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Temperature effects on parental care behaviour in native and invasive *Palaemon* shrimp species

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ABSTRACT

Environmental changes and the spread of non-native species significantly affect wetland ecosystems, such as coastal lagoons. This study investigates the effects of increased temperature on parental care behaviour, specifically pleopod fanning, in ovigerous females of the following three *Palaemon* species: the global invader *Palaemon macrodactylus* and the Mediterranean native *Palaemon elegans* and *Palaemon adspersus*. Under controlled laboratory conditions, we measured pleopod beats per minute across a temperature gradient to assess species-specific responses. Our results showed significant inter-species differences in fanning behaviour, with *P. elegans* exhibiting the lowest pleopod beat rate overall. Temperature showed a strong positive correlation with pleopod beats across all species, whereas dissolved oxygen negatively correlated with pleopod beats in *P. adspersus* and *P. macrodactylus*. Interestingly, *P. elegans* exhibited a unique response compared with its congeneric species, because it was the only species among those studied that did not show a negative correlation between pleopod beat rate and dissolved oxygen concentration. These findings have enhanced our understanding of the behavioural responses of native and invasive *Palaemon* species to environmental alterations, providing valuable insights into how species interact with their changing environments.

Keywords: allochthonous species, aquatic ecosystems, autochthonous species, behavioural ecology, ecological adaptability, Mediterranean lagoons, oxygen availability, reproductive ecology.

Introduction

Environmental stressors and the proliferation of non-native species are among the most important factors affecting wetlands, such as lagoons. These forces exert significant pressure on marine-coastal and transitional environments, which are inherently vulnerable owing to their dynamic nature, structural complexity, and high productivity (Costello and Allen 1966; Turner 1977; Day *et al.* 2012; Vecchioni *et al.* 2022). Marine-coastal and transitional zones exhibit unique ecological characteristics that make them especially susceptible to external alterations. Previous research has underscored the importance of these attributes, illustrating the intricate interplay between biotic and abiotic factors (Costello and Allen 1966; Turner 1977; Day *et al.* 2012). For instance, the Venice Lagoon, one of the largest Mediterranean lagoons, is a highly anthropised environment because of the various phenomena it experiences, such as hydrological events, variation of water level, chemical pollution from large industrial plants located along its coasts, maritime traffic, climate change effects and biodiversity alterations caused by the introduction of non-native species, which are often invasive (Bonato *et al.* 2007; Picone *et al.* 2016; Liuzzo *et al.* 2023). Some of the non-native species that have spread throughout the lagoon are *Celleporella carolinensis* Ryland, 1979, *Caprella scaura* Templeton, 1836, *Xenostrobus* sp., *Dyspanopeus sayi* Smith, 1869, *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, *Ruditapes philippinarum* A. Adams & Reeve, 1850 (Mizzan 1999) and *Palaemon macrodactylus* Rathbun, 1902 (Cavraro *et al.* 2014*a*).

Species such as palaemonid shrimps, owing to their unique life-history strategies (e.g. high abundance, short life span, high mortality rate, extended reproductive seasons and female-biased sex ratio), serve as model organism for studying various ecological and evolutionary phenomena (Cavraro *et al.* 2022). These characteristics align with traits of r-strategist species, facilitating their invasion and enabling rapid responses to external changes (Vejan *et al.* 2023). This adaptability not only promotes the establishment of these shrimps in new environments but also underscores the potential for significant ecological impacts following their introduction and establishment in an invaded area. The Venetian Lagoon hosts *Palaemon macrodactylus*, an invasive shrimp species originating from the north-western Pacific. This species has successfully established populations in various regions worldwide, including the Americas, Australia and several European countries (Ashelby *et al.* 2013). In the Mediterranean Sea, the oriental shrimp *P. macrodactylus* was initially documented in the Balearic Islands in 2009 at the larval stage (Torres *et al.* 2012). Subsequently, adults, including ovigerous females, were found in various Mediterranean regions, such as the northern Adriatic lagoons of Venice, Grado-Marano, and Goro (Cavraro *et al.* 2014*a*; Cuesta *et al.* 2014). The genus *Palaemon* Weber, 1795 is well represented among the nektonic communities of Mediterranean coastal lagoons, with five native species being present (*P. adspersus*, *P. elegans*, *P. longirostris* H. Milne Edwards, 1837, *P. serratus* (Pennant, 1777) and *P. xiphias* Risso, 1816) (Fischer *et al.* 1987). The proliferation of *P. macrodactylus* raises numerous questions about its impact on the indigenous biological community, particularly on native species that are phylogenetically close to *P. macrodactylus*.

In the Mediterranean Sea, *Paleamon elegans* Rathke, 1837 and *Paleamon adspersus* Rathke, 1837 exhibit a sharp niche separation (Bilgin *et al.* 2008; Kuprijanov *et al.* 2017), occupying areas where conditions are suboptimal for each other. *P. adspersus* is known to prefer stable environments with slow-growing, long-living vegetation, such as *Zostera* beds (Cottiglia 1983; Bilgin *et al.* 2008). By contrast, *P. elegans* demonstrates high ecological plasticity, tolerating highly variable environmental conditions (Berglund 1980; Berglund and Bengtsson 1981) and thriving in areas with strong currents (Bilgin *et al.* 2008). Little information is available about the relationship between native and non-native *Palaemon* species (Cavraro *et al.* 2022), particularly concerning the association between reproductive success and environmental parameters (Redolfi Bristol *et al.* 2021; Vejan *et al.* 2023) and how these factors might influence ecological dynamics in transitional ecosystems. Research programs based on laboratory experiments are crucial for better assessing how native and non-native species may be able to face environmental alteration. This research has been planned under controlled laboratory conditions to (i) test the beating behaviour of pleopods, known as fanning, and suggest its role in parental care, and (ii) compare the relationship between temperature and fanning in ovigerous females of three *Palaemon* species to enhance understanding of their adaptability in the context of transitional environments.

Materials and methods

Shrimp collection and housing

Sampling was conducted in the Venice lagoon on the basis of each species' preferred habitat and previous observations (Cavraro *et al.* 2014*b*). Individuals of three *Palaemon* species (*P. macrodactylus*, *P. elegans* and *P. adspersus*) were caught by means of baited fish traps ($25 \times 25 \times 50$ cm; mesh size 4 mm). The bait was PRODAC TABLET-Compound feed in tablets for bottom feeders, because tablets demonstrated to attract animals for the purpose of our research (animal collection for behavioural studies), and they are easy to be conserved and to be managed, compared with fish scraps, which are easily perishable. The traps were left in place for 5 h, and the captured animals were transported to the laboratory in well-aerated containers. *P. macrodactylus* and *P. elegans* were caught in the inner brackish part of the Venice Lagoon, and *P. adspersus* in seagrass beds. This sampling method was selected to minimise animal injuries, because they entered the traps on their own (Cavraro *et al.* 2022). Moreover, the traps were modified to reduce the entrance of crustaceans by adding an iron grid at the trap mouths, and the presence of crabs remained negligible, limited to smaller individuals. Once in the laboratory, *Palaemon* individuals were counted and identified at species level (González-Ortegón and Cuesta 2006). They were then introduced and acclimated (for ~3 days) into separate aquariums, each with a capacity of 120 L, maintained at a salinity of ~30 and a temperature of 20°C. For all the experimental activities, aquarium tanks were equipped with artificial plants (raphia mop) and sedimental material following the protocol of Cavraro *et al.* (2022), simulating the natural conditions during the reproductive period at which the three species were already adapted.

Parental care in response of temperature under controlled laboratory condition

To assess parental care in response to temperature, eight ovigerous females from each species (*P. macrodactylus*, *P. elegans* and *P. adspersus*) were collected from the holding aquarium and weighed using a small plastic container with enough water to submerge one individual at a time (the weight of the container and of water was known); in this way, the handling of the animals was reduced and they were kept in water for most of the analysis. Each individual was placed in an experimental aquarium (48 L) to avoid interaction with the others. To minimise intra-species variability, individuals with similar weights were selected (see Supplementary Table S1). The study of parental behaviour, specifically fanning, was analysed using the focal animal technique (Silva *et al.* 2023). This technique involved video recording the individual for a continuous 10 min by using a tripod-mounted Canon Legria HFS30 camcorder. During this period, an operator monitored all the individual's movements. Within the 10 min of footage, at least 2 min were required during which the individual remained stationary, allowing for clear observation and counting of pleopod beats associated with fanning behaviour. Animals were observed to be less stressed if they were fed prior to recording; so, food was provided each day before the observations.

Recordings were conducted over a period of 5 days for each individual, with the temperature starting at 20°C and increasing by 2°C each day until reaching a final average temperature of 28°C. This temperature range was selected on the basis of preliminary analyses performed on *P. adspersus*, which indicated that individuals exposed to temperatures approaching 30°C exhibited abnormal locomotor performance (C. Facca, unpubl. data). Within each experimental aquarium, both the pleopod beats associated with fanning and the environmental parameters were measured over the 5-day period. The pleopod beats were recorded as beats per minute, whereas temperature (°C) and dissolved oxygen (DO, mg L^{-1}) were recorded using the Hanna HI98509 Checktemp12 thermometer and the LDO optical sensor oximeter HANNA HI98198 respectively.

Data analysis

All considered parameters to assess the pleopod beats and environmental parameters measured in the experimental aquariums underwent Shapiro–Wilk tests for normality and were subsequently analysed using either parametric or non-parametric statistical methods. In particular, the non-parametric Friedman test was used to analyse differences in pleopod beat rate among the three species (*P. macrodactylus*, *P. elegans* and *P. adspersus*). In addition, a Conover's all-pairs *post hoc* test with Bonferroni correction was performed to compare the pleopod beat rate among the species. A Chi-Square test was used to compare weight differences within species. Differences in the inter-species weight were tested with Kruskal–Wallis and *post hoc* Dunn's tests.

To assess the relationship among pleopod beat rate, from three species and environmental parameters, Spearman and Kendall correlation tests were performed. Additionally, to evaluate the variation in pleopod beats in response to increasing temperatures, temperature data were divided into the following five classes of 2°C, each using a graphical approach: T1 (<20°C), T2 (20–22°C), T3 (22–24°C), T4 (24–26°C) and T5 (>26°C). Differences in the pleopod beat rate within each temperature class among species were analysed using the non-parametric Kruskal–Wallis test. Furthermore, a *post hoc* Dunn's test was performed to compare the pleopod beat rate among species within each temperature class. All statistical analyses were undertaken using *R* (ver. 4.4.1, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/).

Results

Significant inter-species differences were detected in the pleopod beat rate ($\chi^2 = 8.4$, $P < 0.05$), which was significantly lower in *P. elegans* than in *P. adspersus* (Conover's test, $P < 0.001$) and *P. macrodactylus* (Conover's, $P < 0.05$) (Fig. 1). The individual weight did not differ significantly within species (*P. macrodactylus*: $\chi^2 = 0.17$, $P = 0.99$; *P. elegans*: $\chi^2 = 0.18$, $P = 1$; *P. adspersus*: $\chi^2 = 0.1$, $P = 1$). On the contrary, significant differences were observed in interspecific weight ($K = 99.60$, $P < 0.001$), confirming that each species differs significantly from the others in terms of weight (Dunn's test, $P < 0.001$).

Significant relationships between pleopod beat rate and environmental variables were shown by the Spearman correlation analysis. A strong positive correlation between pleopod beat rate and temperature was observed for all species (*P. macrodactylus*: $\rho = 0.75$, $P < 0.001$; *P. elegans*: $\rho = 0.75$, $P < 0.001$; *P. adspersus*: $\rho = 0.94$, $P < 0.001$). In contrast, a negative correlation between pleopod beat rate and DO was found for *P. adspersus* ($\rho = -0.88$, $P < 0.001$) and *P. macrodactylus* ($\rho = -0.58$, $P < 0.001$). No significant correlation was detected between pleopod beat rate and DO for *P. elegans* ($\rho = -0.29$, $P = 0.07$) (Fig. 2). Additionally, weight did not show a significant correlation with pleopod beat rate ($\tau = 0.12$, $P = 0.066$).

Significant differences were also observed in the pleopod beat rate among the three species within the different temperature classes (T1, $K = 6.33$, $P < 0.05$; T2, $K = 7.06$, $P < 0.05$; T3, $K = 10.90$, $P < 0.05$; and T4, $K = 7.81$, $P < 0.05$). Specifically, pleopod beat rates were significantly lower in *P. elegans* than in *P. adspersus* in T1, T2, T3 and T4 (Dunn's test, $P < 0.05$). Moreover, pleopod beat rates were significantly lower in *P. elegans* than in *P. macrodactylus* in T3 (Dunn's test, $P < 0.05$) (Fig. 1).

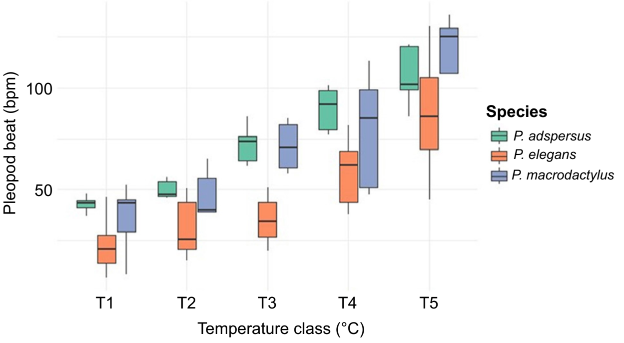

Fig. 1. Boxplot of pleopod beat rates (beats per minute, bpm) in ovigerous females of three *Palaemon* species (*P. adspersus*, *P. elegans* and *P. macrodactylus*) across five temperature treatments (T1–T5). The boxes represent the interquartile range (IQR), with the horizontal line indicating the median.

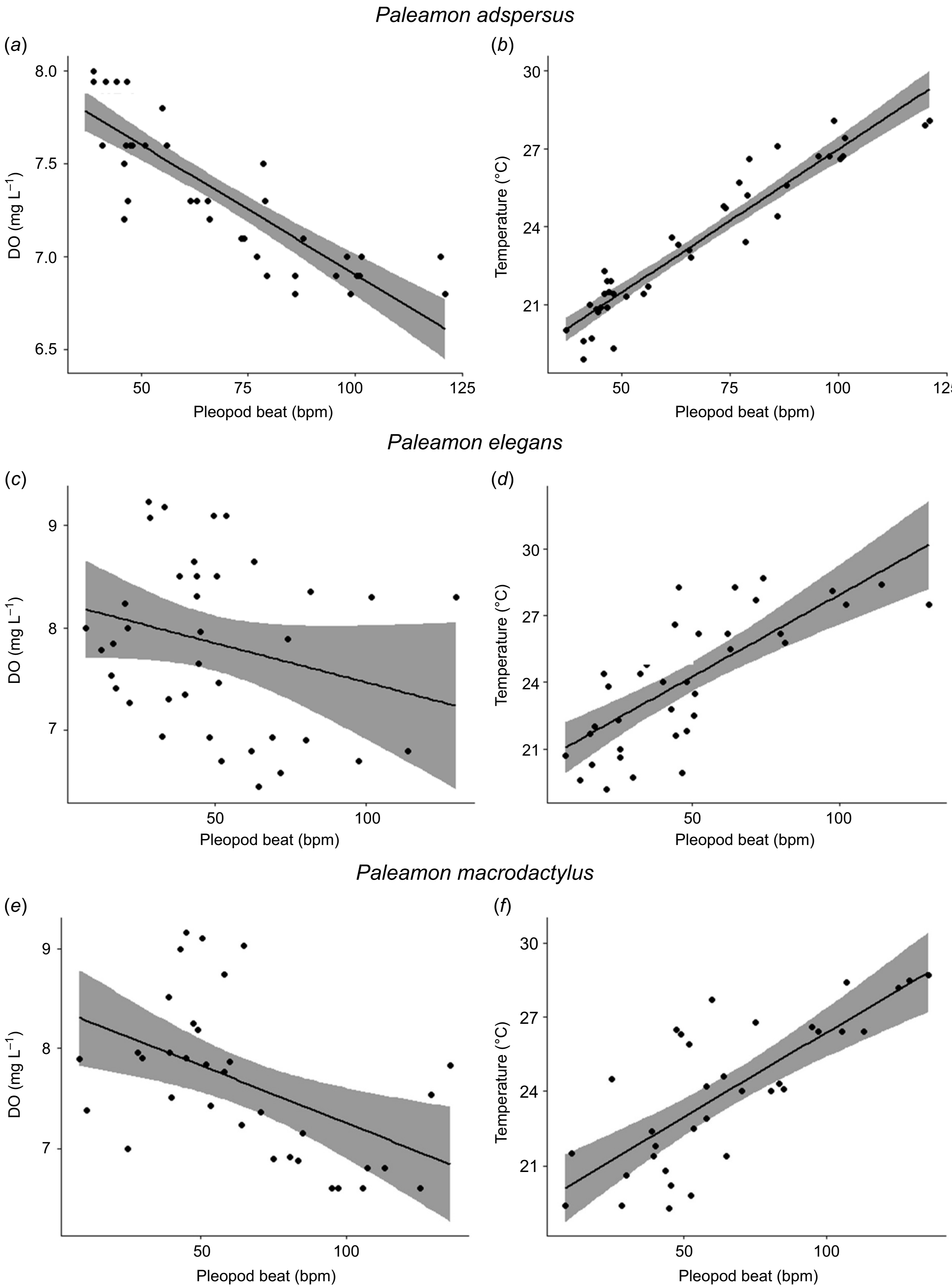

Fig. 2. Relationship among dissolved oxygen (DO, mg L^{-1}), temperature (°C) and pleopod beat (beats per minute, bpm) in ovigerous females of three *Paleamon* species: (*a*, *b*) *P. adspersus*, (*c*, *d*) *P. elegans*, and (*e*, *f*) *P. macrodactylus*. Shaded area represents 95% confidence intervals.

Discussion

The study suggests that pleopod beats serve as a mechanism for parental fanning, particularly in response to environmental factors such as temperature and dissolved oxygen. As temperature increased and dissolved oxygen decreased, the species increased their pleopod beats to ensure the survival of their eggs (Reinsel *et al.* 2014). Similar fanning behaviours have been documented in other crustacean species, such as crayfish and lobsters, where they serve not only to aerate eggs but also to deter potential pathogens and parasites (Baeza and Fernández 2002). This modulation of fanning activity in response to environmental cues highlights the differential ability of the three species to adjust their intensity of parental care in relation to temperature. In particular, the experiment showed differences in parental care behaviour, particularly fanning activity, and performance across different temperatures between *P. elegans* and its congeneric species, *P. adspersus* and *P. macrodactylus*. Significant differences in pleopod beat rates were observed among the three palaemonid species within the temperature classes. Notably, *P. elegans* exhibited significantly lower pleopod beat rates than did *P. adspersus* across T1, T2, T3 and T4. Additionally, *P. elegans* had significantly lower pleopod beat rates than did *P. macrodactylus* in T3. Overall, when pleopod beat rates among the species were compared in relation to temperature, a descending order was observed as follows: *P. adspersus*, *P. macrodactylus* and *P. elegans*. However, in the T4 and T5 temperature classes, which correspond to temperatures approaching 30°C, the data showed greater variability. Interestingly, *P. elegans* exhibited a unique response compared with its congeneric species, *P. adspersus* and *P. macrodactylus*, in relation to dissolved oxygen concentrations. Specifically, *P. elegans* was the only palaemonid species among those studied that did not show a significant negative correlation between pleopod beat rate and dissolved oxygen concentration. The variation in pleopod beat rhythm in response to the analysed environmental parameters could be simultaneously linked to both the ecology and physiology of the species (Morris and Taylor 1984). The analysis showed that *P. adspersus* invests considerable energy in parental care as the temperature increases, because it inhabits more stable environments (Janas *et al.* 2013). In particular, temperature and concentrations of oxygen exert high selective pressure on maximum physiological performance and motor activities (Morris and Taylor 1984; Tarutis *et al.* 2005). The evolution of high metabolic rates can enable organisms to exploit a broader range of environmental conditions, but it also entails higher maintenance costs (Magozzi and Calosi 2015). Consequently, species tend to evolve different levels of metabolic control, suggesting varying levels of vulnerability to warming depending on their habitat (Magozzi and Calosi 2015). *P. elegans*, which inhabits environments naturally subject to significant thermal fluctuations, could have a more efficient cost-effective metabolic strategy to cope with the temperature and oxygen concentration, than do *P. adspersus* and *P. macrodactylus*.

In other congeneric species (e.g. *Palaemon serratus*), a positive relationship between increasing temperature and both the rate and success of embryonic development has been reported (Wear 1974). However, this assumption requires careful consideration, because it has yet to be established whether the increased fanning activity of *P. macrodactylus* is advantageous under higher temperatures, given the potential metabolic costs involved. A study by Cavraro *et al.* (2022) demonstrated that *P. macrodactylus* exhibits a higher hatching success rate under salinity stress than does the native *P. elegans*. This finding suggests that salinity plays a pivotal role in determining reproductive success and may favour *P. macrodactylus* in environments characterised by elevated salinity. Nevertheless, the lack of comparative data on hatching success across a range of temperatures makes it difficult to conclude which species is better adapted to thermal stress.

Further research is needed to assess hatching success and reproductive performance under varying temperature and salinity conditions, and to better understand the competitive dynamics between *P. macrodactylus* and closely related native species. Particular attention should be given to compare reproductive fitness traits, such as fanning behaviour efficiency and hatching success, to determine how these factors potentially influence the competitive advantage of *P. macrodactylus* over native species such as *P. elegans*. Long-term monitoring programs, combined with detailed observations of reproductive strategies, will be essential to assess how the presence of *P. macrodactylus* may affect the reproductive success and population dynamics of the closely related, native species.

Supplementary material

Supplementary material is available online.

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Data availability. All data related to the study are available upon request from the corresponding author.

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