Available online at www.sciencedirect.com
ScienceDirect
Comparative Biochemistry and Physiology, Part A 151 (2008) 423–436
CBP
www.elsevier.com/locate/cbpa

Review

Biochemical and physiological adaptations in the estuarine crab *Neohelice granulata* during salinity acclimation ☆

Adalto Bianchini [a,*], Mariana Machado Lauer [b], Luiz Eduardo Maia Nery [a], Elton Pinto Colares [a], José María Monserrat [a], Euclydes Antônio dos Santos Filho [a]

[a] *Departamento de Ciências Fisiológicas, Fundação Universidade Federal do Rio Grande, Campus Carreiros, Av. Itália km 8, 96201-900, Rio Grande, RS, Brazil*
[b] *Programa de Pós-Graduação em Ciências Fisiológicas – Fisiologia Animal Comparada, Fundação Universidade Federal do Rio Grande, Campus Carreiros, Av. Itália km 8, 96201-900, Rio Grande, RS, Brazil*

Received 3 May 2006; received in revised form 21 November 2007; accepted 3 December 2007
Available online 8 December 2007

Abstract

Neohelice granulata (*Chasmagnathus granulatus*) is an intertidal crab species living in salt marshes from estuaries and lagoons along the Atlantic coast of South America. It is a key species in these environments because it is responsible for energy transfer from producers to consumers. In order to deal with the extremely marked environmental salinity changes occurring in salt marshes, *N. granulata* shows important and interesting structural, biochemical, and physiological adaptations at the gills level. These adaptations characterize this crab as a euryhaline species, tolerating environmental salinities ranging from very diluted media to concentrated seawater. These characteristics had led to its use as an animal model to study estuarine adaptations in crustaceans. Therefore, the present review focuses on the influence of environmental salinity on *N. granulata* responses at the ecological, organismic and molecular levels. Aspects covered include salinity tolerance, osmo- and ionoregulatory patterns, morphological and structural adaptations at the gills, and mechanisms of ion transport and their regulation at the gills level during environmental salinity acclimation. Finally, this review compiles information on the effects of some environmental pollutants on iono- and osmoregulatory adaptations showed by *N. granulata*.

Keywords: *Neohelice granulate*; *Chasmagnathus granulatus*; Crab; Gills; Ionoregulation; Osmoregulation; Salinity; Pollution

Contents

☆ This paper is part of the 5th special issue of CBP dedicated to The Face of Latin American Comparative Biochemistry and Physiology organized by Marcelo Hermes-Lima (Brazil) and co-edited by Carlos Navas (Brazil), Rene Beleboni (Brazil), Carolina A. Freire (Brazil), Tania Zenteno-Savín (Mexico) and the editors of CBP. This issue is dedicated to the memory of Knut Schmidt-Nielsen (1915–2007), a great mind in comparative physiology, with books translated into 16 languages, including Spanish and Portuguese, and Cicero Lima (1934–2006), journalist, science lover and Hermes-Lima's dad.

* Corresponding author. Fundação Universidade Federal do Rio Grande, Departamento de Ciências Fisiológicas, Av. Itália km 8 – Campus Carreiros, 96.201-900, Rio Grande, RS, Brazil. Tel.: +55 53 3233 6853; fax: +55 53 3233 6848.
E-mail addresses: adalto@octopus.furg.br, adalto@vetorial.net (A. Bianchini).

1095-6433/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.cbpa.2007.12.001

1. General aspects

The main goal of the present review is to discuss the biochemical and physiological responses of the estuarine crab *Neohelice granulata* (Crustacea, Decapoda, Brachyura) to environmental saline stress. Aspects covered will include salinity effects on *N. granulata* responses at the ecological, organismic and molecular levels. Crab salinity tolerance and the ionic and osmotic regulation patterns associated with environmental salinity changes will be discussed. Morphological and structural adaptations, as well as the mechanisms of ion transport and their regulation at the gills level during salinity acclimation will also be analyzed and modeled. Finally, this review will compile information on the biochemical and physiological effects of some environmental pollutants on the iono- and osmoregulatory adaptations showed by *N. granulata*.

The burrowing crab *N. granulata*, formerly known as *Chasmagnathus granulata* or *C. granulatus* (Sakai et al., 2006), is the most abundant macroinvertebrate on intertidal mudflats and salt marshes of the South Western Atlantic (Iribarne et al., 2000). It lives in both vegetated and non-vegetated areas (Bass et al., 2005) along the South Atlantic coast from Rio de Janeiro (Brazil) to Patagonia (Argentina) (Boschi, 1964). Density and sex ratio vary among seasonal periods and areas. Spatial and temporal variations in sex ratio and size frequency distributions among microhabitats suggest that the structure of *N. granulata* populations is dynamic, with a clear spatial segregation of sizes and sexes. Interpopulational differences in density, size and reproductive period are not simply attributed to changes associated with a latitudinal cline. Other factors, such as food availability and thermal stress seem to be implicated (Bass et al., 2005).

N. granulata has important ecological roles in intertidal mudflats and salt marshes, controlling or affecting different physico-chemical and biological aspects in these environments. For example, it excavates and maintains large semi-permanent open burrows that work as passive traps for debris, increasing the retention of this material in mudflats (Iribarne et al., 2000). *N. granulata* is also considered as a key species in the energy transfer in mudflats and salt marshes, grazing on the cordgrass *Spartina densiflora* (D' Incao et al., 1990). Evidences suggest that *N. granulata* affects cordgrass production by herbivory on new shoots (Bortolus and Iribarne, 1999). This crab also plays an important role on the structure of the meiofauna community in estuarine intertidal habitats (Rosa and Bemvenuti, 2005). For example, polychaete distribution and availability to shorebirds are affected by *N. granulata* activity, establishing an important shorebird–burrowing organism interaction (Botto et al., 2000; Palomo et al., 2003; Iribarne et al., 2005). Another example of the ecosystem engineering ability of *N. granulata* is related to the fact that the environmental heterogeneity produced by its activity has an effect on the infaunal behavior, risk of mortality, and the zonation pattern (Escapa et al., 2004).

2. Environmental salinity effects

As for other estuarine animals, environmental salinity drives several aspects of *N. granulata* biology. It is a key parameter in the larval biology (Anger, 2003). For example, pre-hatching salinity is very important for larval survival, growth, and duration of development under normal condition or food stress (Gimenez and Anger, 2001; Gimenez, 2002; Gimenez and Torres, 2002; Gimenez and Anger, 2003). Also, interpopulational differences in low salinity tolerance of embryos and larvae are related to environmental differences between habitats (Bass and Spivak, 2003). However, first larval stages and juveniles of *N. granulata* have a better survival and development in high salinities (Boschi et al., 1967; Rieger and Nakagawa, 1995).

Environmental salinity also influences juvenile and adult *N. granulata* distribution and abundance within different populations. For example, highest abundances are observed in the Patos Lagoon estuary (Southern Brazil) during periods of moderate increasing temperature and salinity. Furthermore, high abundance of ovigerous females is reported in saltwater during the summer. These patterns are likely associated with the species reproductive and recruitment strategies (D'Incao et al., 1992). In addition to these ecological effects, environmental salinity changes can also induce several responses at the organismic level.

At the behavioral level, environmental salinity is an external cue involved in the memory control in *N. granulata*. For example, exposure to high environmental salinity (33‰), for at least 4 days, triggers an enhanced long-term memory. This facilitatory effect is induced by synthesis of angiotensin-II-like peptides in several neural structures of *N. granulata*, thus being involved in the association between context and iterative danger stimulus in this crab species (Delorenzi et al., 2000).

At the metabolic level, salinity affects growth and biochemical composition of larvae, influencing directly the number and quality of larvae reaching metamorphosis. For example, exposure of Zoea I larvae to low salinity induces lower increments in dry weight, lipid and protein contents (Torres et al., 2002). In juvenile and adult *N. granulata*, acclimation to low salinity induces lipid mobilization in gills and muscle (Luvizotto-Santos et al., 2003). Carbohydrate metabolism is also modified during environmental salinity changes. Increases in hemolymph glucose levels are observed after hypo- or hyper-osmotic stress (Santos and Nery, 1987; Da Silva and Kucharski, 1992). However, glucose metabolism is seasonal dependent. In the summer, saline stress (hypo- or hyper-osmotic shock) induces gluconeogenesis in gills,