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Chapter 8

The Thalassinidean Mud Shrimp *Upogebia vasquezi*: Life Cycle and Reproductive Traits on the Amazonian Coast, Brazil

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Additional information is available at the end of the chapter

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Abstract

The thalassinideans comprise the infraorders Axiidea and Gebiidea, two distinct groups of decapods that have converged morphologically and ecologically as burrowing forms, commonly known as mud lobsters and mud or ghost shrimps. These groups are an important component of the macroinfauna of intertidal and subtidal environments and are distributed throughout the world, with species diversity increasing from high latitudes toward the equator. These species are burrowing benthic decapods, with more than 95% of species inhabiting shallow waters in marine and estuarine environments, exerting considerable influence over the structure of benthic communities through their ability to bioturbate the sediments, with effects on the infauna and seagrasses in coastal environments. *Upogebia vasquezi* has an ample geographic distribution, it is typically found in rocky outcrops near mangroves. This species reproduces year round, which is subjected to strong seasonal fluctuations in salinity due to the local precipitation regime. The Amazon Macrotidal Mangrove Coast, representing 10% of the Brazilian coastline and encompassing more than 56% of the country's mangrove forests, is a high priority area for conservation. This chapter aims to elucidate the reproductive traits of *U. vasquezi* with a revision about the known ecological information available for thalassinidean species all over the world.

Keywords: Decapoda, Gebiidea, larval biology, reproduction

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1. Introduction

The Thalassinidea (infraorders Axiidea de Saint Laurent 1979 and Gebiidea de Saint Laurent, 1979) designates a group of decapods popularly known as "mud shrimps," "mud lobsters," "ghost shrimps," or "corruptos" in Portuguese [1–3]. They are among the most common burrowing shrimps frequently found in high densities in coastal and sublittoral sediments, from brackish to euryhaline environments [4]. Most species are marine or estuarine and use sheltered sites as habitats, preferably estuaries, bays, lagoons, beaches, and seas, both in tropical countries and in temperate regions worldwide, and their distribution ranges from shallow mid- and infralittoral to deeper zones [5–7].

These species are also very sensitive to any type of disturbance in their environments, thus serving as effective bioindicators [1]. The potential to accumulate pollutants in their tissues is higher than that of other crustaceans such as crabs and sand crabs, which is useful in the assessment of coastal environments polluted by domestic sewage and industrial waste [1, 8]. On the Amazon Coast, for instance, thalassinidean species have not been found on coastal sites that directly receive untreated domestic effluents, and have only appeared in less anthropized, more preserved regions [9].

Some species also have indirect economic value, as they are used as bait in artisanal and recreational fishing [6, 10–15]. Its capture is usually performed using "prawn pumps," with consequent trampling and digging in several locations, resulting in relevant impacts to the ecosystems where they dwell [16], as well as on the associated biota [17]. Furthermore, thalassinidean populations might occasionally suffer a sharp decrease themselves or even be at risk of extinction [14]. They have been reportedly used as food in some eastern countries, e.g., *Austinogebia edulis* (Ngoc-Ho and Chan, 1992), which is commercialized in Taiwan [18]. On the other hand, they might also cause harm in oyster farming, provoking sediment instability, that impacts on the growth of cultivated organisms or even cause their mortality [19–21].

Despite the ecological relevance of this species in benthic communities of the mid-littoral, very little is known about its biology, especially regarding reproduction and larval development [10, 22–24], mostly due to its cryptic habit and difficulties in capturing specimens [25].

The aim of this chapter is to provide a brief revision on the biology of Axiidea and Gebiidea crustaceans and characterize the Amazon coastal habitats where these organisms are found, with emphasis on *Upogebia vasquezi* (Ngoc-Ho, 1989), one of the most abundant species of this group in the region.

2. Systematics and morphology

The evolutionary position of thalassinidean shrimps inside decapods is still quite controversial, and this is reflected in frequent systematic revisions. These species have already comprised the Infraorder Anomura MacLeay, 1838, together with hermit crabs, porcellanids, and galatids, among other different representatives of this taxon [26–28]. Although this classification was based on the morphological characteristics of adults, some similarities concerning larval morphology

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were also observed, e.g., the reduction of a pair of marginal bristles of the telson in the zoeal stage [27], which reinforced indications of a relationship between hermit crab species and this group.

Notwithstanding, important distinctions have also been observed, which indicate a strong association between Callianassidae Dana, 1852 and Axiidae Huxley, 1879 and between Upogebiidae Borradaile, 1903 and Laomediidae Borradaile, 1903 with other Anomurans (**Figure 1**), suggesting a inhomogeneous group [29], which would later be called "nephropoidean" and "anomuran" larvae, respectively [30].

Thalassinideans were later considered a distinct group, at the same hierarchical level as anomurans [31], until they were pointed out as a monophyletic taxon, comprising the infraorder Thalassinidea (Latreille, 1831) [32]. The definition of this infraorder was based on some characteristics shared by the species that comprise it, namely, the complex burrow systems they built and the presence of thick feathery bristles on their second pair of pereiopods [32–34].

However, differences observed between two of the main families that comprise Thalassinidea (Callianassidae and Upogebiidae) suggested that they could have distant phylogenetic origins [35]. Thus, the similar habits between these two taxa (reclusive habits, burrows) would have converged throughout their evolutionary history [35]. This assumption corroborated the indications [28] of the existence of two different groups based on larval morphology. This morphological evidence was supported by molecular phylogeny analyses and resulted in the suggestion of dividing this taxon into two infraorders: Axiidea De Saint Laurent, 1979 and Gebiidea De Saint Laurent, 1979 [36, 37], which has been adopted by several authors [38–42]. Another nomenclature was proposed [43] for these taxa: Callianassidea Dana, 1852 and Thalassinidea Latreille, 1831, respectively. However, the names Axiidea and Gebiidea, which were first proposed by Saint Laurent [44], are the most widely accepted and consistently used to designate the two infraorders, which recognizably comprise thalassinidean decapods [42].

According to the most recent classification [40], the following families are included in the infraorder Axiidea: Axiidae Huxley, 1879; Callianassidae Dana, 1852; Ctenochelidae Manning and Felder, 1991; Micheleidae Sakai, 1992; and Strahlaxiidae Poore, 1994; whereas the infraorder Gebiidea is comprised of: Axianassidae Schmitt, 1924; Laomediidae Borradaile, 1903; Thalassinidae Latreille, 1831; and Upogebiidae Borradaile, 1903 [40]. Since 1792, when the first thalassinidean species were described, currently cataloged as *Upogebia pusilla* (Petagna, 1792),



Figure 1. Representative specimens of infraorders Axiidea (*Lepidophthalmus siriboia*) and Gebiidea (*Upogebia vasquezi*) collected in the Amazon coastal region. Scale in millimeters. Photos: Dalila Silva.

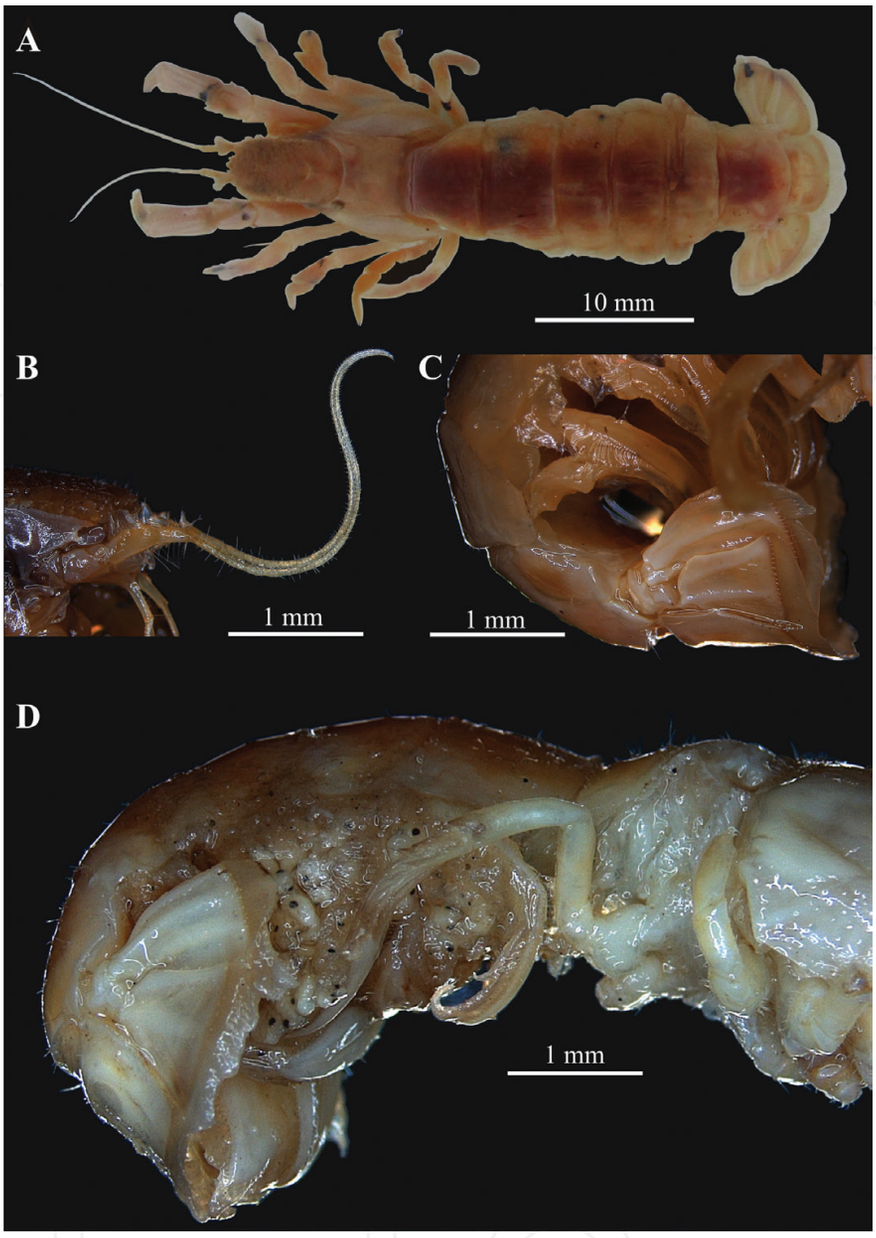


Figure 2. *Upogebia vasquezi*, adult female. (A) Dorsal view; (B) detail of the rostrum; (C) detail of part of the abdomen with pleopods and telson, lateral view; (D) embryos adhered to pleopods in the hatching phase, lateral view. Photos: (A) Rory Oliveira; (B)–(D) Danielly Oliveira.

Callianassa tyrrhena (Petagna, 1792), and *Callianassa candida* (Olivi, 1792), information available on this group has increased considerably, mainly over the last 100 years, and Callianassidae, Upogebiidae, and Axiidae are the most extensively studied ones [7].

Thalassinidean decapods encompass a relatively small number of species, with approximately 646 catalogued species [38, 39]. This number has recently increased to approximately 674 species, with 465 Axiidea and 209 Gebiidea [45]. Morphologically, these organisms share characters such as the presence of a fairly calcified carapace, symmetrical and extended, while the abdomen is feebly calcified, ending on a well-developed tail fan (telson + uropods) [46]. Some

species are more similar to lobsters with a highly calcified exoskeleton (e.g., Thalassinidae and Axiidae); while others have a more elongated body and a slightly calcified exoskeleton, better adapted to the "burrowing" life style (e.g., Callianassidae) [45].

Differences between the representatives of the infraorders Axiidea and Gebiidea are mainly the shape of the anterior part of the carapace, the structure of appendages, and larval morphology [30, 47]. Gebiidea have a chelated or subchelated first pair of pereiopods, and the second pair is subchelated or simple (never are both pairs chelated), whereas Infraorder Axiidea has the two first pairs of pereiopods chelated [40]. In addition, Axiidea are frequently heterochelic, as opposed to Gebiidea, whose first pair of pereiopods (chelipods) are of the same size, as can be observed in the two species frequently found on the Amazon coast: *Lepidophthalmus siriboia* (Axiidea) and *U. vasquezi* (Gebiidea) (**Figure 1**).

U. vasquezi has a triangular rostrum, whose lateral edges are nearly straight and longer than the ocular peduncles, with presence of postocular spine [47]. The abdomen is robust, broader than long (**Figure 2A**), and the entire body is adorned with bristles, from the anterior portion, on the cephalic appendages (**Figure 2B**), to the abdominal appendages (pleopods) and telson (**Figure 2C**). Females carry the eggs on the pleopods until hatching, in zoea I stage (**Figure 2D**), with approximately 0.88 mm of carapace length [48].

3. Distribution

Thalassinideans are distributed around the world, with a higher concentration of species in the regions located at low latitudes; e.g., the three major groups Callianassidae, Upogebiidae, and Axiidae occur mainly between latitudes 25°N and 10°N and between 0° and 15°S [7]. The highest percentage of species (36.5%) was recorded in the Western Indian-Pacific, but they are also found in the eastern and western portions of the Atlantic, including the Caribbean Sea and the Gulf of Mexico; as well as in the Mediterranean region [41, 49, 50].

They are mostly marine species, usually found in sheltered habitats, such as estuaries, bays, lagoons, beaches, and seas, both in tropical countries and in temperate regions worldwide, and their distribution ranges from shallow mid- and infralittoral to deeper zones [5–7]. Most species (95%) occur in shallow waters (0–200 m), and few have been found in depths lower than 2000 m [7, 49].

In Brazil, the occurrence of 43 species has been registered [47, 51], and they are popularly known as "corruptos" [1]. Their distribution ranges from Amapá (Northern region) to Rio Grande do Sul (Southern Region) in different habitats, such as bottoms of calcareous waters, coral reefs, rocks, sand, mud, near seaweed meadows, surrounding mangrove vegetation, and in deeper waters on the continental shelf and slope, down to a depth of 820 m [47].

Species of only two families have occurred on the Amazon coast: Callianassidae (Axiidea) and Upogebiidae (Gebiidea) [47], typically found in very shallow waters (down to a depth of 2 m) of estuarine regions with decreased salinity [7, 47]. Only 13 species has been recorded in the State of Pará [47, 52, 53] Brazil (**Table 1**).

Infraorder	Family	Gender	Species	Geographical distribution
Gebiidea (De Saint Laurent, 1979)	Upogebiidae Borradaile, 1903	*Upogebia* (Leach, 1814)	*U. acanthura* (Coelho, 1973)	Western Atlantic: Gulf of Mexico and the Bahamas, Antilles, northern South America and Brazil – from Pará to Pernambuco and along Espírito Santo.
			U. brasiliensis (Holthuis, 1956)	Western Atlantic: Belize, French Guiana, Suriname, and Brazil – from Pará to Santa Catarina.
			U. marina (Coelho, 1973)	Western Atlantic: Venezuela and Brazil – from Pará to São Paulo.
			U. paraffinis (Williams, 1993)	Western Atlantic: Brazil – Pará and from Ceará to Paraná.
			U. vasquezi (Ngoc-Ho, 1989)	Western Atlantic: south of Florida, Bahamas, Central America, Antilles, Venezuela, and Brazil – from Pará and Maranhão to São Paulo.
Axiidea (De Saint Laurent, 1979)	Callianassidae (Dana, 1852)	*Corallianassa* Manning, 1987	*C. longiventris* (A. Milne Edwards, 1870)	Western Atlantic: Florida, Bermuda, Antilles, and Brazil – Rocas, and from Pará to Pernambuco.
		Cheramus Bate, 1888	*C. marginatus* (Rathbun, 1901)	Western Atlantic: Florida, Antilles, and Brazil – from Amapá to Rio de Janeiro.
		Callichirus (Stimpson, 1866)	*C. major* (Say, 1818)	Western Atlantic: North Carolina to Florida, Gulf of Mexico, Venezuela and Brazil – Rio Grande do Norte, Pernambuco, and from Bahia to Santa Catarina.
		Lepidophthalmus (Holmes, 1904)	*L. siriboia* (Felder and Rodrigues, 1993)	Western Atlantic: Florida, Gulf of Mexico, Antilles, and Brazil – from Pará to Bahia.
		Neocallichirus (Sakai, 1988)	*N. grandimana* (Gibbes, 1850)	Western Atlantic: Florida, Gulf of Mexico, Bermuda, Antilles, and South America, and Brazil – from Pará to Bahia.
		Sergio (Manning and Lemaitre, 1994)	*S. guara* (Rodrigues, 1971)	Western Atlantic: Brazil – from Pará to São Paulo.
		Marcusiaxius (Rodrigues and Carvalho, 1972)	*M. lemoscastroi* (Rodrigues and Carvalho, 1972)	Western Atlantic: Central America, Colombia, Venezuela, and Brazil – Amapá, Pará, and Ceará.
		Dawsonius (Manning and Felder, 1991)	*D. latispinus* (Dawson, 1967)	Western Atlantic: Florida and Brazil – from Amapá to Alagoas.

Table 1. Geographical distribution of thalassinidean species (Gebiidea and Axiidea), with occurrence registered on the coast of Pará.

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The distribution of *U. vasquezi* encompasses the Western Atlantic, ranging from Florida and several islands in the Caribbean Sea region (such as Aruba and Bonaire), through Central America, Bahamas, Dominican Republic, Barbuda, Antigua, Barbados, Tobago, Mexico, Panama, Venezuela, to Brazil: from Pará to São Paulo [47, 50, 53, 54] (**Figure 3**). It occurs in shallow waters, mostly down to depths of 2 m [7], dwelling in burrows excavated in the sediment of the intertidal zone [47].

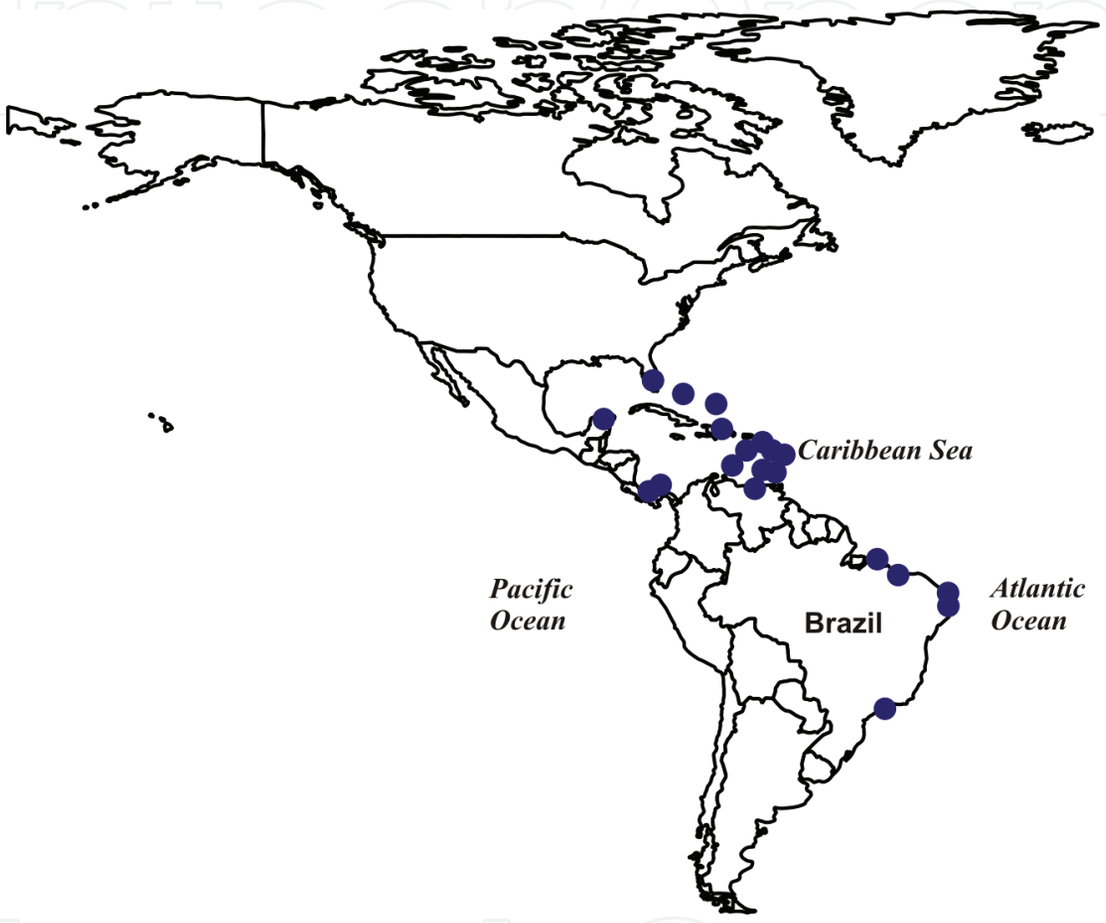


Figure 3. Distribution of *Upogebia vasquezi* in the American continent, according to occurrence records available in references [47, 50, 53, 54].

4. Amazon coastal habitats

The coast of Pará accounts for 6.6% of the Brazilian coast, and the extension of mangrove area covers approximately 2176 km^2 [55] in the northeastern portion of the state alone, corresponding to 1.2% of the global mangrove area (181,000 km^2) [55–57]. The region known as "Amazon Macrotidal Mangrove Coast" extends from Marajó Bay (PA) to São José Bay (MA), totalling 650 km of coast [55]. It is characterized by a wide coastal plain and an extensive adjacent continental shelf (~200 km wide), which is irregular and cut through by several estuaries [55]. This region is subjected to a quite dynamic tidal regime and currents, with semidiurnal macrotides ranging from 4 to 7.5 m of amplitude [48, 55, 58].

Several habitats comprise the Amazon coast, e.g., sandy beaches and estuaries, temporary tide pools, muddy coastal plains, and rocky outcrops, where several decapod species are found, including thalassinideans. For instance, *L. siriboia* occurs mostly on beaches with sandy-muddy sediment [9, 59], *Callichirus major* might be found in habitats similar to *L. siriboia*, on the most exposed portion of the beach (Danielly B. Oliveira, personal observation), whereas *U. vasquezi* inhabits burrows sheltered under rocky outcrops with sandy-muddy sediment [48, 53].

5. Burrows

One of the characteristics shared by thalassinidean shrimps is their reclusive lifestyle, with the construction of burrows, which are among the deepest and most complex systems recorded in transitional marine environments [6]. They are built on sandy and muddy surfaces of the coastal zone, serving as shelter and protection against predators, as well as feeding and reproduction sites [1, 6, 25]. Thanks to the fossilization of burrows on these species, paleontologists gathered important indications about ancient coastlines [6].

Thalassinidean burrows are considered unique environments, whose physical-chemical conditions are strongly influenced by the behavior of these species, mostly due to their bioturbation activities, which have effects on nutrient cycling (for example, see [60–62]) and also ensure high availability of dissolved oxygen, aside from providing protection from the direct action of waves [1]. The process of burrow construction increases the inner surface area of the sediment, in the oxygenated water-sediment interface [33, 63], and causes physicochemical changes, thus increasing the metabolic activity in the sediment [64].

In regions with intense thalassinidean aggregations, there is a change in the sediment structure, which becomes more porous and has increased concentration of smaller particles and organic matter [65]. Such conditions influence the structure of the local benthic community [66], creating, changing, and maintaining a mosaic of habitats for a wide range of organisms [67].

Burrow structure is specific for each species, and it is related to their feeding mode, as well as to environmental conditions and the population density of these crustaceans in their habitats [63]. Externally, they might be divided into two main types: burrows with and without sediment heaps around their openings [63]. Regarding shape, they might be built in a single U- or Y-shaped tunnel, or in several sediment layers or branched, deep tunnels [63], which might be interconnected and might shelter at least one specimen [68].

Most *Upogebia* species, for example, live in relatively shallow, U-shaped burrows, e.g., *U. africana* (Ortmann, 1894) [69], *U. stellata* (Montagu, 1808) and *U. deltaura* (Leach, 1815) [70], *U. tipica* (Nardo, 1869) [71] *U. noronhensis* (Fausto-Filho, 1969) [23] *U. major* (De Haan, 1841) [66] and *U. vasquezi* [72]). Some species of this group build Y-shaped burrows in sandy-muddy habitats, like *U. omissa* (Gomes Corrêa, 1968), *U. yokoyai* (Makarov, 1938), and *U. carinicauda* (Stimpson, 1860) [25, 73, 74].

Burrows of *U. vasquezi* are built in predominantly sandy-muddy sediment, with small and abundant rock fragments, located below extensive outcrops comprised of rocks of several sizes. These outcrops are located near mangroves on some Amazon estuarine beaches, and

are submerged during high tide and exposed during low tide (Danielly B. Oliveira, personal observation). Regarding its morphology, the burrows of *U. vasquezi* are relatively shallow and U-shaped [72], and in its natural habitat, it is possible to observe the opening of the burrows excavated in the sediment by just removing some rocks from the outcrop (Danielly B. Oliveira, personal observation).

6. Ecological relationships

Several organisms associated to thalassinideans occur inside their burrows, using them as shelter and also for feeding. Examples are some alpheid shrimp species, as *Leptalpheus axianassae* (Dworschak and Coelho, 1999), the crabs *Pinnixa gracilipes* (Coelho, 1997); *Pinnixa transversalis* (H. MilneEdwards and Lucas, 1842); and *Austinixa aidae* (Righi, 1967), as well as invertebrates phoronids, polychaetes, nemertins, copepods, and gobiidae fish [20, 68, 75–80]. Some species might be parasitic to thalassinideans; e.g., isopods are prevalent ectoparasites of *Upogebia* (Leach, 1814) (for example, see [4, 5, 81–83]). There are also endoparasites of thalassinids, such as trematode cysts, Acanthocephala [4], and copepods infesting gills, pereiopods, and egg masses (e.g., [68]).

In addition to these species, there is a varying fauna that coexists in the sandy and muddy plains inhabited by thalassinideans, not necessarily inside the burrows, which are also influenced by the dynamics of "corruptos" (mud crabs). For example, gastropods, bivalves, echiura, echinodermata, polychaetes, and anemones comprise of an important fraction of the macrozoobenthos biomass in *Upogebia issaeffi* habitats (Balss, 1913) [84]. Stomatopods species, bivalves, and echiura, along with other sympratic thalassinids (e.g., *Upogebia* sp. and *Lepidophthalmus* sp.) [80], are macrofauna also associated to habitats of *Axianassa australis* (Rodrigues and Shimizu, 1992) on the tropical beaches of the Brazilian coast [80].

The invading intertidal fish species *Omobranchus punctatus* (Valenciennes, 1836) (Osteichthyes: Blenniidae) and the shrimp *Alpheus estuariensis* (Christoffersen, 1984) (**Figure 4**) have been



Figure 4. Species inhabiting burrows of *Upogebia vasquezi* in the Amazon estuarine region. (A) *Omobranchus punctatus*; (B) *Alpheus estuariensis*. Photos: Rory Oliveira.

found in burrows of *U. vasquezi* on the Amazon coast (Danielly B. Oliveira, personal observation). Gobbidea fish are common dwellers of burrows of Upogebiidea, feeding mostly on small crustaceans [85].

7. Reproduction and life cycle

7.1. Larval biology

Information available on larval biology of thalassinidean shrimps (infraorders Axiidea and Gebiidea) is relatively scarce, mainly because the development of larval stages of most species have not yet been described, thereby hindering the identification of specimens captured in natural environments. Among the available descriptions, many of them are based on specimens collected in zooplankton samples, which might mislead species identification [86], and in others, the characterization of the different development stages [63] are frequently poorly understood.

Only 12.5% of thalassinidean species and 25% of thalassinidean genera are estimated to have a known larval development, and *Upogebia* is the group with the highest number of species whose larvae have been described [87]. In absolute numbers, approximately 80 species (including unidentified morphotypes of some genera) have had their larval cycle partially or completely described [87]. Some of these species have also had their post-larval stage (or first juvenile stage) morphologically described (e.g., *Upogebia affinis* (Say, 1818): [88]; *U. paraffinis* (Williams, 1993): [89]; *L. siriboia*: [90]).

Regarding the 13 thalassinidean species whose occurrence in the Amazon coastal region has been recorded, only four have already had their larval and/or juvenile development stages partially or completely described: *C. major*, *L. siriboia*, *U. paraffinis*, and *U. vasquezi* (**Table 2**).

The larval phase of thalassinideans is predominantly planktonic, and in most species, it is the only life-cycle stage where they remain outside their burrows [6]. The complete suppression of larval stages during development is only known for *Upogebia savignyi* (Strahl, 1862), a sponge commensal [91].

Species	Developmental stages	References
Callichirus major	ZI–ZV, M	[95]
Lepidophthalmus siriboia	Prezoea, ZI–ZIII, M, JI	[90]
Upogebia paraffinis	ZI–ZV, M	[89]
Upogebia vasquezi	ZI–ZIV, M	[48]

Note: Z, Zoea; M, Megalopa; J, juvenile. Roman numbers represent the number of developmental stages described.

Table 2. Thalassinidean species with occurrence on the coast of Pará whose larval and/or juvenile development stages have already been partially or completely described.

Thalassinideans have varying developmental patterns, generally one to eight zoeal stages [86, 92]. Among Axiidea, a reduced larval cycle is common, with two to three development stages (e.g., *Callichirus kraussi* (Stebbing, 1900) as *Callianassa kraussi* [93]; *Pestarella tyrrhena* (Petagna, 1792) as *C. tyrrhena* [22]; *Lepidophthalmus sinuensis* (Lemaitre and Rodrigues, 1991), *Lepidophthalmus louisianensis* (Schmitt, 1935) [94], and *L. siriboia* [90]). Some species in this group also have a long planktonic larval development, such as *C. major* and *Callichirus islagrande* (Schmitt, 1935), which undergo 4–5 zoeal stages [95, 96], or *Boasaxius princeps* (Boas, 1880) and *Nihonotrypaea petalura* (Stimpson, 1860), with 7–8 zoea [97, 98].

Regarding Gebiidea, a long larval development is frequent: *Naushonia crangonoides* (Kingsley, 1897) undergoes six to seven zoeal stages until it reaches the post-larval stage [99]; and *A. australis* (Rodrigues and Shimizu, 1992) shows up to eight zoeal stages [100]. The most common larval development pattern of *Upogebiidea* is the presence of three to four zoeal stages (e.g., *Upogebia kempi* (Shenoy, 1967) [101]; *Upogebia darwinii* (Miers, 1884) [102]; *U. major* [10]; *U. pusilla* [103]; *U. issaeffi* [104]; *U. yokoyai* [63]; *U. vasquezi* [48]).

The life cycle of *U. vasquezi* larvae has four zoeal stages [48]. When immature, the eggs of this species are yellowish (**Figure 5A**), their color start becoming more orange by the end of embryo development, in the hatching stage, when the eyes also become visible (**Figure 5B**). Larvae hatch in Zoea I, going through three other zoeal stages and one megalopa until reaching the first juvenile stage (**Figure 5C–H**).

Only *C. major*, *L. siriboia*, and *U. vasquezi* larvae have already been found in estuarine zooplankton samples from the Amazon coast [53]. Among the studies conducted with these species in the region, the taxonomic studies stand out, namely the morphological description of larval developmental stages of *L. siriboia* [90], as well as the description of mouth appendages and stomachs of larvae [105], analysis of the lecithotrophic behavior of this species during larval cycle [24], and abundance of larvae in the estuarine zooplankton [53]. With regard to *C. major*, the importance of feeding during larval development has been analyzed (as opposed to the lecithotrophic behavior of *L. siriboia*) [106], as well as the abundance of estuarine planktonic larvae throughout an annual cycle [53].

U. vasquezi was the most studied thalassinidean species in the region regarding larval biology, with description of larval morphology [48, 107], analysis of the effect of salinity on survival and duration of larval stages, its implication on larval migration [108], and occurrence of planktonic larvae along a salinity gradient in the Amazon estuary [53].

7.2. Effects of biotic factors on larval development

Diverse environmental factors influence developmental rates, number of stages, and survival of larvae of marine invertebrates [109]. Temperature and salinity are among the physicochemical factors that have a higher influence on survival and larval development of marine decapods [110]. Temperature might influence the growth of decapods during different life-cycle phases, from larvae and post-larvae to juveniles and adults [111], and trigger the acceleration or decrease of larval developmental rate, and impact metabolism and development, as well as

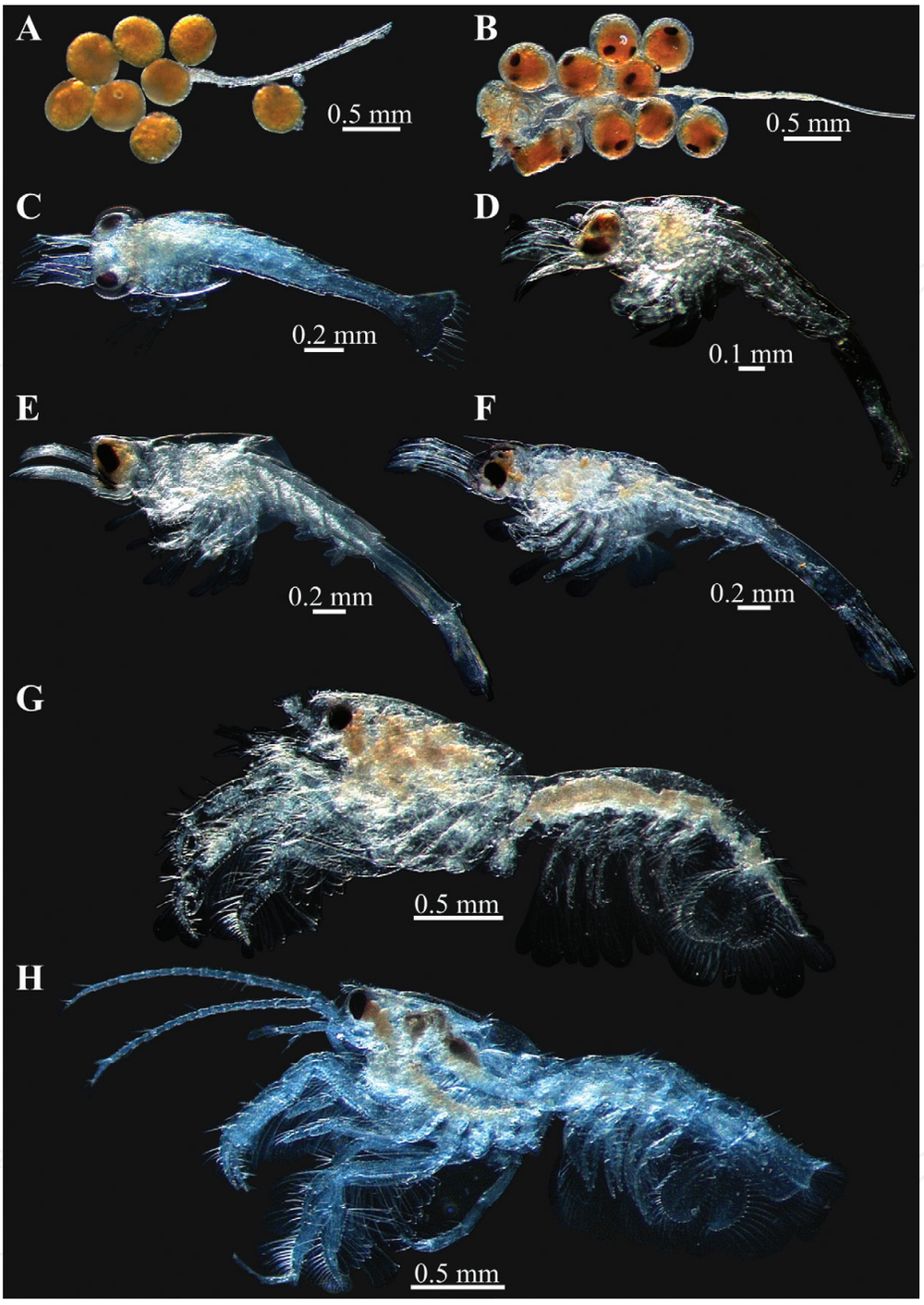


Figure 5. Developmental stages of *Upogebia vasquezi*. (A) Eggs in the initial developmental stage; (B) eggs in the final developmental stage; (C) Zoea I; (D) Zoea II; (E) Zoea III; (F) Zoea IV; (G) Megalopa (without antennas); (H) Juvenile I. Photos: Danielly Oliveira.

the seasonality of larvae emergence in some plankton species [110]. For instance, temperature mainly influences the duration of decapod larval stages, which are prolonged in stressful situations (for example, see [22, 112, 113]).

Saline concentration is generally constant in open sea, whereas it might seasonally fluctuate in coastal and estuarine zones, both regionally and locally [110]. Hence, salinity is considered an

ecological and physiological factor of extreme importance for species in these environments [110], with impact on the development, survival, feeding, and growth rate, as well as on shedding cycles, metabolic rates, and behavior [113].

The reproductive behavior (life-cycle strategies) of decapods might also be influenced by salinity. Most estuarine species export their larvae to marine coastal zones, where salinity is more stable and, on average, higher than in the parental habitat, whereas others retain their initial larval stages inside the estuarine environment [112, 113]. For instance, some typical estuarine crabs increase their swimming activity in higher salinities to avoid being transported outside the estuary [114].

Studies analyzing the effect of salinity on larval development of decapods are also useful to identify which reproductive strategy is adopted by the species (either retention or exportation) due to the fact that saline limits tolerated by decapod larvae under experimental conditions coincide with their distribution along salinity gradients in the field [113]. In the coastal region of Pará, the effect of salinity on larval development of the crabs *Ucides cordatus* (Linnaeus, 1763), *Uca vocator* (Herbst, 1804), and *Uca rapax* was analyzed in the laboratory, obtaining decreased survival rates under lower salinity conditions, thus indicating a strategy of larval dispersal and exportation [115–118].

7.3. Reproduction, dynamics, and secondary production

Studies on the population dynamics and reproductive biology of thalassinideans have been developed in several locations worldwide, thus contributing to understanding the life cycle of these species (for example, see [14, 23, 80, 119–126]). Most of these studies were conducted in temperate and subtropical regions and few have shown estimates of population dynamic parameters for this group. On the Amazon coast, only the population dynamics of *L. siriboia* has been studied [59].

Secondary production might be defined as the production of biomass carried out by heterotrophic organisms, including animals, fungi, and heterotrophic bacteria; it represents an estimated biomass made available for higher trophic levels [127]. Decapod crustaceans have a crucial contribution to secondary production in the habitats they inhabit. For example, even though their abundance is lower than that of other invertebrates, they account for an important fraction of productivity in coral reef ecosystems [128] and on sandy beaches at different latitudes [129].

Secondary production estimates are still quite scarce, mostly in the equatorial region (between latitudes 5°S and 5°N), with absence of studies on benthic macrofaunal populations of sandy beaches [130]. Only 12 decapod populations have been studied [130] at higher latitudes, on tropical and subtropical beaches, including the thalassinids *U. pusilla* [4] and *C. major* [131, 132]. In Brazil, studies of this type have only been conducted in the Southern and Southeastern regions (for example, see [132–139]).

The capture of mud shrimps (Axiidea and Gebiidea) might cause changes in the target species and habitat and might influence resident communities and cause indirect effects on sediment structure [12, 13]). Excessive fishery efforts might lead to overexploitation of naturally abundant populations or even to the total disappearance of some species [12, 14]. Management plans and

efforts for the conservation of these species and recovery of their habitats must be based on their regional population and reproductive characteristics [14]. Thus, studies that investigate population dynamics and reproductive biology of thalassinideans in several locations are of utmost importance, especially in priority conservation areas.

Despite the importance of thalassinidean species on Amazon coastal habitats, very little are known on their ecology, mostly regarding burrow morphology, physiology, population dynamics, behavior, and larval description.

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