### MORPHOLOGY OF THE FIRST ZOEAL STAGE OF *PLATYPODIELLA SPECTABILIS* (HERBST, 1794) (DECAPODA, BRACHYURA, XANTHIDAE) OBTAINED IN THE LABORATORY

Adilson Fransozo<sup>1</sup>, Maria Lucia Negreiros-Fransozo<sup>1</sup>, Joel W. Martin<sup>2</sup>, and Sandra E. Trautwein<sup>2,3</sup>

<sup>1</sup>Departamento de Zoologia, IB, UNESP, 18618-000, Botucatu (SP), Brazil, NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture), E-mail: fransozo@ibb.unesp.br and mlnf@ibb.unesp.br <sup>2</sup>Natural History Museum of Los Angeles County, Los Angeles, California 90007, USA <sup>3</sup>University of California Los Angeles

*Abstract* Ovigerous females of the xanthid crab *Platypodiella spectabilis* (Herbst, 1794) were obtained from 2 widely separated localities: the Ubatuba coast (Félix Beach, São Paulo) of Brazil and Guana Island in the British Virgin Islands (BVI). First stage zoea larvae were obtained from females at both locations. Those from Brazil are described and illustrated. The first zoea bears dorsal, rostral, and lateral carapace spines, plus a well-developed and spinose antennal protopod that bears a greatly reduced exopod with 2 minute setae. This antennal morphology, along with other characters, places the species among the "Group I" xanthid zoeas of Rice (1980) and Martin (1984, 1988). Differences between larvae from Brazil and those from the BVI are minor and are attributed to within-species variation. Characters that serve to separate these larvae from those of co-occuring xanthids are presented. Comments on the distribution and size of *Platypodiella spectabilis* are included.

#### INTRODUCTION

The xanthid crab genus *Platypodiella* was erected in 1967 (Guinot 1967:562) to accommodate 4 species formerly treated as Platypodia Bell, 1835. Two of the species, P. gemmata (Rathbun, 1902) and P. rotundata (Stimpson, 1860), are known from the eastern Pacific. Garth (1991:131), in discussing the Galapagos crab fauna, pointed out that the 2 Pacific species are possibly the adult (described as P. rotundata) and young (P. gemmata) of the same species, with the name P. rotundata having precedence. Other workers feel that the 2 Pacific species are distinct (T. Zimmerman, personal communication, Natural History Museum of Los Angeles County, Los Angeles, CA, USA). The other 2 species are Atlantic, with P. picta (A. Milne Edwards, 1869) restricted to the eastern Atlantic and P. spectabilis (Herbst, 1794) known from the western Atlantic.

*Platypodiella spectabilis* is a relatively small xanthid found in or near coral reefs and rocky shorelines throughout most of the western Atlantic. The species has been reported as far north as Bermuda (Chace et al. 1986:346, plates 115 and 11:11, in Sterrer 1986, as *Platypodia spectabilis*) and as far south as Rio de Janeiro, Brazil, including the Fernando de Noronha Archipelago and Trindade Island (Melo 1998:490). The current report extends the southern range to the São Paulo state of Brazil. Thus, the range of the species is an impressive 7,000 km from northern to southern extent. Distributional records within this range, and extending westward into the Gulf of Mexico, can be found in Rathbun (1930), Felder (1973), Powers (1977), and Abele and Kim (1986). Because of its spectacular coloration and color pattern, *P. spectabilis* is often depicted in faunal or regional guide books (Humann 1992), and the species is sometimes referred to as the calico crab (Chace et al. 1986) or gaudy clown crab (Williams et al. 1989).

The use of crab larval morphology, and in particular characters of the first zoeal stage, in elucidating phylogeny is now well established (see references in Clark et al. 1998) especially within the Xanthidae (Clark and Al-Aidaroos 1996, Clark and Galil 1998, Clark and Ng 1998). To date, nothing is known about larval development in the genus *Platypodiella*, and thus no larval evidence has been brought to bear on the question of how this genus relates to other genera within the Xanthidae *sensu stricta* or to other families within the superfamily Xanthoidea (sensu Martin and Davis, in review). In this paper we provide the first description of zoeal larvae in this genus.

### MATERIALS AND METHODS

In February 1998, 4 ovigerous female *P. spectabilis* were collected by scuba diving along the infralittoral region of a rocky shore (Félix Beach) in Ubatuba, São Paulo, Brazil (23°23'00"S, 44°57'06"W). The crabs were maintained separately in an aquarium provided with

seawater from the collecting site (salinity 35‰, temperature  $24 \pm 1^{\circ}$ C) until hatching. The eggs of 2 of these females, carapace widths 28.1 and 29 mm, hatched. Newly hatched zoeae were fixed in 10% formalin and were then transferred to a mixture (1:1) of 70% ethyl alcohol and glycerin; 15 specimens were dissected for detailed examination and description. Additional ovigerous females were collected from the eastern Caribbean as part of an ongoing survey of the marine invertebrates of Guana Island, British Virgin Islands (BVI) (led by T.L. Zimmerman and J.W. Martin). These specimens came from North Beach, Guana Island, from interstices of dead coral (mostly clumps of dead Porites) in shallow water (1 m and less), on 14 July 2000 (Station 65 of the Zimmerman/Martin survey of Guana Island). A single ovigerous female (later photographed alive, photographic voucher number Vc0796), carapace width 10.5 mm, carapace length (as measured from front to back and excluding the rostrum) 7.1 mm, was kept alive in a small plastic container of fresh seawater until the eggs hatched later that evening. Examination of these larvae occurred in the laboratory of the 3rd and 4th authors in Los Angeles.

Illustrations were made from fixed material and are based on at least 15 specimens (Brazil) or 5 specimens (BVI). First stage zoeae were dissected under a stereomicroscope and mounted on semi-permanent slides. Morphological characters were examined with a Zeiss Axioskop 2 compound microscope attached to a personal computer using an Axiovision Image Analysis system (Brazil) or a Wild M5APO dissecting microscope and Nikon Labophot compound microscope with drawing tube (Los Angeles, for the BVI specimens). For the description of the larvae we followed the format suggested by Clark et al. (1998). Larvae and one parental female from Brazil have been deposited in the collection of the Departamento de Zoologia, Instituto de Biociencias, UNESP, Botucatu, SP, Brazil, NEBECC/LC 00076.1 (larvae) and NEBECC/LC 00076.0 (female). Larvae and the parental female from the BVI have been deposited in the collections of the Natural History Museum of Los Angeles County (LACM CR 20000061), as has a second large ovigerous female from Brazil (LACM CR 19981421).

#### RESULTS

Size. Larvae from the Brazilian female were slightly longer than those from the BVI, averaging  $1.43 \pm 0.18$ mm from tip of rostrum to tip of dorsal spine (compared to 1.20 mm for BVI larvae) and  $0.53 \pm 0.03$  mm total carapace length (compared to 0.42 mm in BVI larvae). However, width of the larvae from the 2 localities was the same; both Brazilian and BVI larvae averaged  $0.79 \pm 0.04$  mm from tip to tip of the lateral carapace spines.

**Carapace (Figure 1a, 3a).** Globose, bearing dorsal, rostral, and lateral spines. Lateral spines shorter than dorsal and rostral spines. Rostral spine with 2 to 6 spinules (always 6 in Brazilian specimens) along mediodistal two thirds. Eyes sessile.

**Abdomen (Figure 1b).** With 5 abdominal somites, each bearing pair of posterodorsal setae. Somite 2 bearing lateral knobs projecting anteriorly and dorsally. Somite 3 bearing small lateral knobs projecting laterally or posterolaterally. Somites 3–5 with acute posterolateral processes. Pleopods absent.

**Telson (Figure 1b, 3b).** Bearing on each branch one large lateral spine, one small seta-like spine directly posterior to large lateral spine, and one short dorsal spine located posterior to these. Three pairs of minutely serrate spines on posterior emargination; innermost pair with 3

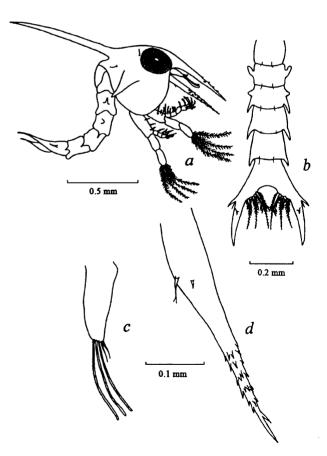


Figure 1. Morphology of the first zoea of *Platypodiella spectabilis* (based on specimens from Brazil). a, entire zoea, lateral view. b, abdomen and telson, dorsal view. c, antennule. d, antenna.

or 4 setules at approximate midlength in addition to serrations.

Antennule (Figure 1c, 3c). Uniramous. Endopod absent. Exopod unsegmented, with 3 aesthetascs (Brazil; only 2 in BVI) and 2 simple setae.

Antenna (Figure 1d, 3c). Protopod well developed, as long as rostral spine, and distally spinulate. Endopod reduced, represented by small spine at 1/3 length of protopod. Exopod greatly reduced, less than 1/10 length of protopod, and bearing 2 minute simple setae.

Mandible (Figure 2a). Incisor process stout. Molar process well developed. Endopod palp absent.

**Maxillule (Figure 2b).** Basial endite with 2 plumodenticulate to cuspidate setae, 2 plumodenticulate setae and 1 plumose setae. Coxal endite with 5 plumodenticulate setae and 1 plumose seta. Endopod 2-segmented, with 1 plumose seta on proximal article and 6 plumose setae (2 subterminal + 4 terminal) on distal article.

**Maxilla (Figure 2c).** Coxal endite bilobed with 4 + 4 plumodenticulate setae. Basial endite bilobed with 4 + 4 plumodenticulate setae. Endopod bilobed with

3 + 5 (2 subterminal + 3 terminal) plumodenticulate setae. Scaphognathite with 4 marginal setose setae and stout posterior process.

**First Maxilliped (Figure 2d).** Coxa with one plumose seta. Basial segment with 10 medial plumose setae arranged 2, 2, 3, 3. Endopod 5-segmented with 3, 2, 1, 2, and 5 plumose setae. Exopod 2-segmented with 4 terminal plumose setae.

Second Maxilliped (Figure 2e). Coxa without setae. Basial segment with 4 medial plumose setae arranged 1, 1, 1, 1. Endopod 3-segmented, with 1, 1, and 2 subterminal + 3 terminal plumose setae. Exopod 2-segmented, with 4 terminal plumose setae.

#### **REMARKS AND DISCUSSION**

### Comparison of larvae from Brazil with those from the eastern Caribbean

Larvae from Guana Island (BVI) differ from those from Brazil only slightly. Brazilian larvae were longer, based on measurements of the rostral-to-dorsal spine

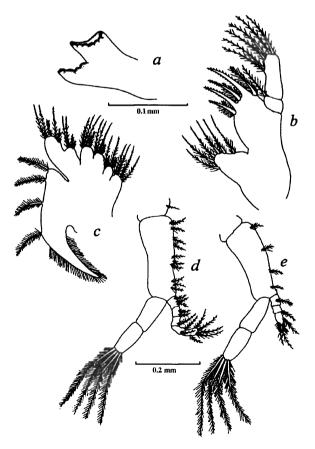


Figure 2. Morphology of the first zoea of *Platypodiella* Island spectabilis (based on specimens from Brazil). a, mandible. b, maxillule. c, maxilla. d, first maxilliped. e, second maxilliped. (right

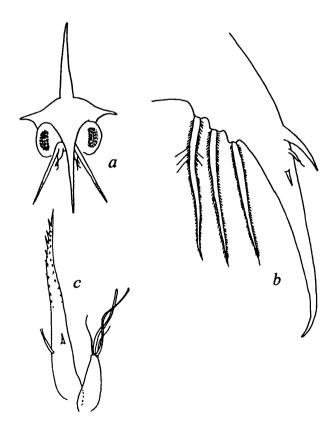


Figure 3. Additional figures of the first zoea of *Platypodiella* spectabilis from a female collected in the British Virgin Islands. a, frontal view showing relative lengths of lateral and dorsal carapace spines. b, right fork of telson and right side setae, dorsal view. c, antenna (left) and antennule (right).

lengths, but were equally wide (lateral spine tip-to-tip length). Rostral spinules were fewer in the BVI specimens, with sometimes as few as only 2 spinules, whereas Brazilian larvae always possessed 6 rostral spinules. Aesthetascs of the antennule usually numbered 2 in the BVI specimens but 3 in the Brazilian specimens. Placement of the 2nd (smaller) lateral spine on the telson appeared to be slightly more posterior in the BVI specimens (compare Figures 1b and 3b), although this may be only a matter of interpretation of the illustrator. Thus, despite the geographic distance separating the parental females, larvae from the 2 areas are quite similar.

## Observations on hatching behavior of the parental female

The parental female collected in the BVI was observed from the time of collection (late afternoon) until about 0130 the following morning. Hatching of the eggs commenced at about 1930 on July 14. As hatching began, the female began rhythmically pumping her abdomen at a rate of about 1 pump per second, with a pattern of 4 or 5 pumps followed by a short pause, followed by 4 or 5 pumps, followed by another pause. This rhythmical pumping continued for several hours, gradually slowing at 0130 the next morning (15 July), at which time the female and her remaining eggs were preserved. At the time of preservation, there were still a large number (we estimate about 1/10) of the original number of eggs remaining on the pleopods. It is not known if these eggs would have continued to hatch throughout the night. Thus, hatching in this species can take at least 5 hours based on these limited laboratory observations. The effects of captivity and confinement in a small container are unknown; these factors also could play a role in the crab's behavior.

# Systematic position of *Platypodiella* based on larval morphology

The reduced antennal expoped, well-developed lateral carapace spines, and setation of the endopods of the maxilla, maxillule, and both maxillipeds all combine to suggest that *Platypodiella* belongs among the Group I xanthid zoeas of Rice (1980) and Martin (1984). Within this group, *Platypodiella* belongs to a subgroup that bears spinules on the protopod of the antenna (see below).

Guinot (1967), when erecting the genus *Platypodiella*, remarked on the similarities between species of this genus and those of *Platyactaea* Guinot, 1967, and to a lesser extent to species of *Atergatis* De Haan, 1833 and *Atergatopsis* A. Milne Edwards, 1862, as well

as to members of Platypodia. The latter 3 genera are usually considered members of the xanthid subfamily Zosiminae (Serène 1984, Clark and Ng 1998). Thus, one might expect to find morphological and zoeal similarities among species of these genera. To our knowledge, within these genera descriptions of the first zoea exist only for Atergatis (Terada 1980) and for Platypodia (Hashmi 1970). Larvae of another Zosiminae genus, Lophozozymous, were recently described by Clark and Ng (1998). Martin (1984) placed Atergatis (based on Terada's description of the larvae of A. reticulatus DeHaan, 1835) in Group I, but was indecisive about Hashmi's (1970) description of the zoea of Platypodia cristata (A. Milne Edwards, 1865), and left it in an "incertae" grouping of xanthid larvae having no clear affinities. Hashmi (1970) did not provide illustrations of any larval features of P. cristata, instead indicating the antennal and telson "types" using a schematic diagram. The antenna of P. cristata was categorized by Hashmi (1970) as "type b," where the antennal exopod was at least 1/2 the length of the protopod. Thus, in this feature there is a significant difference between larvae of Platypodia and larvae of Platypodiella.

Concerning relationships of *P. spectabilis* to the numerous and diverse families of "xanthoids" (treated as the superfamily Xanthoidea, containing 12 families, by Martin and Davis in review): the rostral and antennal morphologies of the zoea of *P. spectabilis* may indicate an affinity with the subfamily Panopeinae (the Panopeidae of Guinot 1978, and Martin and Davis in review). The zoea of *P. spectabilis* is also similar to those of the Indo-Pacific *A. reticulatus* (as described by Terada 1980), sometimes considered a member of the xanthoid subfamily Zosiminae (Serène 1984). Clark and Ng (1998) correctly note that antennal morphology alone is insufficient for determining subfamiliar affinities within the xanthoids.

# Comparison of the larvae of *P. spectabilis* with those of other western Atlantic xanthoids

Martin (1984), in his review of the larvae of xanthid crabs, listed some 25 species of xanthids (*sensu largo*) from the western Atlantic and Gulf of Mexico for which at least the first zoeal stage was described. Most of these (15) belonged to the Group I larvae as described above. Since that time several other descriptions of western Atlantic xanthid larvae have appeared (see Martin et al. 1985 for *Panopeus bermudensis* Benedict and Rathbun, 1891; Iorio and Boschi 1986 for *Platyxanthus patagonicus* A. Milne Edwards, 1879; Negreiros-Fransozo 1986a, b for *Panopeus americanus* De Saussure, 1857 and *Eurypanopeus abbreviatus* Stimpson, 1860, respectively; Fransozo 1987 for *Eriphia gonagra* (Fabricius, 1781; Ingle 1985 for *Panopeus occidentalis* De Saussure, 1857; Ingle 1987 for *Cataleptodius floridanus* (Gibbes, 1850); Montú et al. 1988 for *Panopeus austrobesus* Williams, 1983; Martin 1988 for a review of xanthid larvae and information on phyletic utility of the megalopa stage; Bakker et al. 1989 for *Hexapanopeus schmitti* Rathbun, 1930; Fransozo et al. 1990 for *Hexapanopeus paulensis* Rathbun, 1930; Messerknecht et al. 1991 for *Eurytium limosum* [previously described by Kurata et al. 1981]; and Vieira 1999 for *Hexapanopeus caribbaeus* (Stimpson, 1871).

The first zoeal stage of P. spectabilis is very similar to the first zoea of a large number of western Atlantic xanthids. However, it can be readily distinguished from larvae of any of the previously described western Atlantic species by 2 characters. First, the antennal exopod is greatly reduced (true of all "Group I" xanthid zoeas), while the antennal protopod bears rows of spines on the distal 1/4 to 1/2 of its length. In this character, the first zoea of P. spectabilis is similar to existing descriptions of the first zoeal stage of P. occidentalis, P. herbstii, P. americanus, P. austrobesus, E. limosum, Eurypanopeus abbreviatus, E. depressus, C. floridanus, and H. paulensis. Second, the spinules on the rostral spine are known only for this species and for the first zoeas of Garthiope barbadensis (Rathbun, 1921), formerly Micropanope Stimpson, 1871 (Gore et al. 1981) and C. floridanus (Ingle 1987). The rostral spine of P. spectabilis can bear up to 6 sharp spinules, whereas first zoeal larvae of G. barbadensis and C. floridanus were each described as having only 2 such spinules.

### **Geographical Distribution**

The distribution of P. spectablis as presently understood (i.e., assuming that there is a single species in the western Atlantic rather than a species complex) is in excess of 7,000 km. When we add to this the fact that P. spectabilis is found in the far western Gulf of Mexico (Felder 1973) and far eastern Caribbean (e.g., British Virgin Islands, this report), it becomes clear that the range of the species is extraordinarily large. However, such a range is not unique; there are other species of xanthoid crabs (e.g., Eriphia gonagra and Carpilius corallinus (Herbst, 1783) that have similar ranges (T. Zimmerman, personal communication). It is possible that the spectacular color pattern, from which the species derives its name, has caused workers to quickly and easily "identify" all of the various color forms (see description of color variation in Chace et al. 1986) as P.

spectabilis. Because cryptic species are being discovered frequently on the basis of subtle color differences (see Zimmerman and Felder 1991 for species of Sesarma Say, 1817; Williams and Felder 1989 for species of Menippe De Haan, 1833), it is certainly possible that the wide range of colors and color patterns in P. spectabilis is hinting at a species complex rather than one wideranging species. If such is the case, it is also possible that we have misinterpreted the differences in larvae from the eastern Caribbean and Brazil (where the adult females are nearly 3 times the size of those in the BVI) as being caused by intraspecific, rather than interspecific, variation. On the other hand, this species can exhibit a wide range of colors and patterns within a very small geographic region (T.L. Zimmerman and J.W. Martin, unpublished data). Clearly more work on morphological and color variation in this species across its entire range is needed.

#### **ACKNOWLEDGMENTS**

The first 2 authors are grateful to "Fundação de Amparo à Pesquisa no Estado de São Paulo" (FAPESP (grants #94/4878-8; 95/8520-3; 98/9426-90) for financial support, and to F.P.L. Marques for his helpful suggestions on the manuscript. This work was funded in part by the Biotic Surveys and Inventories program of the US National Science Foundation (NSF) via grant DEB 9972100 to T.L. Zimmerman and J.W. Martin, and in part by a PEET grant (DEB 9978193) from NSF to J.W. Martin and D. Jacobs. We thank NSF and especially D. Causey for support and encouragement. We also thank other members of the Guana Island field team: L. Harris, D. Cadien, R. Ware, T. Haney, K. Fitzhugh, and G. Hendler. Finally, we thank the Falconwood Corporation and especially L. Jarecki for allowing us to conduct this work on Guana Island, and R. Heard and D. Hard for helping us prepare the manuscript. J. Martin extends special thanks to the first 2 authors for graciously allowing us to combine data and observations in order to jointly prepare this note.

### LITERATURE CITED

- Abele, L.G. and W. Kim. 1986. An illustrated guide to the marine decapod crustaceans of Florida. State of Florida Department of Environmental Regulation Technical Series, Vol. 8, no. 1 (in 2 parts).
- Bakker, C. de, M. Montú, K. Anger, and L. L. Fernandes. 1989. Larval development of *Hexapanopeus schmitti* Rathbun, 1930 (Decapoda, Brachyura, Xanthidae) reared in the laboratory. Nerítica 4:137-164.

- Chace, F.A., Jr., J.J. McDermott, P.A. McLaughlin, and R.B. Manning. 1986. Decapoda. In: W. Sterrer, ed. Marine Fauna and Flora of Bermuda. Wiley-Interscience, John Wiley and Sons, New York, NY, p. 312–358.
- Clark, P.F. and A.M. Al-Aidaroos. 1996. The first zoeas of Actaeodes hirsutissimus (Rüppell, 1830) and A. tomentosus (H. Milne Edwards, 1834) (Crustacea: Decapoda: Brachyura: Xanthidae: Actaeinae). Journal of King Abdulaziz University Marine Sciences 7, Special Issue: Symposium on the Red Sea Marine Environment:207-214.
- Clark, P.F., D.K. Calazans, and G.W. Pohle. 1998. Accuracy and standardization of brachyuran larval descriptions. Invertebrate Reproduction and Development 33:127–144.
- Clark, P.F. and B.S. Galil. 1998. The first stage zoca of *Pseudoliomera speciosa* (Dana, 1852) (Crustacea, Decapoda, Brachyura, Xanthidae). Zoosystema 20:193– 200.
- Clark, P.F. and P.K.L. Ng. 1998. The larval development of the poisonous mosaic crab, *Lophozozymous pictor* (Fabricius, 1798) (Crustacea, Decapoda, Brachyura, Xanthidae, Zosiminae), with comments on familial characters for first stage zoeas. Zoosystema 20:201–220.
- Felder, D.L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Center for Wetland Resources, Louisiana State University, Baton Rouge, LA, 103 p.
- Fransozo, A. 1987. Desenvolvimento larval de *Eriphia gonagra* (Fabricius, 1781) (Decapoda, Xanthidae), em laboratório. Revista Brasilicra Zoologie 4:165–179.
- Fransozo, A., F.L.M. Mantelatto, and M.L. Negreiros-Fransozo. 1990. Larval development of *Hexapanopeus paulensis* Rathbun, 1930 (Crustacea, Brachyura, Xanthidae) under laboratory conditions. Revista Brasiliera Zoologie 7:31– 45.
- Garth, J.S. 1991. Taxonomy, Distribution, and Ecology of Galápagos Brachyura. In: M.J. James, ed. Galápagos Marine Invertebrates. Topics in Geobiology, Volume 8, Plenum Press, New York, NY, p. 123-145.
- Gore, R.H., C.L. Van Dover, and K.A. Wilson. 1981. Studies on Decapod Crustacea from the Indian River region of Florida. XX. *Micropanope barbadensis* (Rathbun, 1921): the complete larval development under laboratory conditions (Brachyura, Xanthidae). Journal of Crustacean Biology 1:28-50.
- Guinot, D. 1967. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures III. A propos des affinités des genres Dairoides Stebbing et Daira de Haan. Bulletin du Museum National d'Histoire Naturelle, 2e Série, 39:540–563.
- Guinot, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyoures. Bulletin Biologique de le France et de le Belgique (n.s.) 112:211-292.
- Hashmi, S.S. 1970. The brachyuran larvae of west Pakistan hatched in the laboratory (Decapoda, Crustacea). Pakistan Journal of Zoology 2:81-93.
- Humann, P. 1992. Reef Creature Identification: Florida, Caribbean, Bahamas. New World Publications, Inc., Vaughan Press, Orlando, FL, 320 p.

- Ingle, R.W. 1985. Larval development of the mud crab Panopeus occidentalis de Saussure, from Bermuda (Crustacea: Xanthoidea: Panopeidae). Bulletin of the British Museum of Natural History (Zoology) 48:233-248.
- Ingle, R.W. 1987. The first zoca of three Pachygrapsus species and of Cataleptodius floridanus (Gibbes) from Bermuda and Mediterranean (Crustacea: Decapoda: Brachyura). Bulletin of the British Museum of Natural History (Zoology) 52:31-41.
- Iorio, M.I. and E.E. Boschi. 1986. Studies on the larval stages of the crab *Platyxanthus patagonicus*, from laboratoryrearing and plankton samples. Journal of Aquatics Tropicale 1:7-24.
- Kurata, H., R.W. Heard, and J.W. Martin. 1981. Larval development in the laboratory of the xanthid mud crab *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) from Georgia. Gulf Research Reports 7:19-25.
- Martin, J.W. 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the western Atlantic and Gulf of Mexico. Bulletin of Marine Science 34:220-239.
- Martin, J.W. 1988. Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae. Symposia of the Zoological Society of London 59:69–102.
- Martin, J.W. and G.E. Davis. In review. An Updated Classification of the Recent Crustacea. Science Series, Natural History Museum of Los Angeles County, Los Angeles, CA, 390 ms pages.
- Martin, J.W., F.M. Truesdale, and D.L. Felder. 1985. Larval development of *Panopeus bermudensis* Benedict and Rathbun, 1891 (Brachyura, Xanthidae) with notes on zoeal characters in xanthid crabs. Journal of Crustacean Biology 5:84-105.
- Melo, G.A.S. 1998. Malacostraca-Eucarida. Brachyura. Oxyrhyncha and Brachyrhyncha. In: P.S. Young, ed. Cataloge of Crustacea of Brazil. Museu Nacional (Serie Livros no. 6), Rio de Janeiro, Brazil, p. 455-515.
- Messerknecht, I., M. Montú, and K. Anger. 1991. Larval development and salinity tolerance of Brazilian *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) reared in the laboratory. Meeresforschungen 33:275-296.
- Montú, M., K. Anger, C. de Bakker, V. Anger, and L.L. Fernandes. 1988. Larval development of the Brazilian mud crab *Panopeus austrobesus* Williams, 1983 (Decapoda: Xanthidae) reared in the laboratory. Journal of Crustacean Biology 8:594-613.
- Negreiros-Fransozo, M.L. 1986a. Desenvolvimento pósembrionário de *Panopeus americanus* Saussure, 1857 (Decapoda, Xanthidae), em laboratório. Revista Brasiliera Biologia 46:173-188.
- Negreiros-Fransozo, M.L. 1986b. Desenvolvimento pósembrionário de *Eurypanopeus abbreviatus* (Stimpson, 1860) (Crustacea, Decapoda, Xanthidae), em laboratório. Boletim Zoologia 10:19-39.
- Powers, L. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. Contributions in Marine Science 20:1-190.
- Rathbun, M.J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. Bulletin of the US National Museum 152:1-609.

- Rice, A.L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Transactions of the Zoo-logical Society of London 35:271–424.
- Serène, R. 1984. Crustacés Décapodes Brachyoures de l'Ocean Indien Occidental et de la Mer Rouge, Xanthoidea: Xanthidae et Trapeziidae. Avec un addendum par Crosnier, A.: Carpiliidae et Menippidae. Faune Tropicale 24:1– 400.
- Sterrer, W., ed. 1986. Marine Fauna and Flora of Bermuda. John Wiley and Sons, New York, NY, 742 p.
- Terada, M. 1980. Zoea larvae of four crabs in the subfamily Xanthinae. Zoological Magazine 89:138–148. (in Japanese).
- Vieira, R.R. 1999. Desenvolvimento larval e juvenil de Hexapanopeus caribbaeus (Stimpson, 1871) (Crustacea, Decapoda, Xanthidae) em laboratório. MSc. dissertation, Universidade Botucatu, SP, Brazil, 120 p.

- Williams, A.B. and D.L. Felder. 1989. Analysis of stone crabs: Menippe mercenaria (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). Proceedings of the Biological Society of Washington 99:517-543.
- Williams, A.B., L.G. Abele, D.L. Felder, H.H. Hobbs, Jr., R.B. Manning, P.A. McLaughlin, and I. Pérez Farfante. 1989. Common and scientific names of aquatic invertebrates from the United States and Canada: Decapod Crustaceans. American Fisheries Society Special Publication 17:1-77.
- Zimmerman, T.L. and D.L. Felder. 1991. Reproductive ecology of an intertidal brachyuran crab, Sesarma sp. (nr. reticulatum), from the Gulf of Mexico. Biological Bulletin 181:387-401.