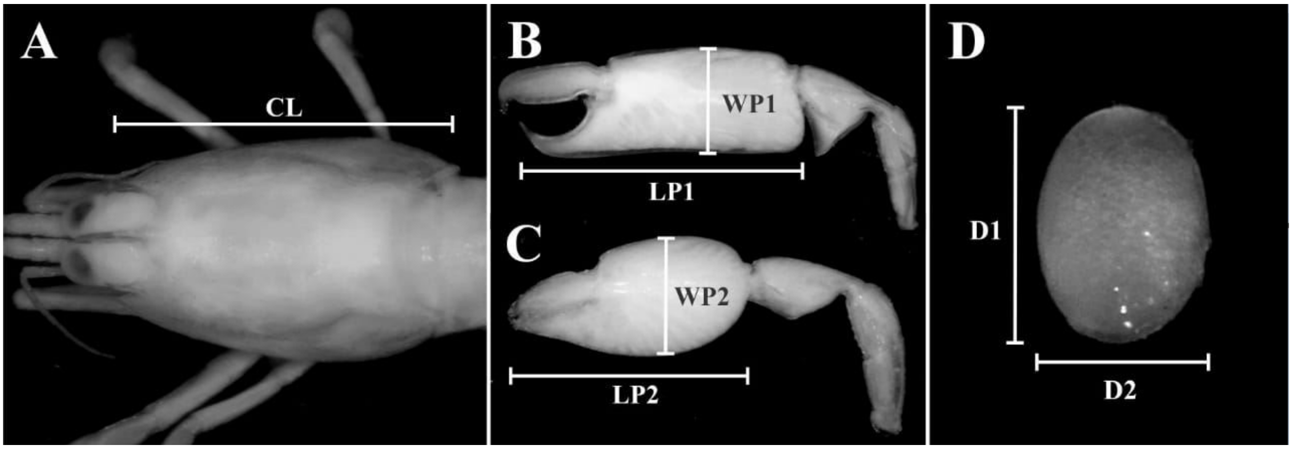

Figure 2. Morphometric dimensions obtained for the sponge-dwelling shrimp *Typton carneus* Holthuis, 1951 from Ponta de Pedras, Pernambuco, northeastern Brazil, sampled between September 2014 and February 2016. **A**, Carapace, dorsal view; **B**, major chela of the second pereiopod, lateral view; **C**, minor chela of the second pereiopod, lateral view; **D**, egg. (CL) Carapace length; (LP1 and WP1) propodus length and width of the major chela, respectively; (LP2 and WP2) propodus length and width of the minor chela, respectively; (D1 and D2) longest and shortest egg diameter, respectively.

RESULTS

A total of 45 individuals were obtained, of which 41 (91.1 %) were found in *Te. ignis*, three (6.7 %) in *H. implexiformis* and only one (2.2 %) in *D. etheria*. In *Te. ignis*, shrimps were present in 25 of the 54 analyzed sponges (prevalence of 46 %).

A total of 24 males and 16 females (10 ovigerous) were considered adults (CL > 1.10 mm, which was the CL of the smallest ovigerous females) and one was considered juvenile (CL = 0.95 mm). The majority of ovigerous females (9) carried stage I eggs, while stage III eggs were observed in only one female. Ovigerous females were observed in six of the 18 sampling months, both in dry (September to March) and rainy (April to August) seasons in the study area (Fig. 3).

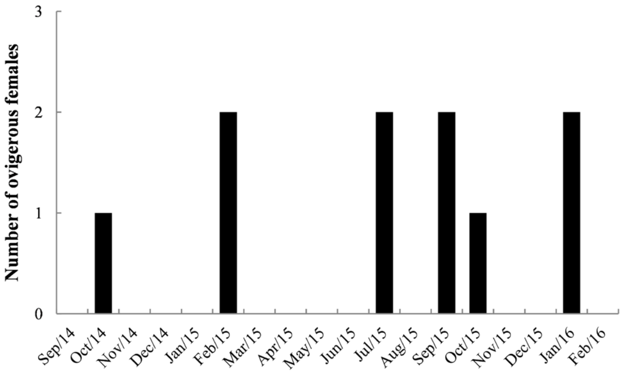

Figure 3. Monthly distribution of ovigerous females of the sponge-dwelling shrimp *Typton carneus* Holthuis, 1951 from Pontas de Pedras, Pernambuco, northeastern Brazil, sampled between September 2014 and February 2016. Dry season: from September to February; Rainy season: from March to August.

Fecundity of females carrying stage I eggs varied from 19 to 56 eggs (37 ± 14, mean ± standard deviation) with a mean volume of 0.033 ± 0.010 mm^3. The female with stage III eggs (1.75 mm in CL) was carrying 22 eggs. The CL of non-ovigerous females and ovigerous females varied from 1.28 to 2.15 mm (1.72 ± 0.31 mm) and 1.10 to 2.16 mm (1.87 ± 0.31 mm), respectively. The CL of males ranged from 1.46 to 2.14 mm (1.78 ± 0.19 mm). Males and ovigerous females differed in mean CL size ($p < 0.05$). No statistical differences in CL were found among the other classes (males *vs.* non-ovigerous females, males *vs.* total females, and non-ovigerous females *vs.* ovigerous females) ($p > 0.05$).

The mean length of the propodus of the major chela did not differ between the sexes (males 2.52 ± 0.83 mm and females 2.54 ± 0.68 mm). On the other hand, the mean length of the propodus of the minor chela was slightly larger in females (1.60 ± 0.33 mm) when compared to males (1.48 ± 0.31 mm). In relation to the mean width of the major and minor chelae, slightly larger values were observed in females (major chela, 1.01 ± 0.24 mm; minor chela 0.74 ± 0.15 mm) than in males (major chela, 0.99 ± 0.28 mm; minor chela, 0.68 ± 0.13 mm). However, such mean values did not differ statistically between the sexes ($p > 0.05$).

Of the 41 specimens obtained in *Te. ignis*, 12 were solitary and 12 were paired (one pair of males and 11 heterosexual pairs) in 22.2 % of the sponge samples. Additionally, a group of five individuals (4 % of the individuals) was found in one sponge sample (1.9 % of *Te. ignis* samples). In 53.7 % of the analyzed samples no shrimp were observed. Within paired individuals, eight females (72.7 %) were ovigerous, seven of them were carrying stage I eggs and one was carrying stage III eggs. Paired females have similar lengths as males (1.89 ± 0.21 mm *vs.* 1.89 ± 0.18 mm, respectively), with no significant difference between the sexes ($p > 0.05$). No CL size correlation (size-assortative pairing) was observed in the heterosexual pairs ($r = -0.10023$; $p = 0.77$) (Fig. 4). The sex ratio was 1:0.64 (M:F) and did not differ statistically from the expected ratio of 1:1 ($p = 0.21$).

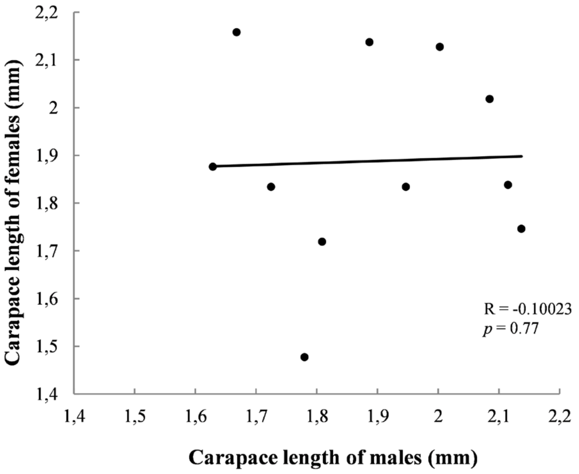

Figure 4. Correlation between the carapace lengths of heterosexual pairs of sponge-dwelling shrimp *Typton carneus* Holthuis, 1951 from Pontas de Pedras, Pernambuco, northeastern Brazil, sampled between September 2014 and February 2016.

DISCUSSION

Distribution of Typton carneus *in sponge hosts*

The number of *Ty. carneus* individuals found indicates a tight symbiotic fit regarding sponges, especially with *Te. ignis*. In fact, some association records of *Typton* spp. with *Tedania* Gray, 1867 sponges (*Tedania klausi* Wulff, 2006 and *Te. ignis*) have been documented (Ďuriš *et al.*, 2011; Santana-Moreno *et al.*, 2013; De Grave and Anker, 2017), probably since these sponges have suitable morphological and chemical characteristics, and are potentially used as a food source, according to Ďuriš' *et al.* (2011) (see below). Herein, we report the occurrence of *Ty. carneus* in *D. etheria* and *H. implexiformis* for the first time, increasing knowledge about sponge hosts of this shrimp. This indicates that *Ty. carneus* has some type of specialization to live in *Te. ignis* in the study area but it can explore other sponge hosts. Along with the sponges analyzed in this study, *Ty. carneus* has been recorded to inhabit others (Chace, 1972; Ramos-Porto and Coelho, 1998; Ďuriš *et al.*, 2011) (see Tab. 1 for a summary of previous association records between species of *Typton* and sponges).

A few species of *Typton* have not been recorded in association with sponges. *Typton ascensionis* Manning and Chace, 1990 and *Typton holthuisi* De Grave, 2010 have both been found in association with algae (Manning and Chace, 1990; De Grave, 2010), whereas *Typton granulosus* Ayón-Parente, Hendrickx and Galvan-Villa, 2015, was associated with the sea-cucumber *Holothuria* (*Halodeima*) *inornata* Semper, 1868 (Ayón-Parente *et al.*, 2015). Further studies regarding such relationships should be carried out to provide more information about the biological aspects of these caridean shrimps. Such refinement is important for a broader understanding of the relationships between these organisms.

Shrimp abundance by host may be explained by a set of factors, including morphological differences between them and chemical influence of their biological compounds, among others. *Tedania ignis* and *H. implexiformis* present high surface rugosity and an abundance of internal spaces, as well as a large body volume which could favor colonization of their internal spaces by symbiotic organisms such as shrimps. The occurrence of only one individual in *D. etheria* suggests that this sponge is not as suitable as *Te. ignis* and *H. implexiformis* for *Ty. carneus* colonization. On the other hand, although *A. compressa* and *A. viridis* have internal spaces suitable for shrimp colonization, they did not harbor any *Ty. carneus* individuals. This may have been caused by factors besides morphology. *Amphimedon compressa* makes an amphitoxin, which is a chemical defense against predation by reef fish (Albrizio *et al.*, 1995), which could explain the absence of *Ty. carneus*. Furthermore, *A. viridis* produces a halitoxin, which is moderately lethal to rats (Berlink *et al.*, 1996) and, in another experiment, may have killed all hydrozoan *Zyzzyzus warreni* Calder, 1988 larvae that settled on this sponge (Campos *et al.*, 2012). However, *Ty. gnathophylloides* has a previous association record with such a sponge (Soledade *et al.*, 2017), indicating that this shrimp may tolerate the toxins produced by this host. Chemical defenses were also experimentally observed in *D. etheria*, which shows low predation by starfish (Waddell and Pawlik, 2000). Information provided herein could be used to test hypotheses about sponge toxicity and *Typton* shrimp host distribution in the future.

Despite having some toxicity, an expressed Tedanolide, which is found in *Te. ignis*, did not prevent the establishment or development of *Z. warreni* larvae under experimental conditions (Schmitz *et al.*, 1984), nor did it prevent a high predation rate by the starfish *Echinaster echinophorus* Lamarck, 1816 and *Echinaster sentus* Say, 1825 (Waddell and Pawlik, 2000). This suggests that this compound may not repel other organisms (Waddell and Pawlik, 2000), making it possible to harbor ecto- and endobionts (Rützler, 2004). Thus, the high prevalence of *Ty. carneus* in *Te. ignis* in the present study suggests a possible lack of toxicity of this sponge to this shrimp.

The orange color of *Ty. carneus* (Fig. 1G) resembles *Te. ignis* coloration (Fig. 1F). Such cryptic coloration could also explain the higher occurrence of this shrimp in *Te. ignis* when compared to the other sponges analyzed here. However, the shrimps were observed in the internal portion, inhabiting the largest and deepest chambers of the host, where cryptic coloration may not be relevant. Such coloration could actually be caused by the sequestration of pigments from its host's tissues, which has already been recorded for other shrimp species that are symbionts of sponges and echinoderms

Table 1. Species of palaemonid shrimps of the genus *Typton* Costa, 1844 and their hosts/habitats.

Species of Typton	Distribution	Host/habitat	References
Ty. anaramosae Neves, 2020	Eastern Atlantic	probably *Spongionella* sp. (sponge)	Neves (2020)
Ty. ascensionis Manning and Chace, 1990	Central Atlantic	algae	Manning and Chace (1990)
Ty. australis Bruce, 1973	Indo-Pacific	*Psammoclema* sp. (sponge)	Bruce (1984), as *Psammopemma* sp.
Ty. bawii Bruce, 1972	Indo-Pacific	Unidentified sponge	Bruce (1972)
Ty. capricorniae Bruce, 2000	Indo-Pacific	Unidentified sponge	Bruce (2000)
Ty. carneus Holthuis, 1951	Western Atlantic	*Dysidea etheria* Laubenfels, 1936 (sponge)	Present study
		Haliclona implexiformis Hechtel, 1965 (sponge)	Present study
		Tedania ignis Duchassaing and Michelotti, 1864) (sponge)	Duris *et al.* (2011); Pachelle *et al.* (2016)
		Tedania cf. *ignis* (sponge)	De Grave and Anker (2017)
		T. cf. *klausi* Wulff, 2006 (sponge)	De Grave and Anker (2017)
		T. klausi (sponge)	Duris *et al.* (2011)
		Unidentified sponge	Ramos-Porto and Coelho (1998); Chace (1972)
Ty. crosslandi Bruce, 1978	Eastern Pacific	no host/habitat reported	Bruce (1978)
Ty. distinctus Chace, 1972	Western Atlantic	*Tedania ignis* (sponge)	Duris *et al.* (2011)
		T. klausi (sponge)	Duris *et al.* (2011)
		Dragmacidon reticulatus (Ridley and Dendy, 1886) (sponge)	Moraes *et al.* (2020)
		Unidentified sponge	Ramos-Porto and Coelho (1998); Chace (1972)
Ty. fapespae Almeida, Anker and Mantellato, 2014	Western Atlantic	*Mycale (Zygomycale) angulosa* Duchassaing and Michelotti, 1864 (sponge)	Almeida *et al.* (2014); Duarte and Nalesso (1996) reported *T. gnathophylloides*, actually *T. fapespae* (see Almeida *et al.*, 2014) in a sponge erroneously identified as *Zygomycale parishii* (Bowerbank, 1875) (see Van Soest, 1984)
Ty. gnathophylloides Holthuis, 1951	Western Atlantic	*Amphimedon viridis* Duchassaing and Michelotti, 1864 (sponge)	Soledade *et al.* (2017)
Ty. granulosus Ayón-Parente, Hendrickx and Galvan-Villa, 2015	Western Atlantic	*Holothuria* (*Halodeima*) *inornata* Semper, 1868 (sea-cucumber)	Ayón-Parente *et al.* (2015)
Ty. hephaestus Holthuis, 1951	Eastern Pacific	no host/habitat reported	Holthuis (1951)
Ty. holthuisi De Grave, 2010	Central Atlantic	algae	De Grave (2010)
Ty. manningi Bruce, 2000	Indo-Pacific	*Ircinia* sp. (sponge)	Bruce (2000)
Ty. prionurus Holthuis, 1951	Western Atlantic	*Callyspongia* sp. (sponge); *T. ignis* (sponge)	Pachelle *et al.* (2015); Santana-Moreno *et al.* (2013)
Ty. serratus Holthuis, 1951	Eastern Pacific	Unidentified sponge	Fransen *et. al.* (1997)
Ty. spongicola Costa, 1844	Eastern Atlantic; Aegean sea; Mediterranean sea; English Channel	*Cliona viridis* Schmidt, 1862 (sponge)	Laubier (1966)
		Desmacidon fruticosum Montagu, 1814 (sponge)	Hunt (1925), as *Desmacidon fructicosa*
		Mycale syrinx Schmidt, 1862 (sponge)	Voultsiadou-Koukouras and Koukouras (1989)
		Unidentified sponge	Costa (1844)
Ty. tortugae McClendon, 1911	Western Atlantic	*Ircinia strobilina* Lamarck, 1816 (sponge)	Santana-Moreno *et al.* (2013)
		Spheciospongia vesparium Lamarck, 1815 (sponge)	Bruce (1978), as *Spheciospongia vesparia*
		probably *I. strobilina* (sponge)	Bruce (1978), as *Stematumenia strobiliana*
Ty. vulcanus Holthuis, 1951	Western Atlantic	*Callyspongia* sp. (sponge)	Pachelle *et al.* (2015)
Ty. wasini Bruce, 1977	Indo-Pacific	*Dysidea* sp. (sponge)	Bruce (2010)
		Haliclona sp. (sponge)	Bruce (1977), as *Reniera* sp.

(*Periclimenes soror* Nobili, 1904, *Tuleariocaris holthuisi* Hipeau-Jacquotte, 1971, *Gnathophylloides mineri* Schmitt, 1933, and *Periclimenaeus caraibicus* Holthuis, 1951) (Castro, 1971; Patton *et al.*, 1985). However, pigment sequestration in *Ty. carneus* needs to be further investigated. Information about the color of shrimps collected in *H. implexiformis*, a typically purple sponge (Fig. 1E), would shed some light on possible pigment sequestration by *Ty. carneus*. However, such information was not recorded in this study.

Although the actual relationship between *Ty. carneus* and its hosts are still unclear, there are morphological indications that suggest a parasitic habit of the species regarding its host. These include, for example, morphology of the fingers of the major chelae on the second pair of pereopods with scissors-like closure, cutting edge of these fingers with grooves caused by intense mechanical abrasion, and a series of small teeth on these cutting edges (see Ďuriš *et al.*, 2011). Another characteristic is a large subtriangular lobe at the proximal end of the cutting edge of the propodus, present on the chelae of *Ty. carneus* and other shrimps living on host sponges; possibly conducting and controlling the movement of the dactyl of the fixed finger (Ďuriš *et al.*, 2011). There is also evidence of parasitism based on the presence of sponge spicules in the stomach contents of this shrimp, as well as for congenerics *Ty. distinctus* and *Typton spongicola* Costa, 1844 (Ďuriš *et al.*, 2011). However, this parasitic feeding habit does not necessarily mean that the damage caused by the shrimp is not offset by some benefit to the host and, any kind of benefit is still unknown in this relationship (Ďuriš *et al.*, 2011).

Breeding biology

Herein, we provide initial information about the breeding biology of *Ty. carneus*. Most females associated with *Te. ignis* were ovigerous (62.5 %), indicating the importance of the host as a reproduction site. The frequency of ovigerous females was low (in six of the 18 sampling months); however, their occurrence in both dry and rainy seasons in the study area suggests continuous reproduction for *Ty. carneus*, which has been observed for other tropical caridean shrimps (Bauer, 1989; Terossi and Mantellato, 2010; Almeida *et al.*, 2011).

Only two other studies (original descriptions of two other *Typton* species) have recorded the number of eggs carried by breeding females. Bruce (1973; 2000) reported ovigerous females of *Typton australis* Bruce, 1973 and *Typton manningi* Bruce, 2000 carrying approximately 10 and 150 eggs, respectively. When redescribing *Ty. spongicola*, Bruce (2009) mentioned that this shrimp produces many small eggs, which suggests higher fecundity for this species. However, comparisons with *Ty. carneus* fecundity are not reliable because Bruce (1973; 2000) only examined the fecundity of one ovigerous female. Different factors may influence fecundity in caridean shrimps, including female and egg sizes (Sastry, 1983; Hartnoll, 1985). The apparent low fecundity in *Ty. carneus* may be related to the small size of the shrimp, which is directly related to the size of the body cavity for oocytes to grow in, as well as the space available for egg incubation in the pleon (Bauer, 1991; Corey and Reid, 1991).

On the other hand, fecundity may be related to an embryonic development strategy. In some crustaceans, the duration of embryonic development is directly proportional to egg size, due to the amount of yolk needed to supply embryonic development. Thus, species with abbreviated or direct development tend to produce larger eggs with more yolk (Bauer, 1991; Wehrtmann and Albornoz, 2002). Furthermore, the low fecundity combined with the large egg size in *Ty. carneus* — up to 0.7 mm in diameter and larger than those of other *Typton* species (*e.g.*, *Ty. granulosus*: 0.4 mm; *Ty. prionurus*: 0.5 mm) (Holthuis, 1951; Ayón-Parente *et al.*, 2015) — may indicate abbreviated or direct development, which could be an adaptation for living inside sponges. A similar example is the direct development presented by some sponge-dwelling and eusocial species of the genus *Synalpheus* C.S. Bate, 1888 (Corey and Reid, 1991; Duffy, 1996). However, the production of small eggs and apparently higher fecundity in *Ty. spongicola,* and the scarce evidence from their larvae, suggest extended larval development in the plankton, at least for this species (Lebour, 1925; 1949; Fincham and Williamson, 1978). Finally, our data suggest an absence of overlapping generations of *Ty. carneus* (only one juvenile observed) in the sponge host, which has also been observed in some sponge-dwelling shrimp species with direct development (*e.g.*, some eusocial *Synalpheus* species) (Duffy, 2003). Future studies about *Typton* species could elucidate if large eggs and low fecundity are consequences of the small size of these shrimps and/or due to any type of developmental abbreviation.

Heterosexual pairing

Characteristics regarding paired individuals, such as the absence of sexual dimorphism in weaponry and body size, presence of paired non-brooding and brooding females carrying eggs in different development stages and a sex ratio that did not differ from the expected 1:1, suggest that the population presents a monogamous mating system (see Bauer, 2004; Baeza *et al.*, 2016; Correa and Thiel, 2003); as documented for some caridean shrimps like alpheids (Knowlton, 1980; Correa and Thiel, 2003; Baeza, 2008; Pescinelli *et al.*, 2017; Soledade *et al.*, 2018). However, the lack of size-assortative pairing, as well as the low proportion of heterosexual pairs (37.93 %), compared to solitary individuals (48 %), does not support monogamy when considering that monogamous populations should present paired shrimps more often than solitary ones (Baeza *et al.*, 2016). Such features have been observed in polygamous mating systems of caridean shrimps (see Correa and Thiel, 2003). Our controversial findings highlight the need for broader studies, with larger sample sizes, that assess demographic data, such as frequency of solitary, paired or more sets of individuals in the environment to address the mating system of *Ty. carneus* populations.

Our results provide further insights into some life history traits of *Ty. carneus*. The frequency of *Ty. carneus* collected in *Te. ignis* indicates that this sponge is an important host for these shrimps in the study area. The observation of heterosexual pairing, as well as the high percentage of ovigerous females in our sample, indicate the importance of the host as a reproduction site for this symbiont shrimp. Furthermore, the occurrence of ovigerous females in both dry and rainy seasons suggests continuous reproduction in the study area. The fecundity of the studied population was low, which may be related to small body-size and/or to the existence of some type of abbreviated development. The results regarding population features of the mating system are controversial with some of the population features assessed herein suggesting a monogamous mating system and other features supporting a polygamous system. Thus, the mating system of *Ty. carneus* remains unknown and should be addressed in future studies based on larger sample sizes and include specific demographic information.

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