Zootaxa 3949 (2): 217–228
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3949.2.4
http://zoobank.org/urn:lsid:zoobank.org:pub:F74491D7-DD55-4737-BA32-5E0B54A278FA

Morphological and morphometric comparison of the first zoeal stage of the mangrove crabs of the genus *Aratus* H. Milne Edwards, 1853 (Decapoda: Sesarmidae)

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Abstract

The mangrove crab *Aratus pisonii* (H. Mile Edwards, 1837) was considered to have an amphi-American distribution but a recent genetic study revealed that the Eastern Tropical Pacific populations represent a new species, *A. pacificus* (Thiercelin & Schubart, 2014). These sister species separated by the Central American Isthmus have developed under different environmental conditions that may influence their larval development. A comparison of morphological and morphometric features (length and width of cephalothorax and length of rostral and dorsal spine, antenna, antennule, telson, and furcae) of recently-hatched larvae of *A. pacificus* (Pacific coast) and *A. pisonii* (Caribbean coast) from Costa Rica revealed that the setation pattern of the antennules differed between the species and the analyzed morphometric features were larger in *A. pisonii* larvae. Difference in size may be a response to different environmental conditions, as the lower primary production in coastal Caribbean waters, which may have forced females of *A. pisonii* to allocate more energy into the offspring, resulting in larger zoeal size. A greater endogenous reserve may allow the larvae to reduce the duration of the planktonic phase and increase the size at metamorphosis, thus enhancing their survival chances during the planktonic phase. These data regarding morphological and morphometric differences in recently-hatched larvae of the Pacific and Caribbean species support the conclusion that specimens of *Aratus* from both coasts of Costa Rica represent indeed different species.

Key words: Larvae, transisthmian sister species, interspecific variability, speciation

Introduction

Most marine invertebrates have a complex life cycle, usually characterized by larvae that drift in the plankton until they metamorphose into a juvenile stage that recruit the habitat of the adults (Giménez & Anger 2003; Anger 2006). The larval phase present a wide array of adaptive traits that differ from subsequent life history stages (Anger 2001, 2006). These traits are genetically hereditable and influenced by past and present environmental conditions (Anger 2006; Giménez 2006). Larval descriptions are therefore often considered in the process to define phylogenetic relationships (Ng & Clark 2000; Felder & Martin 2003; Anger 2006), particularly in cases where adults are difficult to distinguish (Ng & Clark 2000; Cuesta & Anger 2001).

The emergence of the Central American Isthmus, roughly 3.5 million years ago, provides a unique opportunity to study how environmental conditions shaped the expression of early ontogenic characters of species separated by this geographic barrier (Lessios 2008; McAlister 2008). The Isthmus divided a previously continuous oceanic region, causing the formation of two very different marine systems, the Eastern Tropical Pacific (ETP) and Caribbean Sea. Each of these systems presents particular conditions regarding temperature, salinity, seasonality, and primary productivity (Haugh & Tieldermann 1998; Steph *et al*. 2006; Jain & Collins 2007). The latter is especially important since food availability is considered one of the key factors determining the endurance of invertebrate larvae in the pelagic environment (Anger 2001; Giménez & Anger 2005).

Accepted by P. Castro: 16 Mar. 2015; published: 24 Apr. 2015

endogenous nutrient reserves is advantageous to reduce their dependence on external food (Moran & Allen 2007) and improve their fitness in this more competitive environment (Allen *et al.* 2008). In areas with reduced food availability, larger offspring perform better than smaller conspecific; the greater energetic reserve provide them the advantage of reaching metamorphosis sooner, thereby shortening their planktonic phase, which in turn reduces the risk of predation and starvation (Hart 1995; Giménez & Anger 2003; 2005, Bas *et al.* 2007).

Temperature can also influences the embryo development and the larval phase of crustacean larvae (Shirley *et al.* 1987; Wehrtmann & López 2003; Barría *et al.* 2005). At higher temperatures the incubation period is reduced (Wear 1974; Hamasaki 2003), and the hatching larvae tend to attain smaller sizes than those where embryos were incubated at lower temperatures (Shirley *et al.* 1987; Wehrtmann & López 2003). This tendency can also be observed in the case of the two *Aratus* species studied herein: the zoea I obtained from the sampling site with considerably higher average temperature (Pacific; *Aratus pacificus*) were smaller than those (*A. pisonii*) collected from the Caribbean coast with lower average temperature.

Apart of these size differences, larvae from both species studied herein differed significantly in the ratios of dorsal/rostral spine length (Table 4), with *A. pisonii* zoeae having proportionally larger dorsal and rostral spines. Cuesta and Anger (2001) nevertheless compared the TFL/TBL ratio among different sesarmid species and reported for a Caribbean population of *A. pisonii* a lower value (<1.9) than those obtained in this study. Comparisons with additional populations are therefore needed to determine the degree of interpopulational variability of this parameter.

Larval studies between other decapod species occurring at both Caribbean and Pacific coasts have raised doubts about their conspecific status (i.e. Gore 1972; Thatje & Bacardit 2000), especially due to the fact that transisthmian sibling species showed clear form and size variations in early ontogenic stages (Cuesta & Schubart 1999; Bartilotti *et al*. 2012). Thiercelin and Schubart (2014) more recently analyzed *Aratus* specimens collected across the Isthmus, and used genetic as well as male gonopod characteristics to distinguish two *Aratus* species and to describe *A. pacificus* for the Pacific coast of Central America.

The intrageneric variability is typically very low in the first zoea of decapods. As mentioned by Mantelatto *et al.* (2014), there are only very few characters where first zoeal stages show differences among closely related species. The setae and aesthetasc numbers of the zoea I antennules remained constant between specimens of the same coasts, but differed between the Pacific and Atlantic individuals (Table 2). The difference regarding this feature, together with the smaller size of the offspring of the Pacific corroborate the recent separation of the genus in a Pacific and Atlantic species.

Acknowledgments

We are grateful to the Instituto Costarricense de Electricidad (ICE), which provided logistic support for the collection of *Aratus pacificus* in the Térraba-Sierpe's mangrove as part of the Diquís Hydroelectric Project. Special thanks are due to the assistants that collaborated with the sampling of *A. pisonii* in the Gandoca's lagoon. We appreciate the comments of the anonymous reviewers and Zootaxa editor, Dr. Peter Castro, which served to improve the quality of the manuscript. The present study was completed by the first author to partially fulfill the requirements for a M.Sc. degree in Biology at the Escuela de Biología, Universidad de Costa Rica.

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