G Model
ECOIND-2742; No. of Pages 11

ARTICLE IN PRESS

Ecological Indicators xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms

Catarina Vinagre[a,*], Inês Leal[a], Vanessa Mendonça[a], Diana Madeira[b], Luís Narciso[a], Mário S. Diniz[b], Augusto A.V. Flores[c]

[a] MARE – Marine and Environmental Sciences Centre, Universidade de Lisboa, Faculdade de Ciências, Campo Grande, 1749-016 Lisboa, Portugal
[b] UCIBIO-Requimte, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal
[c] Centro de Biologia Marinha, Universidade de São Paulo, Rod. Manoel Hipólito do Rego, km 131.5, São Sebastião, SP, Brazil

ARTICLE INFO

Article history:
Received 13 July 2015
Received in revised form 22 October 2015
Accepted 10 November 2015
Available online xxx

Keywords:
Global change
Warming tolerance
Upper thermal limits
Critical Thermal Maximum
Rocky shore
Intertidal

ABSTRACT

Ecological forecasting on the likely impacts of climate warming is crucial at a time when several ecosystems seem to be responding to this environmental threat. Among the most important questions are: which are the most vulnerable organisms to climate warming and where are they? Recently, there has been debate on whether the tropics or temperate zones are more vulnerable to warming. Vulnerability toward higher temperatures will depend on the organisms' thermal limits and also on their acclimation capacity, which remains largely unknown for most species. The aim of the present work was to estimate (1) the upper thermal limits (Critical Thermal Maximum (CTMax)), (2) the warming tolerance (CTMax – Maximum Habitat Temperature) and (3) the acclimation capacity of tropical and temperate rocky shore organisms. Differences in biological groups (decapod crustaceans *vs* fish) were investigated and the effect of region (tropical *vs* temperate) and habitat (intertidal *vs* subtidal) was tested. Overall, 35 species were tested. For the assessment of the acclimation capacity, tropical-temperate pairs of closely related species of shrimp, crab and fish were selected. Warming tolerance was higher for temperate species than for tropical species and higher for subtidal species than for intertidal species, confirming that species with the highest thermal limits have the lowest warming tolerance. All species tested presented some acclimation capacity ($CTMax_{Trial} - CTMax_{Control}$), with the exception of gobiid fish, which was not observed to acclimate. The tropical species tested showed a lower acclimation capacity than their temperate counterparts. Given that tropical rocky shore organisms are already living very close to their thermal limits and that their acclimation capacity is limited, it is likely that the impacts of global warming will be evident sooner in the tropics than in the temperate zone.

1. Introduction

Understanding the impact of global warming on biodiversity is one of the most important challenges faced by mankind. Equally important is the identification of which ecosystems and species are more vulnerable to this threat. Recently, there has been a debate on whether the tropics or temperate zones are more vulnerable to warming (Ghalambor et al., 2006; Tewksbury et al., 2008). The rate of warming is predicted to be lower in the tropics than in temperate zones (IPCC, 2007), however, species that live in aseasonal environments may suffer disproportionally from small increases in temperature (Tewksbury et al., 2008; Hoffmann and Todgham, 2010; Pörtner and Peck, 2010).

This way, tropical species may be more vulnerable to further warming compared to their temperate counterparts. In fact, thermal studies regarding different taxa from different latitudes, such as terrestrial insects, amphibians and marine invertebrates, have shown that tropical organisms are living quite close to their thermal limits (*e.g.* Stillman, 2003; Deutsch et al., 2008; Tewksbury et al., 2008; Duarte et al., 2012). However, vulnerability toward higher temperatures will depend on the organisms' thermal limits and also on their acclimation capacity, which remains largely unknown for most species.

Acclimation can be described as "any phenotypic response to environmental temperature that alters performance and plausibly enhances fitness" (Angilletta, 2009). It implies the detection of an environmental signal, the transduction of this signal into a cellular response, and the activation of molecules (*e.g.* genes, ribosomes, enzymes) that cause a change in the phenotype (Wilson and Franklin, 2002; Angilletta et al., 2006). Thus, thermal acclimation

* Corresponding author. Tel.: +351 21 750 08 26; fax: +351 21 750 02 07.
E-mail address: cmvinagre@fc.ul.pt (C. Vinagre).

http://dx.doi.org/10.1016/j.ecolind.2015.11.010
1470-160X/

Please cite this article in press as: Vinagre, C., et al., Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms. Ecol. Indicat. (2015), http://dx.doi.org/10.1016/j.ecolind.2015.11.010

comprises regulated responses to diel or seasonal changes in temperature, so as to match physiology to the current environment (Angilletta, 2009).

The ability to acclimate results from existing phenotypic plasticity in populations and it is an important mechanism for coping with environmental temperature changes (Wilson and Franklin, 2002; Lucassen et al., 2006). Through acclimation, ectotherms are able to maintain physiological functions and performance across a wide thermal range. This is a common attribute in species that experience pronounced seasonal variations in temperature, such as the ones inhabiting temperate mid-latitudes (Huey and Hertz, 1984; Guderley and St-Pierre, 2002). The organisms at greatest risk from global warming impacts will be the ones with narrow thermal tolerance ranges, limited acclimation capacity, long generation times and reduced dispersal (see Pörtner and Farrell, 2008).

Predicted increases in frequency, duration, intensity and spatial extent of heat waves (IPCC, 2013) will impose both long and short-term thermal stress on tropical and temperate organisms. Both have the potential to elicit an acclimation response.

Stillman (2003) explored the interspecific variability in response to warming in porcelain crabs (genus *Petrolisthes*) and found that species with the greatest tolerance to high temperatures displayed the smallest acclimation capacity. Additionally, Rezende et al. (2014) demonstrated that the temperature range that an organism can tolerate is expected to narrow down with the duration of the thermal challenge, suggesting that a trade-off exists between tolerance to acute and chronic exposition to thermal stress. These findings suggests that species with the higher thermal limits may be the most vulnerable to small sustained increases in temperature, this way, tropical species appear as the most vulnerable to global warming (Somero, 2010). However, besides thermal limits *per se*, intraspecific variability must also be considered. Species with enough genetic variability to generate phenotypes with a wide range of thermal tolerances may become "winners" in a warming world, since exceptionally physiologically robust individuals can be selected through successive generations resulting in genetic adaptation (Somero, 2010).

One of the habitats where the impacts of climate change are likely to strike first is the intertidal zone. Rocky shore habitats exist at the margins between the terrestrial and the marine realms, thus they are not only subject to the changes in water temperature, but also the aerial climatic regime, functioning as early warning systems for climate change impacts (Helmuth et al., 2006). Scientists have long used rocky shore ecosystems as natural laboratories for studying community dynamics, it is now also considered a particularly interesting model-system for the investigation of global warming impacts (Helmuth et al., 2006).

The present study aimed to test the thermal vulnerability of a wide range of coastal species and compare the capacity of tropical and temperate coastal organisms to acclimate their upper thermal limits when exposed to long-term and short-term increases in temperature. Coastal shrimps, crabs and fish were tested. Key species in coastal rocky shore ecosystems were chosen, and where possible an effort was made to collect tropical species that had a temperate con-generic counterpart, for a more direct comparison. When this was not possible species from the same family were chosen.

More specifically, the aims of the present work was to estimate (1) the upper thermal limits (CTMax), (2) the warming tolerance (Maximum Habitat Temperature – CTMax), and (3) the acclimation capacity of tropical and temperate rocky shore organisms. Differences in biological groups (decapod crustaceans *vs* fish) were investigated and the effects of region (tropical *vs* temperate) and habitat (intertidal *vs* subtidal) were tested.

The warming tolerance was defined as the difference between the critical thermal maximum of each species and the maximum habitat temperature of each respective habitat. The acclimation capacity of each species was defined has each species' ability to significantly increase its CTMax after exposure to a higher temperature for a period of time.

For the assessment of the acclimation capacity, the Critical Thermal Maximum (CTMax) of the selected species was estimated after seven days at a control temperature (CTMaxControl) (26 °C for tropical organisms and 20 °C for temperate organisms) and after a (1) long-term trial (30 days at "control temperature +3 °C") (CTMax1), representing the future summer temperature, and a (2) short-term trial (10 days at "control temperature +6 °C") (CTMax2), representing future heat waves.

Differences in CTMax were investigated, for each species, between the control and the long-term and the short-term trials. Differences of acclimation capacity (CTMax1 – CTMaxControl and CTMax2 – CTMaxControl) and in the coefficient of variation of CTMax were investigated between tropical and temperate organisms.

2. Materials and methods

2.1. Study areas

Coastal shrimps, crabs and fish were collected in a tropical and a temperate rocky shore, in the summer of 2014 in Southeastern Brazil (23°49′ S; 45°25′ W) and Western Portugal (38°41′ N; 9°21′ W). The tropical area studied has an annual mean sea surface temperature (SST) of 24 °C and a mean summer SST of 26 °C, while the temperate study area has an annual mean SST of 17 °C and a mean summer SST of 19 °C (Locarnini et al., 2010).

Data on water temperature of subtidal water and tidal pools was registered, with Hobo V2 probes, in the summer of 2014 and 2015, in both areas, during ebb tides, in 9 tidal pools in the tropical study area and 4 in the temperate study area. The maximum water temperature registered in tropical tidal pools was 41 °C, in February 2014, while in the temperate area it was 30 °C, in June 2014 (see Supplementary material for temperature data).

2.2. Species tested

The tropical decapod crustacean species studied were the shrimps *Palaemon northropi* (Rankin 1898) and *Hippolyte obliquimanus* Dana 1852, and the crabs *Pachygrapsus transversus* (Gibbes 1850), *Menippe nodifrons* Stimpson 1859 and *Eurypanopeus abbreviatus* (Stimpson 1860). The tropical fish species studied were *Scartella cristata* (Linnaeus 1758), *Eucinostomus melanopterus* (Bleeker 1863), *Bathygobius soporator* (Valenciennes 1837), *Parablennius marmoreus* (Poey 1876), *Stegastes fuscus* (Cuvier 1830), *Sphoeroides testudineus* (Linnaeus 1758) and *Malacoctenus delalandii* (Valenciennes 1836).

The temperate decapod crustacean species studied were the shrimps *Crangon crangon* (Linnaeus 1758) and the crabs *Lophozozymus incisus* (Milne-Edwards 1834) and *Pachygrapsus marmoratus* (Fabricius 1787). The temperate fish species studied were *Lepadogaster lepadogaster* (Bonnaterre 1788) and *Pomatoschistus microps* (Krøyer 1838). Data for temperate species was completed with that published in Madeira et al. (2012) (which includes the following species: the shrimps *Palaemon longirostris* (Milne-Edwards 1837) and *Palaemon elegans* (Rathke 1837); the crabs *Carcinus maenas* (Linnaeus 1758) and *Liocarcinus marmoreus* (Leach 1814); and the fish *Dicentrarchus labrax* (Linnaeus 1758), *Diplodus bellottii* (Steindachner 1882), *Diplodus sargus* (Linnaeus 1758), *Diplodus vulgaris* (Geoffroy St. Hilaire 1817), *Gobius cobitis* (Pallas 1814), *Gobius niger* (Linnaeus 1758), *Liza ramada* (Risso 1827), *Paralipophrys trigloides* (Valenciennes 1836) and *Solea lascaris* (Risso 1810)), Vinagre et al. (2013a) (which includes the following species: the shrimp