



Comparing the reproductive success of three Palaemonid species in a Mediterranean coastal lagoon: native and invasive responses to salinity changes

Francesco Cavraro · Chiara Facca · Muhammad Naseer · Stefano Malavasi

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Abstract Salinity changes in transitional water ecosystems are a natural feature, but anthropogenic direct or indirect impacts are drastically altering their equilibrium and, therefore, their biological communities. Females of three species of Palaemonidae shrimps (the invasive *Palaemon macrodactylus* and the native *P. adspersus* and *P. elegans*) were collected in nature and kept in laboratory at salinities 20 and 30. For each species, the reproductive strategy (investment devoted to reproduction) and the reproductive performance (larval output and hatching success) were determined. Significant differences were observed comparing the three species, highlighting an opportunistic r-strategy in *P. macrodactylus* and *P. elegans*, while *P. adspersus* resulted to produce fewer and larger eggs. *Palaemon elegans* showed a lower hatching success than the other two species, and the size-adjusted larval output appeared to be highly sensitive to salinity variations, with a strong increase under euhaline conditions (salinity 30), while this

increase was limited in the other two species. The selected species were used as model organisms to understand which could be the shift in biological communities due to salinity variations. Data suggest that a shift towards euhaline conditions will favor the native populations, while a shift towards mesohaline waters could determine an increase of the invasive shrimps.

Keywords Fecundity · Reproductive strategy · Reproductive performance · Venice lagoon

Introduction

Coastal lagoons and estuaries are transitional water ecosystems naturally characterised by strong spatial and temporal heterogeneity, due to their peculiar geomorphology and the interactions with both terrestrial and marine environments (Roselli et al., 2009; Newton et al., 2014). These ecosystems have been long exploited by human activities. Eutrophication, land-reclamation, aquaculture, tourism and climate changes, in particular, are making them more and more vulnerable (Newton et al., 2014). The sea level rise is expected to lower tidal flats, reduce salt marsh areas and increase water column height, favouring thermal stratification and affecting vertical mixing (Ferrarin et al., 2014). Moreover, it has already been

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F. Cavraro · C. Facca (✉) · M. Naseer · S. Malavasi
Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, via Torino 155, 30172 Venice, Italy
e-mail: facca@unive.it

observed that the increasing air temperature, favouring an earlier snowmelt, may lead to a shift of freshwater runoff from spring to winter, hence, reducing the summer flow and determining an overall rise in coastal salinity (Scavia et al., 2002). As salinity variations naturally characterize lagoons (Kjerfve, 1994 and references within), it is one of the most used parameters to describe coastal ecosystems (see in Tagliapietra et al., 2009; Ghezzi et al., 2011; Pérez-Ruzafa et al., 2011; Newton et al., 2014). However, even small deviations from the local mean salinity regime may alter the distribution, abundance, and production of biological communities (Levin et al., 2001; Scavia et al., 2002; Ferrarin et al., 2014; Newton et al., 2014; García-Oliva et al., 2019).

The Venice lagoon (Italy), in the Northern Adriatic Sea, is an emblematic example of a coastal ecosystem historically affected by human interventions, whose environmental conditions in terms of both hydrological and morphological features are continuously evolving (Solidoro et al., 2010; Ferrarin et al., 2013; Teatini et al., 2017 and reference therein). Due to anthropogenic alterations, including climate change, the Venice lagoon is going to experience an increase in average salinity values (Ferrarin et al., 2014) and in the level of confinement, that is foreseen to favour the shift in the biological community (Ferrarin et al., 2013). Ferrarin et al. (2013) have foreseen that the evolution in biological communities would shift from k-strategy towards r-strategy species with an overall reduction of biodiversity; however, monitoring observations demonstrated that “coastal lagoon assemblages, especially in polyhaline and euhaline lagoons, are not dominated by r-strategists”, which are “more common in freshwater lagoons” (Pérez-Ruzafa et al., 2013). Moreover, it has been often observed that a low biodiversity combined with a high anthropogenic disturbance may also facilitate the colonization of alien and invasive species (Levin et al., 2001; Occhipinti Ambrogi & Savini, 2003; García-Oliva et al., 2019). In addition, lagoons are more susceptible to new invaders than open marine habitats because they generally host harbours and marinas that are the main vectors of alien species introduction and spread (Occhipinti-Ambrogi et al., 2011; Corriero et al., 2016).

As regards the nektonic community, in recent years a new invader has been added to the already long list of alien invasive species colonizing estuarine and lagoon

habitats: *Palaemon macrodactylus* Rathbun, 1902. This species is considered a global invader, as it is found worldwide in many coastal areas outside its native distribution range (Ashelby et al., 2013; Lejeusne et al., 2014a), which includes the Sea of China, a large part of the Sea of Japan (including the coasts of Korea) and the Pacific coast of Japan (Lejeusne et al., 2014b). Its first introduction in non-native range was in San Francisco Bay (U.S.A) in the mid-1950s during the military shipping activity of the Korean War and some decades passed before its further spreading in North Atlantic (North America and Europe) and South Atlantic (Argentina), almost certainly due to increased global trade (Lejeusne et al., 2014b). In the Mediterranean Sea, it was first recorded in Balearic Islands in 2009 at the larval stage (Torres et al., 2012), but adults, including ovigerous females, were soon after collected in various Mediterranean zones, such as the Northern Adriatic lagoons of Venice, Grado-Marano and Goro (Cavraro et al., 2014a; Cuesta et al., 2014). Being the genus *Palaemon* well represented in the nektonic community of the Mediterranean coastal lagoons in terms of native species, the spread of *P. macrodactylus* opens several questions concerning the impact of this species on the local biological community and, in particular, on those native species that are phylogenetically close to *P. macrodactylus*.

In the present paper, these questions were addressed comparing some traits, related to the reproductive strategy and performance, between the alien *P. macrodactylus* and two native, closely related, species. In the Mediterranean Sea, *P. elegans* Rathke, 1836 and *P. adspersus* Rathke, 1836 are both native (Cottiglia, 1983; González-Ortegón et al., 2015; Deli et al., 2018 and reference therein) and tend to be allopatric in tidal areas (Berglund, 1982). Several studies demonstrated that there is a clear niche separation between these two species (Bilgin et al., 2008; Kuprijanov et al., 2017 and references within) and that *P. elegans* preferably colonizes areas where the conditions for *P. adspersus* are sub-optimal. In fact, compared to *P. elegans*, *P. adspersus* was found to prefer stable habitats with slow growing and long living vegetation, such as the *Zostera* beds (Cottiglia, 1983; Bilgin et al., 2008). *Palaemon elegans* was observed to have a high plasticity, to tolerate extremely variable environmental conditions (Berglund, 1980; Berglund & Bengtsson, 1981) also

characterized by strong currents (Bilgin et al., 2008) and to successfully colonize non-native range (Janas et al., 2013). However, the recent coexistence with *P. macrodactylus* may create some concern about other *Palaemon*'s abundance, distribution and survival in the native range. *Palaemon macrodactylus*, in fact, seems to have the potential to become the dominant estuarine shrimp in Europe and one of the most widespread introduced aquatic species (Lejeusne et al., 2014b). This may probably be due to a combination of biological and ecological aspects that make *P. macrodactylus* more successful at colonising new areas than the other *Palaemon* spp. (Ahelby et al., 2013).

The aim of the present paper was twofold: (1) First, to compare the reproductive strategy, in terms of fecundity, reproductive investment and egg size among the three species, analyzing some life history traits related to reproduction in field-collected samples representative of the natural populations of the three species occurring in Venice lagoon habitats (named: field-collected dataset); (2) Secondly, to test for the effects of salinity and species on the reproductive performance of ovigerous females of the three species, under controlled laboratory conditions (named: laboratory dataset). To address this goal, two approaches were adopted and combined: (1) some life history and reproductive traits of field-collected mature females were analyzed and compared, to assess the reproductive investment by each species (fecundity and relative fecundity, reproductive effort, and other parameters as defined below); (2) a laboratory experiment was designed to assess and compare the larval output and the hatching success of ovigerous females of the three species, kept at two different salinity regimes. The two salinity regimes were selected to mimic two main salinity conditions of the Venice lagoon, set at the opposite extremes of polyhaline range (Ghezzi et al., 2011).

The combination of these two approaches allowed to assess: (1) Differences in the female investment devoted to reproduction (reproductive strategy) among the three species; (2) Differences in the reproductive performance, assessed as larval output and hatching success among the three species, in relation to two salinity conditions; (3) The competitive and invasive potential of the alien species with respect to the other two native congeneric species.

The results were discussed in the light of the potential interaction between environmental changes related to salinity variation and spread of an alien invasive species in a coastal lagoon system (the Venice Lagoon), using the *Palaemon* species as study models. The expected results should answer two main questions (1) Are the differences in the reproductive strategies of the three species able to confer a differential advantage in terms of reproductive performance, especially as regards the comparison between the invader and the two native species? (2) Is the reproductive performance sensitive to salinity variations and in what direction?

Material and methods

Shrimp collection and housing

Specimens of three *Palaemon* species (*P. macrodactylus*, *P. elegans* and *P. adspersus*) were caught by means of baited fish traps (25 × 25 × 50 cm; mesh size 4 mm; baited with PRODAC® TABLET—Compound feed in tablet for bottom feeders). The traps were left a couple of hours on site and the trapped animals were transported to laboratory in well-aerated buckets. This capture method was chosen to reduce as much as possible the injuries on animals, as they entered the trap on their own. Catching areas were chosen in the Venice lagoon according to each species preferential niche and previous observations (Cavaro et al., 2014b): *P. adspersus* where seagrass beds are present, *P. elegans* in sheltered canals with algal beds (Cottiglia, 1983; Bilgin et al., 2008) and *P. macrodactylus* near the mainland, where salinity is lower (Ghezzi et al., 2011). In the selected areas, the presence of specimens of the other species was negligible and no records were kept. The experimental activities were carried out from April to June, at the peak of the reproduction (Bilgin et al., 2008). Species macroscopic identification was mainly based on body pigmentation and rostrum shape (Cavaro et al., 2014a).

Once in the lab, *Palaemon* specimens were put in 150 L aquarium tanks, provided with plastic refuges (PVC tube) and artificial plants (raphia mop) as shown in Fig. S1, keeping the population < 50 individuals/tank. Animals were daily fed with PRODAC® TABLET.

A sub-sample of ovigerous females for each species was euthanized both for the assessment of fecundity / life history traits and for the back-calculation of the fecundity in living females (see below).

For all the experimental activities, the temperature was kept in the range 19–22 °C, simulating the natural conditions in late spring (Brigolin et al., 2021) at which the three species were already adapted. Considering the plasticity to temperature variations of the three studied species (Magozzi & Calosi, 2015), we considered that this range of temperature do not affect their reproductive performance. On the other hand, salinity conditions were kept at 20 and 30. These salinity values were selected according to the “Venice System” (Venice System, 1959) and the subdivision of Venice lagoon water bodies proposed by Ghezzi et al. (2011). The water body typologies were identified by superposing annual salinity means and standard deviations with residence time. The Venice lagoon turned out to be characterised by polyhaline (18–30) and euhaline (> 30) waters, with most of the area having moderate (2–4 salinity points) annual variations and different confinement degree on the basis of the distance from the inlets (Ghezzi et al., 2011; Umgieser et al., 2014). Considering that polyhaline waters are the most extensive in the catching areas and the annual standard deviation is in the range ± 2 –4 (Ghezzi et al., 2011), in the present experimental design, the boundary values of polyhaline range were kept as proxy to simulate the *Palaemon* spatial distributions and to discuss possible salinity effects on organisms.

In laboratory, saltwater was prepared by using marine salt having a grade of purity of almost 100% and containing trace elements necessary for ensuring a correct animal’s growth (PRODAC© OCEAN FISH).

Fecundity and reproductive traits of field-collected ovigerous females (field-collected dataset)

In laboratory, 25 ovigerous females for each species were euthanized using eugenol, the essential oil from cloves (Li et al., 2018) and preserved in 70% ethanol. Ovigerous females were selected in order to have the widest range of size. For each female, the total length (TL in mm, from the tip of the rostrum to the tip of the telson along the mid-dorsal line) was measured by means of a Vernier calliper; the wet weight, with and without eggs, was measured by means of a balance

(Bel Engineering S123, Italy, precision 0.001 g) and the number of eggs was counted directly by using ZEISS STEMI V6 Stereomicroscope equipped with a micrometre accurate to 0.01 mm. Each specimen was gently drained before the above-described measures. Eggs’ development stage was limited to the presence/absence of eyes, that were often absent.

The data achieved from euthanized females were used to calculate the parameters describing the reproductive strategy (Table 1).

The fecundity and the body weight allowed to define the parameters of a power function (1) that was used to estimate the fecundity of females in laboratory experiment (see description in the next paragraph), as suggested in Janas & Mańkucka (2010).

$$y = ax^b \quad (1)$$

where “y” is the number of eggs (F); “x” is the body weight without eggs; “a” and “b” are constant characteristic of each species.

Experimental analysis of reproductive success under controlled aquarium conditions (laboratory dataset)

After an acclimation period (approx. 10 days), ovigerous females were wet weighed and placed individually in floating cylindrical mesh cages (mesh size < 0.1 mm, approx. volume 1.5 L; Figs. S1, S2 in supplementary material) in the same tank where they were acclimated. Ovigerous females were selected in order to have the widest size range. For each species the following ovigerous females were available: 12 for *P. adspersus*, 35 for *P. elegans* and 41 for *P. macrodactylus*. Females in the cages were regularly fed with a fraction of PRODAC© TABLET (approx. 0.05 g every day). Once the eggs hatched, the females were wet weighed and set free in nature (in case of indigenous species); the larvae were preserved in 70% ethanol and then counted. Each specimen was gently drained before weighing.

Despite some slight differences at the level of egg stage, the duration of incubation period did not differ among the three species (ANOVA, $P > 0.05$).

The data achieved from the experiments in the tanks were used to calculate the parameters describing the reproductive performance (Table 1). In particular, the reproductive performance of the ovigerous

Table 1 List of parameters that are used to describe the reproductive strategy and the reproductive performance

Reproductive strategy		
Reproductive effort (RE)	Total egg biomass calculated by difference using the female weights with and without eggs.	(Janas & Mańkucka, 2010)
Reproductive output (RO)	Ratio between RE and female weight without eggs	(Oh et al., 2002; Vázquez et al., 2013)
Fecundity (F)	Number of eggs by direct count	
Relative fecundity (RF)	Ratio between F and size. In the present paper, size is total length	(Vázquez et al., 2013)
The average volume of a single egg (VE)	Measured using the ellipsoid's formula on a subsample of 10 eggs for each female.	(Janas & Mańkucka, 2010)
The average weight of a single egg (WE)	Ratio between RE and F.	
Reproductive performance		
Larval output (LO)	Number of larvae released by females.	
Hatching success (HS) of alive females	Ratio between LO and the estimated fecundity calculated by Formula (1), that is the number of eggs hatched with respect to the total number of eggs.	

The parameters of the reproductive strategy were measured using field-collected ovigerous females; the reproductive performance was estimated by means of laboratory experiments under controlled conditions

females was assessed by means of two complementary measures: (1) Hatching success, meaning the ratio between the larval number and the estimated number of eggs. This parameter measures how many eggs hatched in relation to the total number of eggs (back-calculated on the basis of the regression size/number of eggs examined in the field collected samples; power function (1)); (2) The larval output, that is the number of larvae released in relation to body size (size-adjusted larval output, see below for the data analysis).

Statistical analyses

Descriptive statistics were carried out by means of Excel (Office 365), Statistica (StatSoft Italia srl 1984–2005) and R software (R packages emmeans, glmmTMB, performance and DHARMA—v. 3.6.0; R development Core Team, 2019, www.r-project.org). For all the elaboration done, if the *p*-values (*P*) were lower than 0.05, the analysis outputs were considered significant.

All statistical analyses were carried out on log-transformed data ($\log_{10}x + 1$).

One-way ANOVA was used to compare the life history and reproductive traits of field-collected dataset,

and the post-hoc Tukey HSD to explore the differences between pair of means. Pearson correlation coefficients were calculated to highlight the relationship among variables. To verify the effects of body weight (body weight without eggs) on reproductive traits, the analysis of covariance (ANCOVA) was tested and the adjusted means were presented.

The differences in the hatching success (HS) of the experimental ovigerous females across the three species and between the two salinities was tested by means of a two-way ANOVA and a post-hoc Tukey HSD for unequal sample sizes.

To test the for the effects of salinity and species on larval output (LO), the following procedure was followed:

1. At first, for each species, a linear regression was calculated using the number of larvae as dependent variable and the mother weight (without eggs) as independent variable. This aimed at comparing the species' larval output, eliminating the effect of size.
2. A new dataset putting together all the residuals calculated from the three linear regressions (point 1) was built.
3. A Generalized Linear Model (GLM with binomial distribution) was applied to the residual dataset

(point 2) using salinity and species as predictive variables.

Statistical analyses were performed after checking for normality and homogeneity of variance and a binomial function was considered the best fit.

Results

Fecundity and reproductive traits of field-collected ovigerous females

Palaemon adspersus ovigerous females resulted to be larger than the other two species; but more than length, it was the body weight to demonstrate the main differences, being *P. adspersus*'s weight twofold that of *P. macrodactylus* and almost four times higher than *P. elegans* (Table 2). The body size, both in terms of body weight (without eggs) and total length, was significantly correlated ($P < 0.05$) with all the traits related to reproduction, such as fecundity, egg volume and reproductive effort.

The body weight affected fecundity more than species (F values in Table 3), so adjusting the values, it turned out that the number of eggs was higher in *P.*

elegans than in *P. macrodactylus* and *P. adspersus* (Fig. 1a). Likewise, body weight had significant effects on the reproductive effort (Fig. 1b) and on the weight of a single egg (Fig. 1c), although species was more discriminant (F values in Table 3). After the adjustment, the pattern for RE and WE was *P. adspersus* > *P. elegans* > *P. macrodactylus* (Fig. 1b and c). Egg volume, on the contrary, was characteristic of each species, independently by their size, and followed the pattern *P. adspersus* > *P. elegans* > *P. macrodactylus* (Tables 2 and 3, Fig. 1d). *P. elegans* and *P. macrodactylus* had similar (HSD Tukey test $P > 0.05$) fecundity, reproductive effort, and single egg volume and weight. On the contrary, *P. adspersus* had significantly lower fecundity (HSD Tukey test $P < 0.05$), but larger and heavier eggs than the other two species (HSD Tukey test $P < 0.001$). The reproductive effort of *P. adspersus* was similar to *P. elegans*'s (HSD Tukey test $P > 0.05$), but significantly higher than *P. macrodactylus*'s (HSD Tukey test $P < 0.001$). The interaction term between species and weight was significant for the reproductive effort and the single egg weight (Table 3).

In Fig. 2, the power functions (1) for each species are displayed. The equations were used to assess the

Table 2 List of the parameters describing the average traits of the three Palaemonidae species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*)

	<i>P. adspersus</i>	<i>P. elegans</i>	<i>P. macrodactylus</i>
Total length (mm)	62.82 ± 4.14 (54.00 ÷ 69.90)	38.73 ± 9.81 (25.20 ÷ 58.20)	49.22 ± 6.72 (34.50 ÷ 58.20)
Body weight without eggs (g)	2.525 ± 0.423 (1.724 ÷ 3.340)	0.656 ± 0.423 (0.116 ÷ 1.750)	1.285 ± 0.437 (0.475 ÷ 2.001)
Fecundity (number of eggs)	1920 ± 554 (1080 ÷ 2892)	639 ± 528 (100 ÷ 2326)	1147 ± 406 (464 ÷ 1871)
Reproductive effort (RE = eggs weight, g)	0.716 ± 0.190 (0.384 ÷ 1.123)	0.165 ± 0.080 (0.037 ÷ 0.334)	0.256 ± 0.181 (0.057 ÷ 0.792)
Reproductive output (% RE/body weight)	28.18 ± 4.56 (20.15 ÷ 36.72)	31.17 ± 15.99 (11.27 ÷ 76.72)	18.90 ± 8.82 (4.02 ÷ 42.86)
Relative Fertility (% Fecundity/Total length)	30.24 ± 7.24 (20.00 ÷ 43.82)	14.64 ± 8.65 (3.97 ÷ 39.97)	22.79 ± 5.99 (13.24 ÷ 32.99)
Single Egg volume (mm ³)	0.149 ± 0.029 (0.117 ÷ 0.268)	0.083 ± 0.019 (0.060 ÷ 0.136)	0.069 ± 0.016 (0.050 ÷ 0.101)
Single Egg weight (mg)	1.37 ± 0.23 (1.04 ÷ 1.79)	1.15 ± 0.30 (0.75 ÷ 2.17)	1.14 ± 0.23 (0.85 ÷ 1.80)

Each mean value ± standard deviation (minimum ÷ maximum) was calculated on 25 preserved specimens (field-collected dataset). See Table 1 for the description of the parameters

Table 3 Outputs of analysis of covariance (ANCOVA) carried out on the field-collected females comparing the three Palaemonidae species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*)

	Species		Weight		Species × Weight	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Fecundity (number of eggs)	302.2	< 2e−16	492.3	< 2e−16	2.579	0.0832
Reproductive effort (RE = weight of the egg batch, g)	105.88	< 2e−16	61.43	3.34E−11	5.864	4.45E−03
Single Egg weight (RE/fecundity, g)	16.79	1.07E−06	8.91	0.00389	7.572	0.00106
Single Egg volume (mm ³)	103.1	< 2e−16	0.6	0.441	4.087	0.021

F value indicates which variable has the main discriminant effect for each parameter and *p*-values is the level of significance. Significant values (*P* < 0.05) are in bold

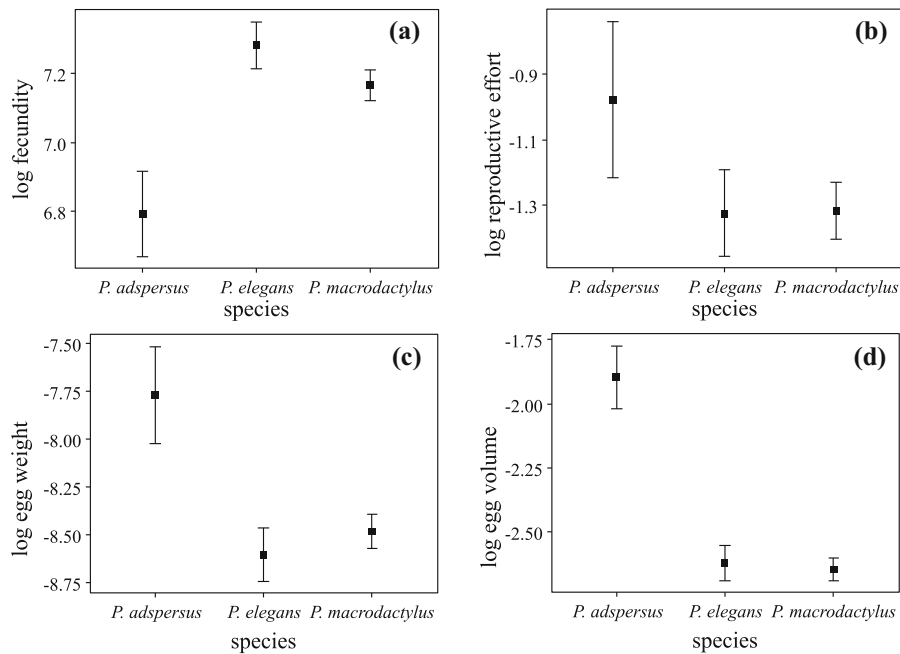


Fig. 1 Main parameters for the field-collected Palaemonidae species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*) after the ANCOVA elaboration. The values are different from Table 2, because they are the logarithm values adjusted after using the ‘body weight without egg’ as covariate. The whisker

plot (mean ± standard error) compares for the three species: **a** the Fecundity (no of eggs), **b** the Reproductive effort (weight of the egg batch), **c** the single egg weight (weight of the egg batch/number of eggs); and **d** the single egg volume

fecundity of alive female used in laboratory experiment.

Experimental analysis of reproductive success under controlled aquarium conditions

The hatching success (HS) of *P.elegans* was significantly lower (two-way ANOVA *P* < 0.001) than that of the other two species (Table 4; Fig. 3), while there was no significant salinity effects on this parameter

(two-way ANOVA *P* > 0.05). However, the Tukey test revealed that the significant differences among species was salinity dependent. The HS of *P. elegans* was, in fact, significantly lower than that of *P. adspersus* at salinity 30 and than that of *P. macrodactylus* at salinity 20 (Tukey HSD, *P* < 0.05, Fig. 4).

The GLM tested on Larval Output (LO) highlighted significant differences when comparing species, salinities and the interaction between the two (*P* < 0.001, Fig. 4, Table 5). All species had higher LO at salinity

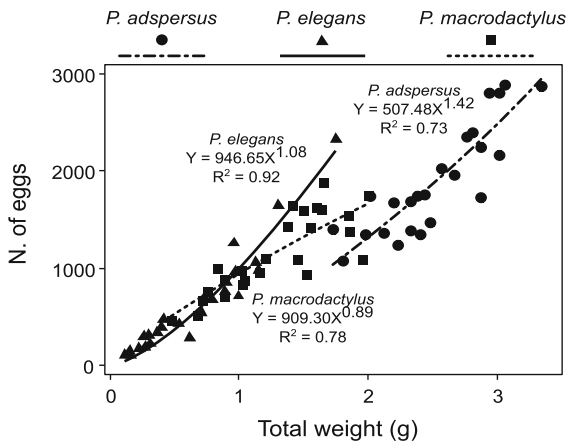


Fig. 2 Relationship between body weight (without eggs) and the number of eggs of the field collected Palaemonidae species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*). The best fit was represented by the power function in (1), being all *P*-values < 0.05. In the graph, the power functions with all coefficients and the R^2 are shown for each species (from above to below: *P. adspersus*, *P. elegans*, *P. macrodactylus*.)

30 than at 20. However, *P. elegans* had the highest LO, being several times higher than that of the other two species. The GLM shows that at salinity 30, *P. elegans* released 3 times more larvae than at salinity 20, while the other two species just doubled the LO (Fig. 4).

Discussion

The comparative analysis here conducted on field-collected ovigerous females of the three investigated species showed important differences in terms of

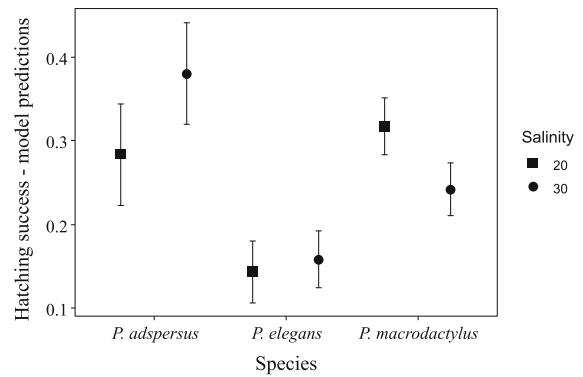


Fig. 3 Mean model prediction (\pm St. Err.) of the hatching success (parameter describing the reproductive performance, see Table 1) for the three Palaemonidae species at the two salinity treatments

reproductive strategy. In particular, *P. adspersus* seemed to produce, after controlling for body size, fewer and larger eggs than the other two species. This different investment in reproduction can be related to habitat preferences: *P. adspersus* was observed to be a habitat specialist, while *P. elegans* is considered a generalist (Berglund, 1984). In their native range, *P. adspersus* and *P. elegans* were found to be both sympatric and allopatric (Bilgin et al., 2008 and references therein), but they prefer different aquatic vegetation cover: the former is generally present in *Zostera* beds (least fluctuating environment), while the latter where seaweeds or bare bottoms are present (Berglund, 1982; Cottiglia, 1983; Bilgin et al., 2008; Reuschel et al., 2010; Cuesta et al., 2014). *P. elegans* is commonly referred as rockpool prawn (Janas &

Table 4 List of the parameters describing the average traits of the females from laboratory experiments. Each mean value \pm standard deviation (minimum \div maximum) was calculated for each species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*)

Species	<i>P. adspersus</i>		<i>P. elegans</i>		<i>P. macrodactylus</i>	
	20	30	20	30	20	30
Body weight without eggs (g)	3.456 \pm 0.895 (2.47 \div 4.71)	3.234 \pm 0.469 (2.87 \div 4.137)	0.667 \pm 0.509 (0.24 \div 2.016)	0.622 \pm 0.399 (0.18 \div 1.50)	1.696 \pm 0.599 (0.86 \div 2.745)	1.636 \pm 0.475 (0.873 \div 2.30)
Calculated fecundity	2983 \pm 1086 (1828 \div 4544)	2685 \pm 568 (2257 \div 3786)	624 \pm 518 (202 \div 2018)	576 \pm 399 (149 \div 1467)	1446 \pm 459 (795 \div 2233)	1403 \pm 367 (806 \div 1911)
Days of hatching after capture	14 \pm 3 (12 \div 18)	15 \pm 3 (13 \div 18)	20 \pm 7 (10 \div 32)	22 \pm 8 (8 \div 32)	19 \pm 11 (9 \div 40)	21 \pm 8 (12 \div 36)
Larval output (LO)	766 \pm 287 (410 \div 1079)	979 \pm 140 (739 \div 1116)	78 \pm 89 (1 \div 305)	105 \pm 139 (0 \div 544)	452 \pm 257 (64 \div 824)	354 \pm 278 (0 \div 939)
Hatching success	0.28 \pm 0.12 (0.09 \div 0.46)	0.38 \pm 0.09 (0.20 \div 0.44)	0.14 \pm 0.13 (0.003 \div 0.43)	0.16 \pm 0.14 (0 \div 0.41)	0.32 \pm 0.17 (0.04 \div 0.61)	0.24 \pm 0.19 (0 \div 0.62)
Number of observations	6	6	16	19	19	22

See Table 1 for the description of the parameters. In grey, the variables tested at the 2 salinity treatments

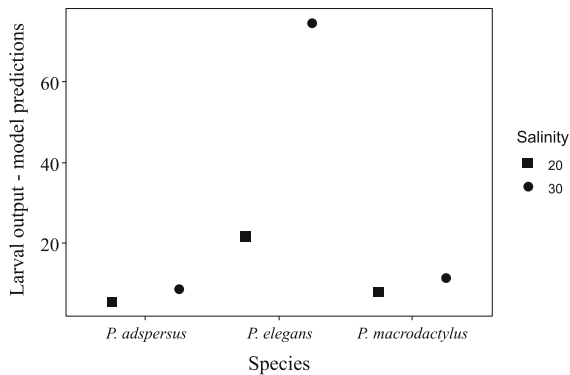


Fig. 4 Mean model prediction of Larval output (parameter describing the reproductive performance, see Table 1) for the three Palaemonidae species at the two salinity treatments. Data in the graph are the outputs of a GLM binomial model, calculated using the residual from 3 linear regressions (one for each species) between larval output and mother weight (without eggs). Standard errors are not displayed because they were < 1 for all cases except for *P. elegans* at salinity 30 that was 2

Table 5 Outputs of GLM carried out on the laboratory dataset of larval output comparing the three Palaemonidae species (*Palaemon adspersus*, *P. elegans*, *P. macrodactylus*) at the two salinity values

	Chisq	DF	<i>P</i>
Species	456835.23	1	$< 2.2e-16$
Salinity	1208816.57	2	$< 2.2e-16$
Salinity*Species	248.31	2	$< 2.2e-16$

Chisq is the value of Chi-squared test, DF indicates the degrees of freedom and *P* is the level of significance (*P* values). Significant values ($P < 0.05$) are in bold

Mańkucka, 2010), but in Venice lagoon it is usually present in the small creeks and ponds inside salt marshes along the mainland (unpublished data), where specimens were collected for the experimental activities here described. The production of few larger eggs favours the hatching of larger larvae that can better survive (Janas & Mańkucka, 2010). Despite the differences in egg number and size in the specimens from the Venice lagoon, *P. adspersus* and *P. elegans* showed a similar Reproductive Output (0.28–0.31), that was averagely higher than the data from literature for other Palaemonidae species (0.12–0.22 in Oh et al., 2002). Therefore, both species seemed to be well-adapted in coastal habitats, although *P. adspersus* was demonstrated to be more sensitive to oxygen depletion than *P. elegans* (Berglund, 1981). Moreover, no

competition has been reported between these two species.

A completely different reproductive strategy was observed in the case of *P. macrodactylus*, that was first recorded in Northern Adriatic in 2011 (Cuesta et al., 2014) and in Venice lagoon in 2012 (Cavraro et al., 2014a). The population collected in the Venice lagoon tended to produce a higher number of small eggs than the native species, displaying also a low Reproductive Output (0.19). The lower investment compared to body size, but the high absolute fecundity, can be related to the reproductive strategy of an opportunistic species. The advantages of opportunistic species are the ability to rapidly colonize new areas and *P. macrodactylus* was widely demonstrated to have a higher invasive potential than the other *Palaemon* spp., because no other species achieved a similar global spread (Ashelby et al., 2013; Lejeusne et al., 2014a). This strategy, with a significant lower reproductive output than the native species, can depend on a more recent introduction in this area and an adaptation process in progress. However, observations done worldwide, before the first records in the Northern Adriatic Sea, highlighted a haplotypic diversity very high in the introduced populations, and, in some cases, even higher than the populations in the native range, excluding the bottleneck or founder effects (Lejeusne et al., 2014b). Such a high haplotypic diversity is a common trait in Palaemonidae shrimps, that appear to have a strong gene flow by natural larval dispersal (Dennenmoser et al., 2010; Reuschel et al., 2010), but the geographic distances from the native range (Japan and Korea) let suppose multiple anthropogenic introductions, mainly by means of ballast water from international shipping vessels (Lejeusne et al., 2014b). Already in 2010, the Venice lagoon was demonstrated to be the hotspot of alien species introduction in Italy (Occhipinti-Ambrogì et al., 2011), and this can suggest that the local populations would soon benefit from the intense naval traffic of the commercial and passenger port of Venice.

Results from our experimental analysis on the hatching success and larval output of the three species in relation to salinity showed that, despite the higher LO of *P. elegans*, the hatching success of *P. adspersus* and *P. macrodactylus* was higher than that of *P. elegans*, once accounted for size-effect. *P. adspersus* tended to have a higher hatching success at salinity 30, while *P. macrodactylus* at salinity 20, although a

significant and clear effects of salinity on this parameter was not revealed by the present study. This suggests that, in terms of hatching success, differences among species have a more significant effect than differences in salinity, with *P. adspersus* and *P. macrodactylus* performing better than *P. elegans* at both salinity conditions. Different results were obtained considering larval output, after adjusting for body size.

P. elegans is, on average, the smallest species (Table 2), but it has the potential to release far more larvae than the other two at both salinity conditions. It resulted to be the species investing more effort in egg production and larval release, according with the fecundity data measured on field collected females in the present study. Further, the GLM model predicted that its larval output to be particularly sensitive to salinity variation, with a general increasing tendency at euhaline conditions (salinity 30). The magnitude of this increase is much higher in *P. elegans* than in the other two species.

On the whole, the present results suggest that *P. elegans* and *P. macrodactylus* invest in large number of eggs and larvae while *P. adspersus* seems to invest more in the survival of the single egg. This result would suggest a clearer adaptation of *P. macrodactylus* and *P. elegans* to more unstable habitats, such as the more tidally influenced areas. On the other hand, *P. elegans* seems to be the most vulnerable species in terms of hatching success, suffering from a high level of egg lost. Further, this species seems to be the most sensitive one to salinity change, strongly increasing the larval output at higher salinity. Although the distribution of the three species in the Venice lagoon and their habitat partitioning are not available at present, some considerations and preliminary conclusions could be drawn in the light of the present data.

Based on observations carried out between 2014 and 2020, *P. macrodactylus* distribution seems to be limited to few, restricted zones of the Venice lagoon, along the mainland (Redolfi Bristol et al., 2021).

This species could therefore successfully occupy the oligohaline and mesohaline areas of the Venice lagoon, without suffering any strong decrease in reproductive performance with salinity change, as also happened in other European areas, such as the Spanish Guadalquivir and the French Gironde estuaries (González-Ortegón et al., 2010; Béguer et al., 2011). By contrast, *P. elegans* shows a typical strategy

adapted to unstable habitats but with higher performance under euhaline conditions and a general lower performance in terms of hatching success. These observations suggest a potential for a competition between the two species, with the alien species appearing in general more opportunistic.

Moreover, *P. macrodactylus* was found to have a significant higher hatching success than *P. elegans*, to be particularly aggressive towards the congeneric (unpublished data in preparation) and other carideans (Béguer et al., 2007) and to have good respiratory performances during hypoxic crises (González-Ortegón et al., 2010; Lejeusne et al., 2014a). Despite well-adaptable to a wide salinity range (Janas et al., 2013), *P. elegans* appears to be generally more vulnerable also because it has a limited resistance to heat shock and one of the lowest critical thermal maximum in the Palaemonid family (Ravaux et al., 2016). *P. macrodactylus* have been already found to have a certain competitive advantage compared to *P. elegans*, *P. adspersus*, *P. serratus*, *P. longirostris* and *Crangon crangon* (Omori & Chida 1988; Ashelby et al., 2004; Béguer et al., 2007; Micu & Niță, 2009). In California, *P. macrodactylus* was responsible for the disappearance of the native *Crangon* spp. (Ricketts et al., 1968). In laboratory crowded conditions, evidence of cannibalism where observed, hence, *P. macrodactylus* can be supposed to prey on other carideans (Béguer et al., 2007). Worldwide, *P. macrodactylus* was demonstrated to have a higher eurythermality and consistently consumed less oxygen than the native species (Chícharo et al., 2009; González-Ortegón et al., 2010; Lejeusne et al., 2014a). Moreover, this species has a wide tolerance to salinity variations (Vázquez et al., 2016), but successful reproduction and embryonic development can occur in different range depending on geographic distribution and local adaptation: between 12 and 34 in Mar de la Plata (Argentina; Vázquez et al., 2013; Vázquez & Bas, 2019) or at low salinities in Guadalquivir estuary (SW Spain), where the population (adults and larvae) was more abundant in the inner estuary (González-Ortegón et al., 2006, 2010).

In the Mediterranean Sea, numerical model scenarios foresee a homogenization of coastal ecosystem hydrology at the end of the century, with consequence on the site-specific species richness. In particular, it seems that the effects would be more marked in the environments with limited exchanges with the sea,

where the combination of decreased freshwater inputs and increased evaporation will favour salinity rise (Ferrarin et al., 2014). Hence, the combination of climate changes and anthropogenic interventions is expected to have a significant impact on hydrology, salinity regimes, and, hence, on biological communities (Ferrarin et al., 2013, 2015). Although coastal lagoons are inhabited by euryhaline species, able to tolerate wide salinity ranges, long-term climate change scenarios predict greater fluctuations than the tolerated ones, compromising local populations and increasing the invasive potential of alien species (Hänfling et al., 2011).

Changing the hydrological conditions due to morphological interventions, combined with the sea level rise, as it is happening in the Venice lagoon, is expected to increase the degree of confinement towards a choked lagoon (Ferrarin et al., 2013) and to modify the tidal regime (Ferrarin et al., 2015). Following the present trends, the foreseen scenarios showed that the Venice lagoon is going to experience an increase of salinity (Ferrarin et al., 2014). This could suggest that the reproductive performance of *P. adspersus* would be favoured to the detriment of the more mesohaline species. Although, it is recognized that euhaline conditions may favour a biological community dominated by K-strategy species (Pérez-Ruzafa et al., 2013), the uncontrolled shift towards marine conditions may significantly alter the community structure, that is characteristic of coastal transitional ecosystems (Pérez-Ruzafa et al., 2013).

Intervention aiming at hampering the marinization, such as salt marsh construction or freshwater input restoration, may favour a re-equilibrium of lagoon environments but, in turns, they can also favour the spreading of r-strategy (Pérez-Ruzafa et al., 2013) and alien species such as *P. macrodactylus* and *Procambarus clarkii*, and leading to some competitive disadvantages for a native species, such as *Palaemon elegans*. The shift in Palaemonidae species can be a significant signal of deep biological changes and, hence, a helpful model to monitor coastal ecosystem evolution.

Conclusions

The high reproductive performance of the alien species *P. macrodactylus* seems to confer an adaptive

advantage in terms of spreading out successfully mainly in mesohaline conditions and to be a more successful competitor in those lagoon areas where it is sympatric with native species (e.g. in Venice lagoon with *P. elegans*, as suggested by the present paper, and *Crangon crangon*, as suggested by the available literature). By contrast, the better performance of *P. adspersus* to more stable, euhaline habitats, such as the seagrass beds, supports some kind of habitat segregation between this species and the alien invader. In the light of these considerations, this alien species has the potential to significantly impact the local biological communities inhabiting temperate coastal and lagoon systems. Future research is needed to address in deeper detail the issue concerning the relationships between *P. macrodactylus* and the closely related native species.

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Author contribution FC, CF, and SM participated in conceptualization, fieldwork, laboratory analyses, statistical elaboration, writing, editing and review. Muhammad Naseer participated in fieldwork and laboratory analyses.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval Field specimen collection was authorized by Veneto Region, Venice, Italy.

Consent to participate Not applicable.

Consent for publication All authors consent to the publication.

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