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ORIGINAL ARTICLE

Population dynamics of two invasive amphipods in the Southwestern Atlantic: *Monocorophium acherusicum* and *Ericthonius punctatus* (Crustacea)

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ABSTRACT
Harbours are important sites for the containment and dispersal of invasive species throughout the world, so the study of life history traits of species is important to understand the success of their invasion and their potential effects on the habitat. In recent years several invasive species have been reported in Argentinian harbours; however, studies of the ecology and life history of these species are scarce. We studied the population dynamics and reproductive biology of *Monocorophium acherusicum* and *Ericthonius punctatus*, in order to update the published information on the introduced amphipods in Mar del Plata harbour. Both species showed a seasonal pattern characterized by high densities in warmer months, related to the highest reproductive activity and the increase of recruitment in summer and early autumn, and lower densities in the cold season. The sex ratio was always female-biased and the number of eggs carried by females was positively correlated to the size. The present study suggests that both species have colonized Mar del Plata harbour successfully, showing viable populations (cohorts of juveniles, males, females and ovigerous females). This work provides the basis for monitoring the impact generated by introduced amphipods over the existing fauna.

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Ericthonius punctatus; harbour; invasive species; *Monocorophium acherusicum*; population dynamics

Introduction

In recent years the study of biological invasions has acquired significant relevance related to the negative impact of invasive species on native ecosystems, such as: native biodiversity loss, habitat modification and introduction of pests or predators of commercial species (Hallegraeff 1998; Schwindt et al. 2001; Darrigran 2002; Long et al. 2012; Smith et al. 2012). In this regard, the study of life history traits of invasive species is important to understanding the success of their invasion and its potential effects on the habitat (McClary & Nelligan 2001; Hutchings et al. 2002; Penchaszadeh et al. 2005; Smith et al. 2012).

Amphipods are small peracarids that live from seawater (e.g. deep-sea, tidal flats and estuaries) to freshwater environments (Martin & Davis 2001, 2006; Väinölä et al. 2008). In benthic marine habitats they are one of the most abundant groups and the main food source for many organisms (Chintiroglou et al. 2004; Albano et al. 2006; Eckmann et al. 2008; Väinölä et al. 2008; Wang et al. 2010). Some species exhibit the typical life history traits of invasive species, such as great phenotypic plasticity, high fecundity and reproducibility, early maturity and a wide tolerance to environmental changes (Grabowski et al. 2007; Beermann & Franke 2011), which has allowed them to invade a large number of habitats around the world (Coles et al. 1999; McClary & Nelligan 2001; Orensanz et al. 2002; Lovell et al. 2006).

Harbours are important sites for the retention and dispersal of alien species throughout the world, and the study of these areas constitutes a mechanism of early detection of potential invasive species (Carlton & Geller 1993; Orensanz et al. 2002; Stevens et al. 2002; Ros et al. 2013). In some Argentinean harbours biodiversity is well studied and new invasive species are constantly reported (Orensanz et al. 2002; Albano et al. 2006, 2013; Schwindt et al. 2014; Rumbold et al. 2015a). Despite this, studies of the ecology and life history of invasive species are scarce (but see Kittlein 1991; Vázquez et al. 2012), and thus the status of these organisms and their possible impact on native populations is unknown.

In Mar del Plata harbour, several invasive amphipods were detected (Orensanz et al. 2002; Rivero et al. 2005; Rumbold et al. 2015a), but in recent studies it has been shown that the introduced amphipods *Monocorophium acherusicum* (Costa, 1853) and *Ericthonius punctatus* (=

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E. brasiliensis) (Bate, 1857) are dominant, while native species declined (Albano 2012). Both species are native in the North Atlantic and their presence on ship fouling have facilitated their invasion to the Mediterranean Sea and the north coast of Europe, southeast Africa, India, Korea, Japan, China, Australia and New Zealand (Haruhiko 1956; Myers & McGrath 1984; Costello et al. 2001; Lee et al. 2005; Inglis et al. 2006; Rilov & Crooks 2009; Ponti et al. 2010; Beermann & Franke 2011; Galil et al. 2011). In South America, both species have been reported in Brazil and *M. acherusicum* in particular has been recorded from the south coasts of Chile (Myers & McGrath 1984; Neves & Rocha 2008; Pérez-Schultheiss 2009). In Argentina, *M. acherusicum* was first recorded in 1969 in La Lucila (Buenos Aires province) by McCain (1969) and subsequently Bastida et al. (1977) reported specimens of *Corophium* sp. in Mar del Plata harbour, but it was Albano et al. in 2013 who confirmed the presence of *M. acherusicum* in the harbour. Moreover, *E. punctatus* has been reported in Argentina by Albano (2012), so their introduction would be recent.

The aim of this paper was to study the population dynamics and reproductive biology of *M. acherusicum* and *E. punctatus*, in order to update the published information on these introduced amphipods into Mar del Plata harbour and establish their current status.

Materials and methods

Study area

Mar del Plata harbour (38°02′29′′S, 57°32′16′′W) (Figure 1) is one of the most important harbours in Argentina because of its fishing fleet, naval traffic, commercial trade and recreational sailing (Rivero et al. 2005; Albano et al. 2013). This harbour was built between 1913 to 1924 and consists of a semi-closed area limited by two artificial breakwaters made of concrete blocks and has a narrow mouth of about 300 m. Mean water depth is lower than 5 m, and a navigational channel is maintained by dredging (at 10 m). The bottom is composed of fine sand in the mouth, and silt in the inner area. This harbour presents typical characteristics of a polluted environment: high levels of total hydrocarbons from fuel discharges, polycyclic aromatic hydrocarbons, copper (Rivero et al. 2005; Albano et al. 2013), tributyltin (Penchaszadeh et al. 2001; Goldberg et al. 2004), organic matter (from industrial and sewage effluents) and reduced dissolved oxygen, pH and salinity (Rivero et al. 2005; Albano & Obenat 2009; Albano et al. 2013).

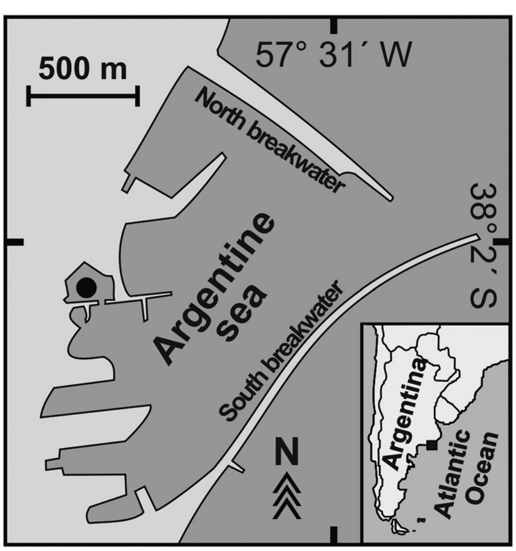

Figure 1 . Geographic localization of Mar del Plata harbour, Buenos Aires, Argentina (● sampling site).

Despite this highly polluted environment, in the recreational area, the wooden docks and marinas are covered by an abundance of ascidians, mussels, algae and tubicolous polychaetes that generate refuges for a great variety of fish, flatworms, molluscs, nematodes and crustaceans (Rivero et al. 2005; Albano et al. 2006, 2013; Albano & Obenat 2009).

Field sampling and laboratory procedures

Samples were collected monthly from December 2010 to November 2011. Three sampling units were extracted from the fouling community adhering to the wooden docks using spatulas. Samples were subtidal (at a depth less than 1 m) and in shaded areas of approximately 0.05 m^2. The extracted material (i.e. ascidians, mussels, algae and tubicolous polychaetes) was placed in containers of 830 cm^3 and fixed in 70% alcohol. In the laboratory, samples were placed in sieves (0.35 mesh) for 15 minutes to drain out the water and alcohol. All extracted material was weighed on a digital balance (±0.01 g). Samples were then washed in running water through a 0.35 mm mesh-sieve, and the amphipods *Monocorophium acherusicum* and *Ericthonius punctatus* were sorted from the fouling community and counted using a stereo microscope. After specific identification, organisms were classified into three population groups: juveniles, males and females. In addition, females were subdivided in two sub-categories: ovigerous females (with brood pouch with eggs) and non-ovigerous females (with empty brood pouches or without brood pouches). Population densities were calculated and expressed as number of individuals per 100 g of sample (wet weight).

Dissolved oxygen and pH were measured *in situ* each time using a portable multiprobe instrument (HACH sensION 156) and salinity was measured with an optical refractometer. From December 2010 to February 2011 no data were collected, due to a lack of instruments. The amplitude and mean monthly seawater temperatures were obtained from the Argentine Oceanographic Data Center (CEADO – Argentina).

Population structure and reproductive parameters

Population biology was assessed by the following parameters: monthly mean density (individuals/100 g of sample ± standard deviation); percentage of males and ovigerous females, used as an estimate of reproductive activity (Kneib 1992; Rumbold et al. 2012); proportion of ovigerous females (number of ovigerous females/ total females); and sex ratio (males/males + total females) which was calculated seasonally due to the low density of amphipods detected in some months. Fecundity was estimated from 50 ovigerous females randomly selected from the total ovigerous females collected during the sampled period; they were measured (total length), and their eggs removed from the brood pouch and counted.

Statistical analysis

Parametric tests were used preferentially, but when the assumptions of parametric statistics were violated, an appropriate non-parametric test was applied. For all tests, significance was assessed at $\alpha = 0.05$ (Zar 2009). Variations in monthly densities of each species were tested using a parametric one-way ANOVA (factor: months). To determine if the density of juveniles, males and females varied among population groups and months sampled, a parametric two-way ANOVA was employed (factors: population groups and months). A Student–Newman–Keuls (SNK) test was applied when statistically significant differences of means were found. Deviations from a 1:1 sex ratio were calculated by non-parametric analysis (χ^2 test). Linear regression and the parametric Pearson's correlation coefficient were calculated to assess the relationship between female size and the number of eggs in the brood pouch (fecundity index). All tests were performed using the R statistical software (R Development Core Team 2011).

Results

Environmental parameters

Temperatures of shallow seawater ranged from 20.9°C in March 2011 to 9.3°C in July 2011 (Figure 2). Oxygen concentrations ranged from 7.5 to 11.2 mg/l, pH values varied between 7.99 and 8.4, and salinity was constant at 33–34 PSU (Table I).

Population structures and brood sizes

Monocorophium acherusicum was present over the whole sampling period (431.86 ± 795.03 ind/100 g) and their density varied significantly between months (one-way ANOVA, $P < 0.001$) (Figure 2; Table II). It was high during December 2010 (*c.* 2500 ind/100 g, SNK test, $P < 0.05$) and remained below 780 ind/100 g during the rest of the study period (SNK test, $P > 0.05$).

The density of males, females and juveniles differed significantly among population groups and months (two-way ANOVA, $P < 0.001$) (Figure 3a; Table III). The density of males was homogeneous, remaining below 230 ind/100 g (SNK test, $P > 0.05$). Females were at their maximum value in December 2010 (*c.* 500 ind/ 100 g, SNK test, $P < 0.05$), while from January to November 2011 mean density was lower than 240 ind/100 g (SNK test, $P > 0.05$). Juveniles showed highest densities in December 2010 (*c.* 1700 ind/ 100 g, SNK test, $P < 0.05$), and in January and April 2011 (*c.* 420 ind/100 g, SNK test, $P < 0.05$; in both cases), remaining below 200 ind/100 g during the rest of the study period (SNK test, $P > 0.05$). The significant interaction detected between factors (two-way ANOVA, $P < 0.001$) revealed that juveniles were more abundant than females and males during December,

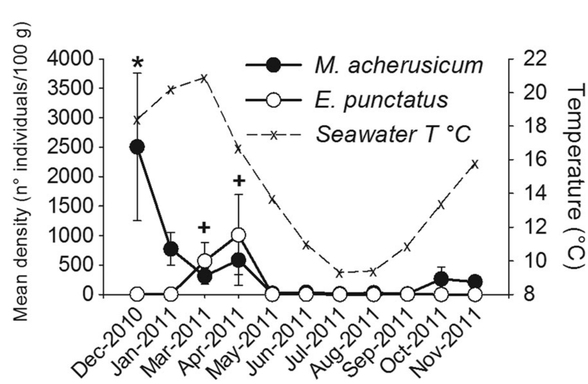

Figure 2. Monthly variation of seawater temperature and total population density (mean ± standard deviation) of (a) *Monocorophium acherusicum* and (b) *Ericthonius punctatus*. Significant difference between months (SNK test, $P < 0.05$) were denoted with: *, *M. acherusicum*; +, *E. punctatus*.

Table I. Monthly variations of environmental variables of Mar del Plata harbour. DO, dissolved oxygen; PSU: practical salinity unit.

Month	DO (mg/l)	pH	Salinity (PSU)
Mar–2011	11.20	8.08	33
Apr–2011	8.94	7.99	33
May–2011	7.88	8.14	33
Jun–2011	8.52	8.33	34
Jul–2011	10.29	8.32	33
Aug–2011	9.23	8.40	34
Sep–2011	9.73	8.18	33
Oct–2011	7.50	8.18	33
Nov–2011	9.54	8.16	33

January and April (SNK test, $P < 0.05$); females showed higher densities than males only in December (SNK test, $P < 0.05$), and density did not differ between population groups during the rest of the months sampled (SNK test, $P > 0.05$). The proportion of ovigerous females with respect to total females reached their maximum during March and June, *c.* 46 and 54%, respectively, while for the rest of the months sampled they remained close to 30%, except for July when a total absence of ovigerous females was registered.

The sex ratio differed significantly from the expected 1:1 (male:female) and was always female biased (χ^2 test, $P < 0.01$). In summer the mean sex

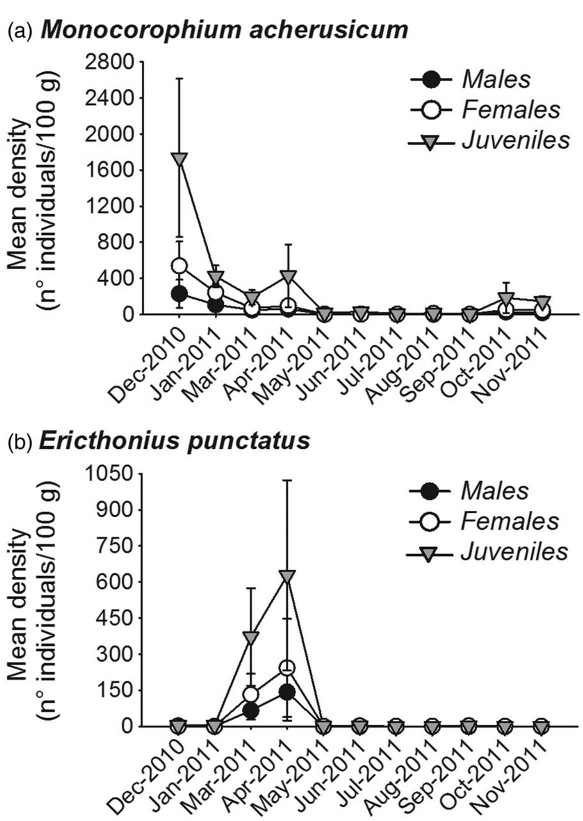

Figure 3. Seasonal variation of density (mean ± standard deviation) of males, females and juveniles of (a) *Monocorophium acherusicum* and (b) *Ericthonius punctatus*.

Table II. Results of one-way ANOVA for comparison of total densities between months of *Monocorophium acherusicum* and *Ericthonius punctatus*. df, degrees of freedom; MS, mean squares.

Population	Source of variation	df	MS	*F*	*P*
M. acherusicum	Month	10	2147883.60	12.43	<0.001
	Error	33	172745.60		
E. punctatus	Month	10	446594.87	8.77	<0.001
	Error	33	50945.12		

ratio was 0.31 (χ^2 test: 251.02), 0.37 in autumn (χ^2 test: 17.84), while in winter and spring it was 0.23 (χ^2 test: 7.22) and 0.32 (χ^2 test: 30.06), respectively. The proportion of males and ovigerous females of *M. acherusicum* remained below 20% with respect to the total population, reaching maximum values in spring and summer, and the minimum in autumn and winter (Figure 4a). A linear regression was found between the number of eggs per brood and female length ($r = 0.787$, $P < 0.001$; Figure 5a), and the mean number of eggs observed per female was 7.14 ± 5.02.

For *Ericthonius punctatus*, the mean density was 145.30 ± 378.10 ind/100 g and varied significantly between months (one-way ANOVA, $P < 0.001$) (Figure 2; Table II). The highest densities were recorded in March and April 2011 (*c.* 550 and 1000 ind/100 g, respectively, SNK test, $P < 0.05$), remaining unchanged during the rest of sampling period (*c.* 10 ind/100 g; SNK–test, $P > 0.05$), although no specimens were recorded from June to August 2011 and from October to November 2011.

The density of males, females and juveniles showed significant differences among population groups and months (two-way ANOVA, $P < 0.001$) (Figure 3b, Table III). Males and females did not show significant differences in mean density (19.04 ± 54.74 ind/100 g and 34.39 ± 96.45 ind/100 g, respectively; SNK test, $P >$ 0.05), but their highest values were recorded in April (*c.* 200 ind/100 g; in both cases). Meanwhile, juveniles reached maximum densities in March and April

Table III. Results of two-way ANOVA for comparison of densities between sampling months and population groups (males, females and juveniles) of *Monocorophium acherusicum* and *Ericthonius punctatus*. df, degrees of freedom; MS, mean squares.

Population	Source of variation	df	MS	*F*	*P*
M. acherusicum	Month	10	715961.20	22.23	<0.001
	Group	2	723012.59	22.45	<0.001
	Month × Group	20	214417.21	6.66	<0.001
	Error	99	32206.01		
E. punctatus	Month	10	280726.01	14.82	<0.001
	Group	2	208839.27	11.03	<0.001
	Month × Group	20	99690.45	5.26	<0.001
	Error	99	18938.30		

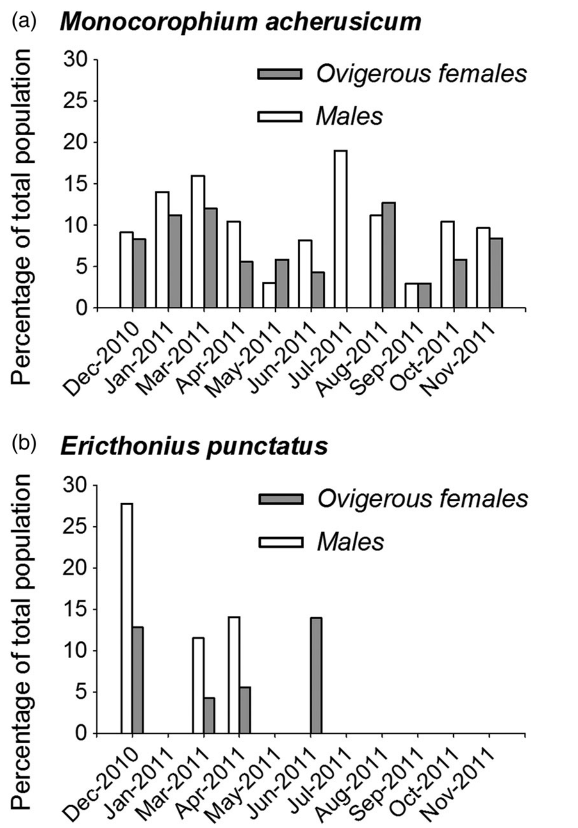

Figure 4. Proportion of males and ovigerous females during the sampling period, with respect to the total population of (a) *Monocorophium acherusicum* and (b) *Ericthonius punctatus*.

(*c*. 350 and 650 ind/100 g, respectively; SNK test, $P <$ 0.05), while density remained below 4 ind/100 g during the rest of the months sampled (SNK test, $P >$ 0.05). In addition, a significant interaction was detected among factors (two-way ANOVA, $P < 0.001$) showing that only from March to April was juvenile density higher than that of other population groups (SNK test, $P < 0.05$), while during the other months, no significant differences were registered between population groups (SNK test, $P > 0.05$). Moreover, ovigerous females were recorded only in December (100% with respect to total females), March (18.36%), April (23.27%) and June (30.67%).

The sex ratio showed significant differences from 1:1 and was skewed toward females (χ^2 test, $P < 0.01$). Their values varied from 0.33 to 0.37 in summer (χ^2 test: 37.37) and autumn (χ^2 test: 43.68), respectively. On the other hand, the proportion of males with respect to the total population was higher (12–28%) than ovigerous females (5–15%) in summer and early autumn (Figure 4b). Fecundity analysis showed that the number of eggs increased with female size ($r = 0.585$, $P < 0.001$; Figure 5b); however, the regression line could not be considered a good predictor of fecundity, due to the high variance associated with the data ($r^2 =$ 0.342). The mean number of eggs observed was 10.3 ± 8.61 per female.

Discussion

The present work established that *Monocorophium acherusicum* and *Ericthonius punctatus* showed a seasonal pattern characterized by high densities in warmer months and lower during the cold season; this seasonal variation has also been reported in other non-native environments, such as the Mediterranean and Korean Seas (Lantzouni et al. 1998; Emara & Belal 2004; Jeong et al. 2006; Bedini et al. 2011). In their native environment *M. acherusicum* did not show a common pattern; in some populations of California, monthly density was constant and in others the maximum values were recorded during summer and winter or even in autumn, mainly related to differences in salinity values (Hopkins 1987). In the case of *E. punctatus* native populations have not been studied yet. On the other hand, several explanations have been suggested to

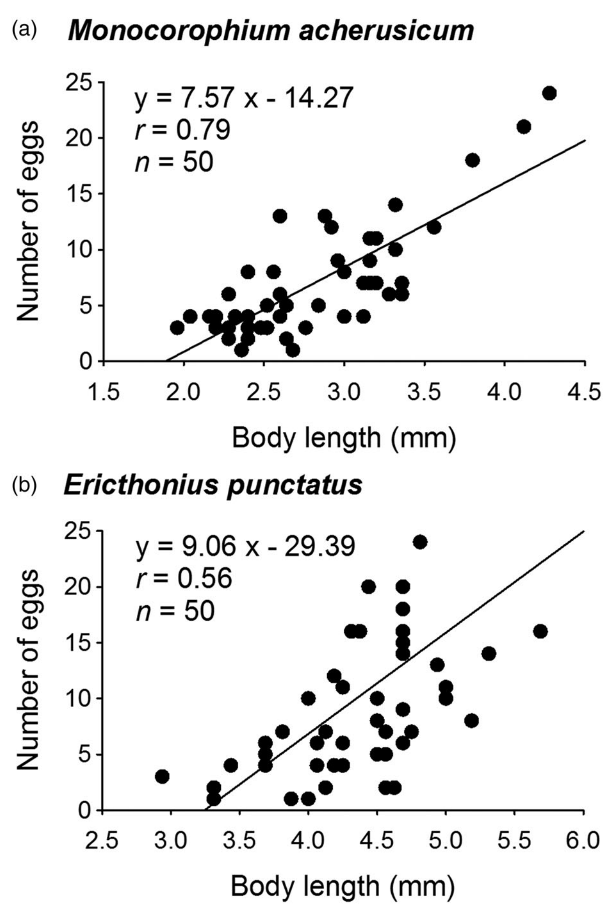

Figure 5. Relationship between the number of eggs and the total body length of ovigerous females of (a) *Monocorophium acherusicum* and (b) *Ericthonius punctatus*.

understand the seasonal variation of both species in non-native habitats (Lantzouni et al. 1998; Emara & Belal 2004; Jeong et al. 2006; Bedini et al. 2011). According to those authors, lower densities of *M. acherusicum* and *E. punctatus* would be related to drastic changes in salinity, poor food availability, higher competition for resources, and a synergistic effect of pollutants and environmental factors (e.g. salinity, temperature and pH). In Mar del Plata harbour other peracarids showed the same seasonal pattern, such as the tanaidacean *Tanais dulongii* (Audouin, 1826) (Rumbold et al. 2015b) and the introduced isopod *Sphaeroma serratum* (Fabricius, 1787) (Kittlein 1991). Rumbold et al. (2015b) determined that except for temperature, the other factors (e.g. salinity, pH and dissolved oxygen) were constant in the harbour, suggesting a close relationship between density and temperature. In peracarids, temperature plays an important role in population dynamics (Pöckl 1992; McKenney & Celestial 1995; Maranhão & Marques 2003; Fockedey et al. 2005; Tsoi et al. 2005; Henninger et al. 2010; Hosono 2011). It has been shown that high temperatures cause an increase in growth rate and sexual maturation, which explains the highest reproductive activity and the increase of recruitment in summer and early autumn (Wilson & Parker 1996; Lee et al. 2005; Scinto et al. 2007; Beermann & Purz 2013). Meanwhile lower temperatures result in a reduction of density, due to high mortality and lower maturation of adults (Alonso 1984; Prato & Biandolino 2006). Unfortunately, studies of the effects of pollutants and ecological factors on amphipods in Mar del Plata harbour are lacking, so the explanation of the proximal causes of the observed differences would require more studies and detailed laboratory and field experiments.

Some significant differences were observed between species: *M. acherusicum* appears to be a well-established population, with males, females and juveniles throughout the study period, suggesting a continuous reproduction, while *E. punctatus* reproduction was restricted to summer and autumn, so their presence could be described as casual. However, Albano (2012) found specimens of *E. punctatus* at the same sampling site throughout the year at 3 m depth, suggesting a migration process of this species from the bottom to shallower areas in the warmer months, explaining their absence in the colder season, as occurs in Mediterranean populations, in which during summer the highest densities of *E. punctatus* were recorded in shallow areas related to higher food availability (Bedini et al. 2011).

The sex ratio was favourable for females in both populations, a common trait in other amphipods (Nair & Anger 1979; Rajagopal et al. 1999; Prato & Biandolino 2006; Scinto et al. 2007, Flynn et al. 2009). The lack of information about population dynamics in native environments makes comparisons difficult, but, in non-native environments the sex ratio was close to 0.5 in both species (Onbe 1966; Costello & Myers 1989), showing that the invasion of new habitats, with differences in biotic and abiotic factors, could affect their reproductive traits. Some explanations for female dominance have been proposed: a sex difference in reproductive behaviour, due to males leaving their refuges while searching for partners resulting in a high exposure to predation while females remain in their shelters (Boates & Smith 1989); or a difference in the onset of sexual maturity, because in some populations males die before females due to reaching their sexual maturity at smaller sizes than females, reducing their longevity (Kevrekidis 2005). On the other hand, Beermann (2014) showed that the sex ratio of some amphipods from fouling populations depend on sampling location; thus, it cannot be excluded that sex ratios in neighbouring locations may favour males or an equal sexual ratio.

The wide range of sizes of ovigerous females of *M. acherusicum* and *E. punctatus* were indicative of iteroparity. The fecundity index in both species showed a positive linear relationship, indicating a high correlation between female body size and their brood size, as has also been observed in other amphipods (Steele & Steele 1991; Cunha et al. 2000; Tsoi & Chu 2005; Prato & Biandolino 2006) and were similar to those recorded in other exotic species of amphipods in the Southwestern Atlantic such as *Melita palmata* (Montagu, 1804) (Obenat et al. 2006), *Monocorophium insidiosum* (Crawford, 1937) (Garrido 2004) and other peracarid species from Mar del Plata harbour (Kittlein 1991; Rumbold et al. 2015b). Moreover, brood size could be affected by several factors, such as female size, stage of development of female, season and egg loss (e.g. by human manipulation or removed by females), so any of these factors could explain the high variance observed in the regression line in *E. punctatus* (Sheader & Chia 1970; Sheader 1983; Beermann & Purz 2013).

The present study suggests that both species have colonized Mar del Plata harbour successfully, showing viable populations (cohorts of juveniles, males, females and ovigerous females), with main reproductive and recruitment periods in warm seasons, iteroparity and high fecundity. On the other hand, as mentioned above the impacts of this introduction are unknown, but the high density of *M. acherusicum* suggests that this species has been incorporated in local food webs, which has probably altered the natural balance of the environment favouring an increase in the number of predators, and consequently resulting in a negative impact on native amphipods (Kelleher et al. 2000; Grabowski et al. 2007). Finally, future studies of ecology and population dynamics of native and invasive species of Mar del Plata harbour are needed in order to determine the possible effect of these species on the ecology of the ecosystem and their impact on biodiversity.

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Disclosure statement

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