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Interspecific Aggression and Food Competition between the Global Invader *Palaemon macrodactylus* and the Native *Palaemon elegans*

Francesco Cavraro , Chiara Facca *, Luca Altavilla and Stefano Malavasi

Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, 30123 Venice, Italy
* Correspondence: facca@unive.it; Tel.: +39-041-234-7733

Abstract: The impact of invasive alien species on native communities can act at different levels both by affecting the ecosystem's structure (i.e., mainly in the case of vegetation) and through direct interactions (i.e., competition for food or space). Behavioral studies under controlled conditions can provide relevant information on both the invasive potential of alien species and the potential impact of the invaders on the local native species. In the laboratory, the competition for food resources between the invasive oriental shrimp *Palaemon macrodactylus,* Rathbun, 1902, and the Mediterranean native shrimp *Palaemon elegans,* Rathke, 1836, was analyzed. These species are typical residents of coastal transitional and estuarine waters, so the experiments were carried out using two salinity conditions that characterize the coastal lagoon of Venice. Although at both salinity treatments the alien species tended to be more aggressive than the native one, significant differences between the two species were mainly observed at a salinity of 30. In particular, at a salinity of 30, *P. macrodactylus* spent more time attending to the food source than the native species. The results are discussed in light of the potential inter-specific competition between the two species within the conditions of the Venice lagoon.

Keywords: *Palaemonidae*; salinity; aggressive behavior; coastal lagoons

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1. Introduction

It is well known from the scientific literature that Invasive Alien Species (IAS) can severely impact native biological communities, as their introduction may produce an ecological imbalance, altering the relationship between abiotic and biotic components [1,2]. In the context of marine environments, most studies describe the interactions between native and alien macrophyte communities and far fewer studies are dedicated to invertebrates [1,2], which are the most numerous IAS [1,3]. In the Mediterranean Sea, almost 60 among the 100 worst invasive species [1] are invertebrates and, along Italian coasts, they constitute almost 74% of all recorded species [3]. Among invertebrates, invasive Crustaceans (mostly Amphipoda and Decapoda) are particularly abundant in all aquatic habitats. In 2001, worldwide, 87 marine and freshwater decapod species were recorded outside their original areas of distribution, 20 of them being caridean shrimps [4], and the number is increasing (see references in [5]). The updated number of invasive decapod species is 119 according to the database AquaNIS [6].

Palaemon macrodactylus, Rathbun, 1902, resulted in having a higher invasive potential than the other *Palaemon* spp., because no other species achieved a similar global spread [5,7]. Indeed, in the last 30 years, it successfully colonized the coastal areas of the Atlantic Ocean and of the Mediterranean Sea, potentially becoming the dominant estuarine shrimp in Europe and one of the most widely introduced aquatic species [7]. In the Mediterranean range, the native species whose habitat preferences are similar to those of *P. macrodatylus* is *Palaemon elegans,* Rathke, 1836 [8].

Worldwide, *P. macrodactylus* has been demonstrated to be more euryhaline and eurythermal and to consistently consume less oxygen than the respective native species [9–14]. In estuarine/coastal habitats, hypoxic/anoxic crises—generally occurring during warm season—may compromise species' survival; hence, the abilities to tolerate high temperature and reduce oxygen consumption represent important competitive advantages [9]. Moreover, in California, *P. macrodactylus* was responsible for the disappearance of the native *Crangon* spp. [15]. Nevertheless, it was demonstrated that *P. macrodactylus* is a generalist feeder, and a dietary overlap with native species might occur [16].

As mentioned above, the available literature supposes a higher aggressiveness of *P. macrodactylus*, but, to our knowledge, no direct observations are reported that quantify this behavior.

Intraspecific aggression was observed under laboratory conditions in female *P. elegans* [17], while inter-specific aggression was observed between *Palaemon adspersus* Rathke, 1836, and *Palaemon varians* Leach, 1814 [18]. Adults of *P. macrodactylus* showed cannibalistic behavior in crowded laboratory conditions [19]. On the other hand, Correa and Thiel [20] reported that free-living shrimps are relatively unaggressive during reproductive mating and that they have an efficient escape mechanism. However, the same authors also stated that species within the family Palaemonidae have common intraspecific aggressive behaviors regarding space and food acquisition. Other authors suggest inter-specific competition between the invasive *P. macrodactylus* and the native shrimps [14]. Hence, the available literature seems to suggest a wide spectrum of behaviors in relation to the microhabitat's morphology (i.e., presence/absence of refugees), population density, predator pressures, resource availability, congeneric competition, etc., (see references in [14,20]).

The aim of the present study is to test, under controlled laboratory conditions, whether there is direct interference between *P. macrodactylus*, an alien species, and *P. elegans*, a native palaemonid shrimp. Using an experimental arena, food competition was elicited, where direct interference and inter-specific aggression in dyadic encounters between the two species were observed. The main goal was to assess whether one of the two species showed a higher resource-holding potential through aggressive interactions when comparing two salinity conditions.

2. Materials and Methods

2.1. Shrimp Collection and Housing

P. macrodactylus and *P.elegans* were caught in five marginal areas within the Venice lagoon, representing natural salt marshes, artificial habitats, and small creeks. The two species co-occurred in a salinity range from 20 to 25 PSU. The individuals were caught by means of fish traps (25 × 25 × 50 cm; mesh size 4 mm), using bait (PRODAC© TABLET Cittadella-Padua Italy—Compound feed in tablets for bottom feeders) to lure the prey inside. The traps were left for a couple of hours during the high-tide peak and the shrimps captured in the site were transported to the laboratory in well-aerated buckets. This capture method was chosen to reduce as much as possible the injuries to the animals, as they entered the trap on their own. After species identification, the animals were housed in 150 l aquarium tanks under two salinity conditions (20 and 30). Each tank was provided with plastic refuges (PVC tube) and artificial plants (Raphia strings), keeping the population at <50 individuals. Animals were fed daily with PRODAC© TABLET. Acclimatization period lasted at least 1 week in light-controlled conditions (13 h of light), synchronized with the natural photoperiod.

The experimental design was set up in order to reproduce the lagoon conditions where the two species were naturally found. In particular, salinity conditions were selected in the polyhaline range that is characteristic of the *Palaemon elegans'* native conditions in the Venice lagoon, where *P. macrodactylus* was recently introduced [21].

Salinity was controlled by means of a refractometer (sensitivity 1 salinity point) and the temperature by means of a digital thermometer (sensitivity 0.1 °C). Temperature was kept constant by means of thermostats at 25 °C (sensitivity 1 °C).

2.2. Experimental Apparatus and Procedure

The inter-specific interactions were recorded by means of a Digital Camera (Canon LEGRIA HF S30—Tokyo, Japan) in 60 l tanks with the same conditions of temperature and salinity of the 150 l acclimatation tanks. For each trial, two individuals, one *P. elegans* and one *P. macrodactylus*, were selected with respect to their similar body sizes, with a weight difference never exceeding 0.1 g. Electronic precision balance (Bel Engineering S123, Italy, precision 0.001 g) was used to weigh individuals. Individuals were selected to be as similar as possible in terms of body size, to exclude any advantage related to size difference. Moreover, ovigerous females were not used, to exclude reproductive effects on these interactions.

Each shrimp couple was kept together (with no barrier between the individuals) for 24 h in the experimental recording tank, without food. Two refuges were placed in the recording tank to provide shelter for each animal (see Figure 1). The food arena was prepared in the middle of the tank using a small portion (about 0.1 g) of *Solea solea,* Linnaeus 1758. The food was anchored to a plate to elicit the interactions between the species, thus constraining and focusing all the interactions, the permanence of the food resource, and feeding acts on this central food arena (Figure 1). Each record lasted 30 min and a total of 16 observations were carried out (8 at salinity 20 and 8 at salinity 30).

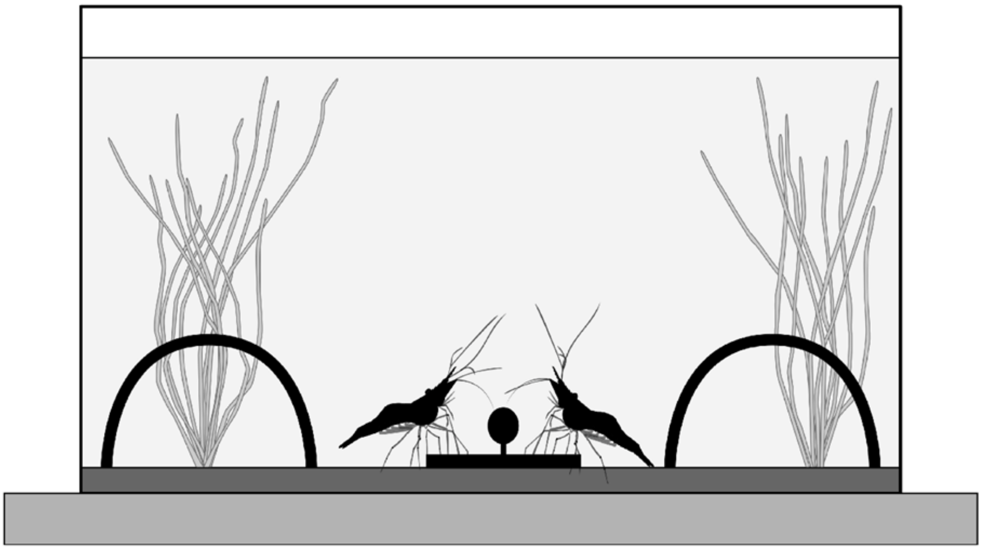

Figure 1. Experimental setup: disposition in the recording tank of shelters and food arena in the middle with a portion of *Solea solea,* Linnaeus, 1758, anchored to a plate.

2.3. Analysis of Behavioral Data

Each replicate (30 min long video-recordings) was analyzed by means of an open-source media player (Media Player Classic-Home Cinema-MPC-HC software-v1.7.13; original MPC version © 2002-2006 by Gabest) and the behavioral acts were measured in terms either of frequency (on the standard 30 min) or duration in seconds (sec), for a total of 16 replicates. For each video-recording, the following behavioral parameters were considered:

- Latency time (LT): time in seconds (s) between the introduction of food and the first access to the resource. It is considered as access when the individual has begun moving towards the resource.
- Residence time (RT): total time in seconds (s) spent for the consumption or protection of the food.
- Number of chases (CN): the number of instantaneous aggressive behaviors enacted by an individual towards the other, as proposed by Eglė and Ulrika [22].
- Number of escape (EN): number of tail-flip escapes after a chase or display.

2.4. Data Analysis

The statistical analysis was carried out using the STATISTICA software (V 7.0–Statsoft Italia Srl–Vigonza-Padua Italy). Data were tested for normality; latency and residence times were not normally distributed (Shapiro test $p < 0.05$) and they were, therefore, log-transformed, while the number of escapes and chases were normally distributed. Considering the normal distribution, the number of observations, the experimental design, and the size of experimental animals, we analyzed the dataset taking into account 2 factors: salinity (2 levels: 20; 30) and species (2 levels: *P. elegans*; *P. macrodactylus*). As the sizes of the organisms tested at 20 were significantly larger than those of the organisms tested at 30, we analyzed the dataset in two steps:

- A *t*-test for dependent, paired observations was carried out to compare the inter-specific differences in frequency or duration of each behavioral parameter within each salinity condition.
- GLM (Generalized Linear Model) was used with salinity and species as predictors together with the individuals' weight as covariate.

For all the above tests, the differences were considered significant per *p*-value < 0.05.

3. Results

The average individual weight did not differ significantly between the two species (see *t*-test results in Table S1): at salinity 20, the average weight of *P. macrodactylus* was 0.81 ± 0.22 g, while that of *P. elegans* was 0.82 ± 0.22 g; at salinity 30, the former was 0.67 ± 0.22 g and the latter 0.68 ± 0.24 g (Figure 2A).

The individuals of the two species exhibited variable levels of inter-specific aggression with respect to the access to the food source, consisting of aggressive displays, chasing, escapes, and, in a few cases, fights constituting relatively long bouts.

At salinity 20, the individuals of both species tended to start feeding earlier than at salinity 30; the mean latency time was 66 ± 80 s at salinity 20 and 179 ± 164 s at salinity 30 (Figure 2B). However, the inter-specific differences at a given salinity were not statistically significant (see *t*-test results in Table S2). Similarly, the behaviors did not change when comparing the two salinity conditions (GLM; $F_{1,27} = 3.80$, $p = 0.062$).

P. macrodactylus spent more time in contact with food than *P. elegans*. The former stayed for on average 1096 ± 693 s at salinity 20 and 1417 + 265 s at salinity 30, while the latter stayed for 277 ± 395 s at salinity 20 and 151 ± 214 s at salinity 30 (Figure 2C). The difference was significant at salinity 30, but not significant at salinity 20 (see *t*-test results in Table S2). The GLM confirmed significant differences between the species (GLM; $F_{1,\,27} = 20.64$, $p < 0.001$).

Almost all *P. elegans* individuals (14 out of 16) exhibited escape behaviors, at least once in half an hour, while only a few *P. macrodactylus* individuals (3 out of 16) displayed this behavior (Figure 2D). Therefore, during aggressive interactions, *P. elegans* tended to give up the food more frequently than *P. macrodactylus*, and this was particularly evident at salinity 30, where *P. macrodactylus* never escaped, while *P. elegans* did (see *t*-test results in Table S2 and Figure 2D).

In terms of chasing, at salinity 20, both species showed similar behavioral patterns (see *t*-test results in Table S2 and Figure 2E), with *P. elegans* individuals displaying 3.5 + 3 chases in half an hour and *P. macrodactylus* 4.5 ± 6 chases in half an hour. At salinity 30, this behavior was rare in *P. elegans* (mean 1.6 ± 2.3), while *P. macrodactylus* showed a frequency in the same range as in the other salinity conditions (see *t*-test results in Table S2 and Figure 2E).

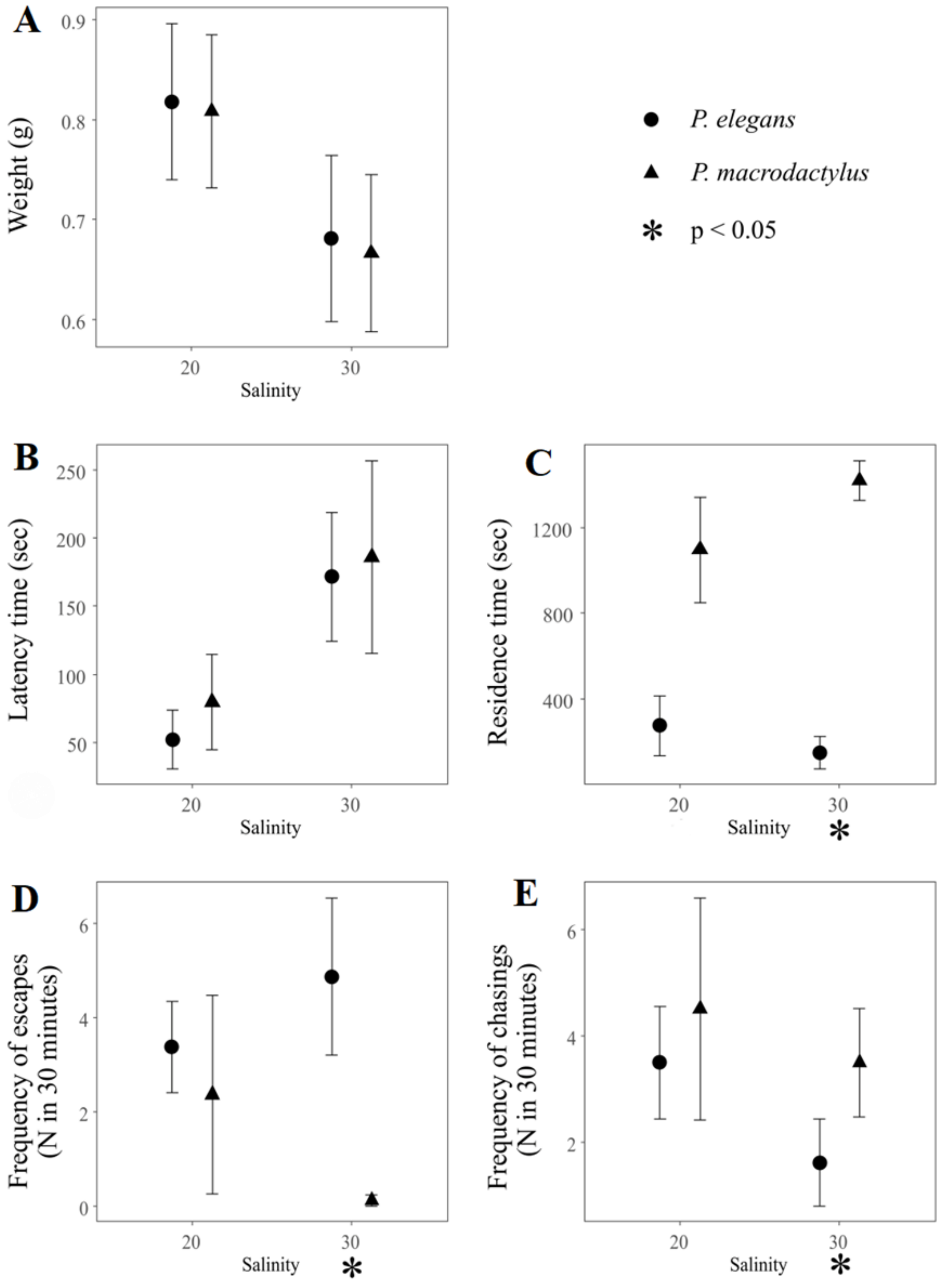

Figure 2. Mean values (±S.E.) of (**A**) the weights in grams, (**B**) the latency time in seconds, (**C**) the residence time in seconds, (**D**) the frequency of escapes expressed in number of events in 30 min and (**E**) the frequency of chasing expressed in number of events in 30 min. The asterisks indicate the significant differences according to the t-test (p-values < 0.05).

The GLM outputs carried out to compare the interaction between species at the two salinities were not statistically significant ($p > 0.05$) regarding the frequency of escape and that of chasing.

4. Discussion

In this paper, we investigated inter-specific aggression within the context of food competition as a trait that can potentially favor alien species invasion. Ashelby et al. [16] found that *P. macrodactylus* and the congeneric *P. longirostris,* H. Milne Edwards, 1837, have similar diets, being amphipods their dominant prey. In summer, both species largely feed on chironomid larvae, but a high degree of dietary overlap occurs during winter when chironomid larvae are absent. These authors suggest that the competition may occur on a seasonal basis depending on the food availability.

Indeed, Chavanich et al. [23] highlighted the potential role of invaders in displacing the native shrimps or effecting their local extinction, studying the behavioral dominance of the non-native white shrimp *Litopenaeus vannamei,* Boone, 1931, towards the native shrimps of the genera *Penaeus* and *Metapenaeus* (Penaeidae family). Our results confirmed that the invasive species, *P. macrodactylus*, tended to spend more time on the food source and to be more successful in aggressive encounters than the native species.

The individuals of each species, once introduced in the small tanks, tended to find a refuge and to remain isolated without any interactions, despite the lack of a barrier separating the individuals. As the refuges and space were not a limiting resource, the species began interacting only when stimulated by food. Previous observations conducted on mixed aquarium populations of the two species indicated that the two species coexist without showing any significant level of direct interference (aggression). The food release is the only trigger observed, able to evoke an inter-specific aggression.

In the present experimental design, the food can be considered a limiting resource, as the individuals were kept under fasting for 24 h. The introduction of food was the mechanism that triggered the interaction. The latency time represents a measure of “no competition” between the species. Even though it was longer at salinity 30, there were no significant differences between species and salinity, indicating that the awareness towards food availability was similar and it was not affected by the salinity values.

In contrast, the time spent on the resource changes significantly at the two salinities analyzed. In this case, *P. macrodactylus* was observed as being dominant and kept control over the food significantly longer than *P. elegans* (GLM $p < 0.05$). Focusing only on salinity 30, it was evident that the behaviors of the two species were significantly different, and this was also the case for the escape behaviors and chases. *P. elegans* showed more frequent escape attempts, fewer aggressive chases, and spent less time on the food source. The escape mechanism seems to be the most frequent behavior in front of other species, such as larger Decapoda (i.e., crabs) [23] or small fishes [14,20].

Although the statistical analysis did not reveal significant differences between the two salinity treatments, once the effect of weight was removed, the salinity conditions appeared to play a major role, confirming the ability of *P. macrodactylus* to better tolerate variations and to modulate its behavior, increasing its level of aggression even in euhaline conditions. The two studied species are known to be extremely euryhaline, but salinity variations can significantly affect their physiology and reproductive performance (see references in [8]). Therefore, the ability to adapt to salinity variations can influence their population distribution and interactions.

P. macrodactylus has been proven to have a wide tolerance to salinity variations [13], being successfully present both in the range between 12 and 34 in Mar de la Plata (Argentina) [14,24] and at low salinities (<5) in the Guadalquivir estuary (SW Spain), where the population (adults and larvae) was more abundant in the inner estuary and negligible at salinities >24 [10]. In the Venice lagoon, where the individuals were collected, the highest densities of *P. macrodactylus* were recorded between salinities of 4 and 23. Its distribution was correlated with low values of salinity and high values of water turbidity [25]. Regarding the Venice lagoon, recent data on the current *P. elegans* distribution are not available, but its presence was generally observed in areas similar to those of *P. macrodactylus*. In the Baltic Sea, *P. elegans* is an invasive species that was demonstrated to tolerate a wide salinity range (from 1 to 35), but to be better resistant to low salinities [26]. Even though both species demonstrated a wide salinity tolerance and a similar behavior at low salinities, *P. macrodactylus* appears to be more competitive and aggressive at salinity 30. Therefore, the evolution of transitional waters towards marine-like salinities would not limit the spread and abundance of this invasive species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse10111593/s1, Table S1: Weight (g) of the animal used in the 16 trials (8 trials at 2 salinities, *t*-test values are also presented with df = degree of freedom).; Table S2: Mean ± SD of each analyzed parameter. *t*-test values are also presented with df = degrees of freedom. (In bold the significant values per $p < 0.05$).

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Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

Data Availability Statement: Not applicable.

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Conflicts of Interest: The authors declare no conflict of interest.

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