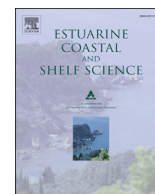




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Do invaders always perform better? Comparing the response of native and invasive shrimps to temperature and salinity gradients in south-west Spain



Christophe Lejeusne*, Oihana Latchere, Nicolas Petit, ¹ Ciro Rico, Andy J. Green

Estación Biológica de Doñana-CSIC, EBD-CSIC, Department of Wetland Ecology, Avenida Américo Vespucio s/n, E-41092 Sevilla, Spain

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ABSTRACT

Invasive species are often thought to benefit from climate change, outcompeting native species as temperatures increase. However, the physiological tolerance has been little explored as a potential mechanism explaining biological invasion success. In this study, we used empirical data from both invasive and native estuarine species as a case study to address the hypotheses that (1) invasive species show a better resistance to acute thermal stress, (2) invasive species present lower oxygen consumption rates owing to greater resistance to environmental stressors, and (3) native species have lower survival rates under chronic temperature and salinity stress. We conducted various comparative experiments on three sympatric and syntopic closely related shrimp species (one invasive *Palaemon macrodactylus*, and two natives *Palaemon longirostris* and *Palaemonetes varians*). We evaluated their critical temperature maxima, their oxygen consumption rates under different salinities and temperatures, and their survival rates under chronic salinity and temperature. We found that the invasive species was the most tolerant to rapid increase in temperature, and consistently consumed less oxygen over a broad range of temperatures and salinities. *Palaemon macrodactylus* also had lower mortality rates at high temperatures than *P. longirostris*. These results support previously reported differences in physiological tolerance between native and invasive species, with the invasive species always performing better. The consistently higher tolerance of the non-indigenous species to temperature variation suggests that climate change will increase the success of invaders.

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1. Introduction

Invasive species often have large-scale ecological impacts on invaded ecosystems and native species (Nentwig, 2007; Richardson and Pysek, 2008). They also have very high economic impacts estimated at more than five per cent of the global economy (Burgiel and Muir, 2010). Together with climate change, they constitute a “deadly duo” threatening worldwide biodiversity (Halpern et al., 2008; Burgiel and Muir, 2010; Barnosky et al., 2012). Both factors can act individually on species abundances, distributions and biotic interactions, inducing local and regional extinctions (Grosholz, 2002; Parmesan, 2006; Lejeusne et al., 2010; Durrieu de Madron et al., 2011), but they also can act synergistically (Dukes and Mooney, 1999; Stachowicz et al., 2002; Hellmann et al., 2008).

To become established then invasive, a non-indigenous species (NIS) has to successfully pass through a series of biotic and abiotic filters acting as barriers between the different steps of the invasion process (see Blackburn et al., 2011 for synthesis). However, the mechanisms leading to a successful invasion are poorly understood in most cases. The numerous non-exclusive hypotheses proposed to explain invasion mechanisms, include evolutionary hypotheses (e.g. hybridisation) and ecological hypotheses (e.g. enemy release) (Hufbauer and Torchin, 2007; Sax et al., 2007; Catford et al., 2009). Another potential mechanism, the physiological tolerance hypothesis, is as yet relatively unexplored (Zerebecki and Sorte, 2011). This hypothesis predicts that invasive species have a greater and/or broader physiological tolerance than native species occupying the same habitat. Predictions of this hypothesis have been verified in a large taxonomical panel of species and stress factors (e.g. Lenz et al., 2011). However, owing to the importance of climate change, most of the studies dealing with this hypothesis have focused on temperature effects and eurythermality of invasives compared to a more stenothermal tolerance of natives (Dukes and Mooney, 1999;

* Corresponding author.

E-mail address: lejeusne@ebd.csic.es (C. Lejeusne).¹ Present address: School of Marine Studies, The University of the South Pacific, Lower Laucala Campus, Suva, Fiji.

McMahon, 2002; Rahel et al., 2008; Zerebecki and Sorte, 2011). In the present study, we address tolerance to two major environmental factors (salinity and temperature) as potential contributors to the success of an invasive estuarine species.

Estuaries are very productive ecosystems providing nursery habitats for many marine and commercial species. These marine-freshwater ecotones show strong fluctuations of physical and chemical parameters at both spatial and temporal scales (e.g. tidal-based salinity fluctuations with a decreasing spatial gradient from the inner mouth). Estuaries are particularly impacted by climate change but are also especially susceptible to biological invasions (Ruiz et al., 1997; Cohen and Carlton, 1998; Wasson et al., 2001; Grosholz, 2002). In the San Francisco estuary, one new NIS is recorded every 14 weeks, and in Europe one fifth of estuarine species are NIS (Cohen and Carlton, 1998; Reise et al., 2006). One key question is whether NIS have more resistance to environmental stressors than native estuarine species, being better adapted to strong fluctuations in temperature and salinity.

The oriental shrimp (also known as migrant prawn, or grass shrimp) *Palaemon macrodactylus* is an estuarine caridean shrimp native to China, Japan and Korea. It was initially introduced to San Francisco Bay, CA in the 1960s, before spreading northward and southward along the US coast. Since 1992, it has reached Europe, Argentina and the north-eastern US coast (Newman, 1963; Cuesta et al., 2004; Spivak et al., 2006; Warkentine and Rachlin, 2010). In European estuaries, the species has spread rapidly and extensively since its first introduction. It is now present from SW Spain to Germany and England, and in the western Black Sea. On the Atlantic coast, the species can interact with two other commercially exploited native species: the Atlantic ditch shrimp *Palaemonetes varians* (a brackish water species found mainly in non-tidal ponds, marshes and canals with hydrological connections to estuaries) and the delta prawn *Palaemon longirostris* (an estuarine species). Despite its relatively small size, *Palaemonetes varians* is often captured for human consumption, use as fishing bait, or use as live diet for aquaculture (Palma et al., 2008), while traditional fishing of *Palaemon longirostris* has local economic importance (Holthuis, 1980; Béguer et al., 2012). Both native Palaemonidae can be very abundant and they occupy a central position in the estuarine trophic network (Salgado et al., 2004), being prey of many European native and commercial fishes (e.g. the European sea bass *Dicentrarchus labrax* for *P. longirostris*) (Salgado et al., 2004; Dauvin and Desroy, 2005).

Competitive interactions between the NIS *Palaemon macrodactylus* and the native *Palaemon longirostris* may be strong, especially for space and food. Both species are estuarine with strong overlap in habitat and trophic preferences (González-Ortegón et al., 2010; Béguer et al., 2011a). In the Guadalquivir estuary (SW Spain), this habitat overlap is maximal in autumn during low abundance of their shared mysid prey *Mesopodopsis slabberi* (González-Ortegón et al., 2006, 2010). Since the NIS was first recorded, an increase in *P. macrodactylus* density records in some European estuaries has coincided with a decrease in density of the native *P. longirostris* (González-Ortegón et al., 2010; Béguer et al., 2011a). A previous study comparing the osmoregulatory capacities of *P. macrodactylus* with the two natives *P. longirostris* and *Palaemonetes varians* indicates that the three species have similar osmoregulatory capacities (González-Ortegón et al., 2006). However, oxygen consumption rates measured under different salinities and dissolved oxygen concentrations suggested that the NIS has a more efficient metabolism and higher tolerance to hypoxic conditions (González-Ortegón et al., 2010). Nevertheless, despite field surveys showing the salinity-related and spatial distribution patterns of these estuarine species (González-Ortegón et al., 2006; Béguer et al., 2011a), little is known of the ecophysiology of the NIS *P. macrodactylus* compared to the natives *P. longirostris* and

Palaemonetes varians, in particular regarding the influence of temperature variations. Taking into account the climate change expected in the Euro-Mediterranean area, the interaction between temperature and salinity might be central to the success of NIS and to changes in status of native species (see Coccia et al., 2013 for an example from the Guadalquivir delta).

Studying the relative performance of NIS and natives under a range of environmental conditions allows evaluation of the likely mechanisms of a successful invasion, and testing of the physiological tolerance hypothesis. We therefore conducted a series of three experiments to test if *Palaemon macrodactylus* performs better under extreme conditions of temperature and salinity, the two main abiotic stress factors found in estuaries. We evaluated behavioural activity and the critical temperature maxima of different shrimp species under an acute short-term thermal stress. We hypothesized that the NIS would show greater resistance to acute thermal stress, reflected in a higher critical thermal maximum. We also measured oxygen consumption under different conditions of temperature and salinity to test whether the NIS species present lower consumption rates owing to greater resistance to environmental stressors. Finally, we quantified survival under different chronic thermal and salinity stress to test whether the native species had lower survival rates.

2. Materials and methods

2.1. Shrimp collection and laboratory acclimation

The oriental shrimp *Palaemon macrodactylus* and the delta prawn *Palaemon longirostris* were collected in the Guadalquivir estuary, SW Spain (see Fig. 1) at three distinct, tidal sites S1–S3, with *P. macrodactylus* only found at site S2 (environmental parameters at each site are described in Appendix A). The Atlantic ditch shrimp *Palaemonetes varians* was sampled in Veta La Palma (S4 and S5), a complex of fish ponds connected to and supplied with water from the Guadalquivir estuary (Fig. 1 and Appendix A) and protected within Doñana Natural Park, where it is abundant and harvested commercially (see Rodríguez-Pérez and Green, 2012 for details of the study site). Living individuals were collected in 2011 using shrimp keep-nets (mesh size 4 mm) placed at low tide for S1–S3 and recovered 24 h later. The size of the shrimps was estimated by measuring the carapace length from the orbital edge of the eye to the edge of the cephalothorax under a stereomicroscope SteREO Discovery V8 (Zeiss) using AxioVision Rel 4.8.2 (Zeiss) software. In order to reduce catching and manipulation stress, living shrimps were acclimated during at least 48 h before any experiment in aerated aquaria with artificial saltwater at 20 °C and a salinity of 5, obtained by dissolving dry sea-salt Instant Ocean (Aquarium Systems, Mentor, Ohio) in distilled water. Salinity was measured using the Practical Salinity Scale. Aquariums were placed in a climatic chamber (Fitoclima 10000EHHF, Aralab) on a 12 h:12 h dark:light photoperiod. Shrimps were fed daily *ad libitum* with commercial aquarium food (gammarids) before and during all the experiments. In order to reduce stress and injury associated with its determination, sex was characterized after the experiments by looking for the presence or absence of the masculine appendix on the endopodite of the second pleopod (Siegfried, 1980). A summary of size and sex ratio of the specimens used in each experiment is given in Table 1.

2.2. Experiment 1: critical thermal maximum (CT_{max}) experiment

In order to compare thermal stress resistance between the shrimp species, Critical Thermal maximum (CT_{max}) experiments were conducted in May and August 2011. Carapace lengths were

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