



Contents lists available at ScienceDirect

## Comparative Biochemistry and Physiology, Part A

journal homepage: [www.elsevier.com/locate/cbpa](http://www.elsevier.com/locate/cbpa)

## Ecophysiology of native and alien-invasive clams in an ocean warming context

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## ARTICLE INFO

## Article history:

Received 16 January 2014

Received in revised form 4 May 2014

Accepted 7 May 2014

Available online xxxx

## Keywords:

Biological invasions

Metabolism

Oxidative stress

*Ruditapes decussatus**Ruditapes philippinarum*

Thermal tolerance

## ABSTRACT

Both climate change and biological invasions are among the most serious global environmental threats. Yet 22  
 mechanisms underlying these eventual interactions remain unclear. The aim of this study was to undertake a 23  
 comprehensive examination of the physiological and biochemical responses of native (*Ruditapes decussatus*) 24  
 and alien-invasive (*Ruditapes philippinarum*) clams to environmental warming. We evaluated thermal tolerance 25  
 limits (CTMax), routine metabolic rates (RMRs) and respective thermal sensitivity ( $Q_{10}$  values), critical oxygen 26  
 partial pressure ( $P_{crit}$ ), heat shock response (HSP70/HSC70 levels), lipid peroxidation (MDA build-up) and anti- 27  
 oxidant enzyme [glutathione-S-transferase (GST), catalase (CAT) and superoxide dismutase (SOD)] activities. 28  
 Contrary to most studies that show that invasive species have a higher thermal tolerance than native congeners, 29  
 here we revealed that the alien-invasive and native species had similar CTMax values. However, warming had a 30  
 stronger effect on metabolism and oxidative status of the native *R. decussatus*, as indicated by the higher RMRs 31  
 and HSP70/HSC70 and MDA levels, as well as GST, CAT and SOD activities. Moreover, we argue that the alien- 32  
 invasive clams, instead of up-regulating energetically expensive cellular responses, have evolved a less demand- 33  
 ing strategy to cope with short-term environmental (oxidative) stress-pervasive valve closure. Although efficient 34  
 during stressful short-term periods to ensure isolation and guarantee longer survival, such adaptive behavioural 35  
 strategy entails metabolic arrest (and the enhancement of anaerobic pathways), which to some extent will not be 36  
 advantageous under the chronically warming conditions predicted in the future. 37

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## 1. Introduction

Estuaries are among the most socio-economically and ecologically 58  
 important coastal ecosystems and are known to be constantly subjected 59  
 to anthropogenically derived pollution and natural stressors (e.g. tem- 60  
 perature, pH, dissolved oxygen, salinity). Additionally, it has been re- 61  
 cently shown that these coastal areas are warming at a faster rate in 62  
 comparison to many other ecosystems (MacKenzie and Schiedek, 63  
 2007). According to the most recent report of the Intergovernmental 64  
 Panel on Climate Change (IPCC), it is expected that by the end of the 65  
 21st century global mean surface temperature will increase by 66  
 0.3–4.8 °C (IPCC, 2013). Since many coastal organisms already live 67  
 close to their thermal tolerance limits (Stillman and Somero, 2000; 68  
 Helmuth et al., 2006; Hoegh-Guldberg et al., 2007; Tewksbury et al., 69  
 2008), ocean warming is expected to negatively impact their perfor- 70  
 mance and survival (Rosa et al., 2012, 2013, 2014). As a consequence, 71

this future thermal challenge will especially affect marine ectothermic 58  
 organisms (e.g. bivalve molluscs) since their metabolism is constrained 59  
 by oxygen supply at high (and low) temperatures with a progressive 60  
 transition to an anaerobic mode of energy production [the “oxygen- 61  
 and capacity-limitation of thermal tolerance” concept (Pörtner and 62  
 Knust, 2007)]. The changes in aerobic scope of ectotherms with global 63  
 warming are assumed to not be caused by lower levels of ambient 64  
 oxygen, but rather by limited capacity of oxygen supply mechanisms 65  
 (ventilatory and circulatory systems) to meet an animal's temperature- 66  
 dependent oxygen demand (Pörtner and Knust, 2007). 67

There is increasing evidence that climate change will influence the 68  
 dynamics of biological invasions, by affecting alien species entry path- 69  
 ways, establishment, spreading and colonization of new habitats 70  
 (Capdevila-Argüelles and Zilletti, 2008). It is expected that, with global 71  
 warming, inter-specific competition will occur with the more warm- 72  
 adapted species replacing native species. The latter usually display 73  
 lower thermal tolerance and, consequently, are unable to physiological- 74  
 ly respond to extreme conditions (Calosi et al., 2008; Somero, 2010). 75  
 Thus, the differential biological responses to future warming will have 76  
 serious ecological (e.g. impact on ecosystem structure and function) 77

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and economic implications (Hellmann et al., 2008). In Portugal, an example of native and alien species interactions is the closely related clam species: the grooved carpet shell clam *Ruditapes decussatus* (native species in the Atlantic and Mediterranean waters) and the Manila clam *Ruditapes philippinarum* (native species from the Indo-Pacific region). The latter was introduced in the beginning of the 1970s for aquaculture purposes in North European Atlantic and Mediterranean coastal waters (Flassch and Leborgne, 1992). This species has been recognized as one of the most successful invaders, being among the “100 worst invasive species in the Mediterranean” (Streftaris and Zenetos, 2006). Its high potential for dispersal, fast growth and ability to adapt new environments can have a major impact on local macrobenthic fauna and flora since it competes for food and space with other filter-feeding invertebrates (Otero et al., 2013).

Studies suggesting that invasive species are more eurythermal (ability to maintain physiological function over a wide range of temperatures) than native species have typically relied on latitudinal range as a proxy for both habitat temperature ranges and physiological temperature tolerance (Rejmánek, 1995, 1996; Rejmánek and Richardson, 1996). Yet although there is a growing interest in the study of physiological responses to environmental stress between alien-invasive and native organisms (Braby and Somero, 2006; Henkel et al., 2009; Lockwood and Somero, 2011; Zerebecki and Sorte, 2011; Coccia et al., 2013), the mechanisms underlying the interaction between climate change and successful biological invasions remain unclear.

The aim of this study was to undertake, for the first time, a comprehensive examination of the physiological and biochemical responses of native (*R. decussatus*) and alien-invasive (*R. philippinarum*) clams to thermal stress. More specifically, we investigated possible differences in: i) thermal tolerance limits (CTMax), ii) routine metabolic rates (RMRs), iii) thermal sensitivity ( $Q_{10}$  values), iv) critical oxygen partial pressure ( $P_{crit}$ ), v) heat shock response (HSP70/HSC70 levels), vi) lipid peroxidation (MDA buildup) and vii) antioxidant enzyme [glutathione-S-transferase (GST), catalase (CAT) and superoxide dismutase (SOD)] activities.

## 2. Materials and methods

### 2.1. Specimen collection and stocking conditions

Specimens of *R. decussatus* (mean  $\pm$  standard deviation; total weight:  $6.7 \pm 1.1$  g; soft-tissue weight:  $3.0 \pm 0.9$  g; shell length:  $31.2 \pm 1.8$  mm; shell width:  $14.8 \pm 0.9$  mm; shell height:  $22.5 \pm 1.2$  mm) and *R. philippinarum* (mean  $\pm$  standard deviation; total weight:  $13.2 \pm 3.9$  g; soft-tissue weight:  $2.3 \pm 0.4$  g; shell length:  $35.3 \pm 3.0$  mm; shell width:  $18.8 \pm 1.8$  mm; and shell height:  $26.6 \pm 2.3$  mm) were harvested up to 10 and 30 m, respectively, through diving in active bivalve fishing areas of the Sado and Tagus estuaries (Western coast of Portugal; see Supplemental Fig. S1), during summer season (August–September 2012). Additionally, collection of sediment from clam harvest sites was also performed. After collection, *Ruditapes* sp. specimens were immediately transported in thermal boxes, to Guia Marine Laboratory (Centre of Oceanography, Faculty of Sciences, University of Lisbon, Cascais, Portugal) and randomly placed in 14 flat-bottom cylindrical fibreglass tanks (10 L capacity each and 4 cm bottom filled (height) with collection site sediment), within a recirculating aquaculture system, filled with natural seawater (0.2  $\mu$ m and UV filtered). The recirculating aquaculture system was equipped with biological (ouriço®, Fernando Ribeiro Lda, Portugal), mechanical (100  $\mu$ m, TMC-Iberia, Portugal) and physical (ReefSkimPro 850, TMC-Iberia, Portugal) filtration, in addition to UV disinfection (Vecton 600, TM-Iberia, Portugal). Ammonium and nitrite levels were determined daily by means of colorimetric test kits (Aquamerck, Merck Millipore, Germany) and kept below detectable levels. Additionally,

salinity was daily checked and kept at  $35 \pm 1$  PSU (V2 refractometer, TMC, UK). Water temperature was maintained at  $22.0 \pm 0.2$  °C, by means of a water chiller (Frimar, Fernando Ribeiro Lda, Portugal) and submersible heaters (300 W, Eheim GmbH & Co. KG, Germany), while pH was kept at  $8.2 \pm 0.1$ . Up and down pH regulation was performed through a CO<sub>2</sub> and filtered atmospheric air (soda lime) injection system, controlled by a Profilux control system (Profilux 3.1N, GHL, Germany). Photoperiod was kept to 14-h light–10-h dark. The acclimation temperature (22 °C) was chosen since it reflects the average thermal value that both clam species face throughout the summer months in the estuaries. Clams were acclimated during seven days and fed 4× a day, with a commercially available microalgal mix (*Isochrysis*, *Pavlova*, *Tetraselmis*, *Thalassiosira* and *Nannochloropsis* spp.; Acuinuga, Coruña, Spain) with the exception for the day prior to the experimental assays (respirometry and thermal tolerance experiments).

### 2.2. Thermal tolerance limits

Thermal tolerance was determined by the dynamic method described in Mora and Ospina (2001). The measured parameter was the Critical Thermal Maximum (CTMax given in degrees Celsius), defined as the “arithmetic mean of the collective thermal points at which the end-point is reached” (Mora and Ospina, 2001).

In order to determine the CTMax, organisms were subjected to a thermostable bath and placed into separated plastic containers, 20 specimens of each species, comprising three replicates (total  $n = 60$ ). The bath temperature was set to the acclimation temperature and maintained for 30 min. Thereafter, temperature was increased at a rate of 1 °C per 30 min and clams were observed continuously, until they reached the end-point. Every 30 min, seawater was aerated and temperature in each container was checked, using a digital thermometer (TFX 430, Ebro, Germany). Afterwards, for each temperature gradient (from 22 °C to the temperature at which 50% of the clams died—LT50) and species, four individuals were immediately frozen in liquid nitrogen and stored at  $-80$  °C for subsequent biochemical analyses. In order to distinguish between live and dead specimens, inactive individuals were mechanically stimulated. All dead clams showed the valves completely open and no reaction to the stimulus (end-point). Since environmental variables that could influence results (e.g. oxygen levels, salinity, pH, feeding and temperature) were monitored during the acclimation and experiments, it is assumed that the observed results were due to temperature.

### 2.3. Routine metabolic rates, valve closure behaviour and thermal sensitivity

Oxygen consumption rates (routine metabolic rates; RMRs) were determined according to previously established methods (Rosa and Seibel, 2008, 2010; Aurélio et al., 2013). Individual clams were placed within an intermittent flow-through respirometry system (250 mL chambers; Loligo Systems, Tjele, Denmark). Five specimens of each species were used per temperature (from 22 °C to LT50). Respiration chambers were placed in thermostable water baths (Lauda, Lauda-Königshofen, Germany) in order to control the temperature. Oxygen concentrations were recorded with Clarke-type O<sub>2</sub> electrodes (SI130 microcathode oxygen electrode, Strathkelvin instruments Limited, North Lanarkshire, Scotland) connected to a multichannel oxygen interface (929, Strathkelvin Instruments Limited, North Lanarkshire, Scotland), during 2 h for each temperature gradient. System calibration was performed using oxygen-saturated seawater and checked for electrode drift before each run and at each experimental temperature. Due to weight dissimilarity between specimens of both species, RMRs were standardized to 2.5 g of soft-tissue wet weight assuming a scaling coefficient of  $-0.25$  (3/4 power law; see also Rosa et al., 2009).

During respirometry runs, valve closure behaviour was also monitored, i.e., clams were continuously observed in order to detect opened

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