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Biological invasions in artificial habitats: factors that determine the presence of native and exotic peracarid Crustacea species in Southwestern Atlantic

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ABSTRACT

The aims of this study were to compare the richness and the population traits of exotic and native peracarid species in two ports of the Southwestern Atlantic (Mar del Plata: MDP, Puerto Madryn: PMY), in order to discuss the vulnerability of these environments to biological invasions, to explore the current status of these assemblages and to study the life history traits that could favour the establishment of exotic species in these ports. Five biofouling samples were taken each season from 2016 to 2017. The present study showed that exotic species were dominants in both ports but profound differences were registered between environments: MDP port is characterized by the absence of native species and highest richness of exotic species ($n = 7$ spp.); while in PMY port two native species were registered and exotic species ($n = 2$ spp.) showed lower richness than MDP port. The analysis of species assemblages and life history traits allows us to discuss the potential invasive pattern of peracarids in the Southwestern Atlantic, suggesting that factors, such as propagule pressure, port infrastructure, pollution levels are closely related to the differences in vulnerability of these artificial environments to biological invasions. In addition, the population dynamics and the reproductive traits of exotic species could explain their establishment and proliferation in the marine environments studied.

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Introduction

Exotic species, defined as organisms introduced outside of their natural habitat, can become invasive when they successfully establish and proliferate in the new invaded environment (Davis 2009; Rilov and Crooks 2009; Blackburn et al. 2011). These species can alter the natural characteristics of native habitats, through several processes such as competition, predation, parasitism, habitat modification, hybridization and disease transmission, among others (Davis 2009; Rilov and Crooks 2009; Blackburn et al. 2011). In this regard, the study of biological invasions has acquired a great relevance, in order to mitigate its negative consequences on the invaded habitat (Carlton 1996; Sala et al. 2000; Blackburn et al. 2011).

In marine environments, human activities have favoured the introduction of exotic species, producing an enormous cost in terms of ecological and economic damages (Carlton 1996; Ruiz and Carlton 2003; Galil et al. 2011). Several human-mediated vectors have been proposed as pathways for the spread of marine exotic species, among which vessels (via ballast water

or hull fouling) are considered the main ones, making anthropic environments (e.g. ports and aquaculture facilities) important sites for the introduction of exotic species worldwide (Ruiz and Carlton 2003; Rilov and Crooks 2009; Galil et al. 2011; Schwindt et al. 2014).

Port areas present a great number of characteristics that favour the settlement of exotic species in comparison to natural environments, such as the presence of anthropogenic materials (e.g. concrete, wood, stone, plastic, metal, among others) that offer a variety of surfaces to be colonized by these species (Glasby et al. 2007; Tyrrell and Byers 2007); the creation of coastal defense areas in wave-exposed habitats (e.g. breakwaters), which provide sheltered sites for the establishment of exotic organisms (Glasby et al. 2007; Tyrrell and Byers 2007); higher levels of pollutants that reduce the native diversity and increase the proliferation of exotic species (Piola and Johnston 2008; Airolidi and Bulleri 2011); and the continuous vessels movement, that increase the risk of successful establishment of exotic species (i.e. propagule pressure) (Carlton 1996; Johnston et al. 2009). However, other factors related to

the life history traits of these species could determine the subsequent proliferation of these organisms in the port area invaded (e.g. seasonal density, population structure, reproductive patterns, among others) (Sakai et al. 2001; Smith 2009). In this context, the knowledge of port characteristics on the one hand, and the life history traits of exotic species on the other, allows us to determine the susceptibility of ports to biological invasions and to infer their potential impact on native biodiversity (Orensanz et al. 2002; Strauss et al. 2006; Rilov and Crooks 2009; Galil et al. 2011; Schwindt et al. 2014).

Peracarids are small crustaceans (including amphipods, isopods, tanaidaceans and others) that inhabit all kind of environments from the tropics to the poles, both in terrestrial and in aquatic environments (e.g. freshwater ecosystems, estuaries, tidal flats and deep sea) (Schram 1986; Martin and Davis 2006). These organisms are one of the most diverse groups in marine habitats, playing an important role as trophic linkers between primary producers and higher trophic levels (Duffy and Hay 2000). On the other hand, despite the fact that their life cycles are characterized by the presence of larval stages restricted to the female brood pouch and that juveniles show a low dispersal rate (Schram 1986; Martin and Davis 2006), several species have invaded a large number of environments worldwide (mainly by shipping), making them an excellent model for invasion studies (Ros et al. 2015; Martínez-Laiz et al. 2019; Rumbold 2019).

Several works have been shown that invasive peracarid species may affect the natural structure of the invaded habitat through different processes: modifying the trophic interactions inside the community (e.g. feeding on eggs and larvae of native species, increasing the density of predators and monopolizing or depleting food resources for other species) (Orav-Kotta et al. 2009; Piscart et al. 2010, 2011; Ros et al. 2014; Beggel et al. 2016; Taylor and Dunn 2017); parasitizing native organisms, which can result in fecundity loss and population dynamics alterations (Dumbauld et al. 2011); and producing habitat modifications (e.g. creating galleries and reducing sediment stability) (Talley et al. 2001). Therefore, the study of exotic and native species is considered an essential step to evaluate the potential effect of invasive species on native communities (Davis 2009; Rilov and Crooks 2009; Blackburn et al. 2011).

Argentina is currently investing a considerable effort in order to determine the presence of exotic species in marine environments (Orensanz et al. 2002; Albano et al. 2013; Schwindt et al. 2014, 2020; Schwindt and

Bortolus 2017; Albano and Obenat 2019; Rumbold 2019; Castro et al. 2020; among others). However, although peracarid species in artificial habitats of Argentina show high densities, comparative studies focused on the exotic species status, their geographical distribution and their impact on native biodiversity are scarce (Schwindt et al. 2014, 2020; Rumbold 2019); mainly due to taxonomic difficulties of some groups, the small size of these organisms and the high sampling effort needed.

The aim of this work was to compare the composition and status of exotic, native and cryptogenic peracarid species between two very distinct ports of the Southwestern Atlantic in order to discuss the differences in vulnerability of these artificial environments to biological invasions in terms of maritime infrastructure, environmental conditions and shipping traffic; and to analyse some life history traits that could favour the persistence of exotic species in these environments. This initial survey will provide important information to design further detailed studies in port environments, serving as a starting point to develop monitoring programmes and to understand the biological invasion patterns of exotic species in South America.

Material and methods

Study sites

The study was conducted in two marine ports of Argentina: Mar del Plata port (38°02'S – 57°32'W; hereafter MDP; Figure 1) and Puerto Madryn port (42°44'S – 65°01'W; hereafter PMY; Figure 1).

MDP port was built in 1922 and consists of a semi-enclosed area (1.4 km²; mean depth 9 m) limited by two artificial breakwaters (North: ca. 1 km long; and South: ca. 2.5 km long) with a port entrance of approximately 300 m wide. This port shows an intense domestic and international traffic of yachts, sailing and fishing vessels. The existence of several industries, sewage pipes and intense fishing activity, result in high levels of hydrocarbons, copper, tributyltin (TBT), high water turbidity, low pH and high levels of organic matter from industrial and urban effluents (Schwindt et al. 2010; Albano et al. 2013; Rumbold et al. 2015b). Despite these high levels of contamination, docks and marinas are densely covered by ascidians, algae and tubicolous polychaetes that provide sheltered areas to fish, flatworms, molluscs, crustaceans and nematodes (Schwindt et al. 2010; Albano et al. 2013; Rumbold et al. 2015b, 2016, 2018b). The monthly seawater temperature showed a mean value of ca. 15°C in MDP port (varying between 9.30°C and

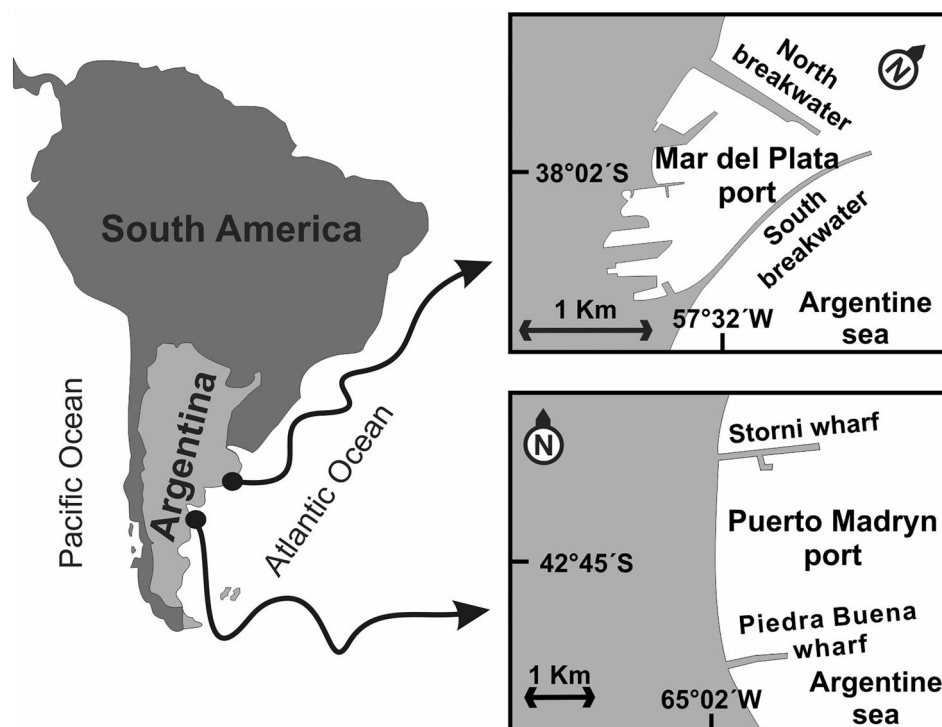


Figure 1. Map of the coast of Argentina with indication of the sampling localities (●): Mar del Plata port and Puerto Madryn port.

20.9°C; **Figure 2A**; data obtained from CEADO-Argentina: <http://www.hidro.gov.ar/ceado>), and the mean salinity and dissolved oxygen values varied between 32.28 and 33.70 PSU and 5.03–6.71 ml/l, respectively (**Figure 2B** and **C**; **Schwindt et al. 2010**).

PMY port is an open port located in a natural bay in the Nuevo Gulf (mean depth 16 m). The port area is composed of two large concrete wharves: the Almirante Storni wharf (ca. 1.5 km long) and the Comandante Piedra Buena wharf (ca. 1 km long), separated by a distance of approximately 3 km. The Almirante Storni wharf was inaugurated in 1910 and is used to transport aluminium and supplies between near industries and vessels, and as docking area for fishing boats. The Comandante Piedra Buena wharf became operational in 1975 and serves as a cruise terminal. Several studies have shown that the fishing and aluminium industries are responsible for moderate eutrophication, presence of heavy metals, hydrocarbons and TBT (**Gil et al. 1999**; **Schwindt et al. 2010**). Nevertheless, a great diversity of algae, molluscs, ascidians, crustaceans, polychaetes, fish and echinoderms among others, can be found in both wharves (**Gil et al. 1999**; **Bigatti et al. 2009**; **Schwindt et al. 2010, 2014**; **Giachetti et al. 2019**). Seawater temperature in PMY registered a mean value of 13.50°C (varying between 9.80°C and 17.5°C; **Figure 2A**; data obtained from CEADO-Argentina: <http://www.hidro.gov.ar/ceado>), while salinity ranged between 33.43 and 33.57 PSU (**Figure 2B**;

Schwindt et al. 2010) and dissolved oxygen between 5.23 and 7.01 ml/l (**Figure 2C**).

Field sampling and laboratory procedures

To compare the port activity between study sites, we analysed the annual mean of total cargo movement of domestic and international ships (i.e. port movement expressed in tons) and the mean total number of vessels entering at each port (i.e. ship movement) from 2010 to 2016 (MDP port: <https://www.gba.gov.ar/produccion>; PMY port: <https://www.appm.com.ar/>).

Five sampling replicates units of 0.04 m² (quadrat of 0.20 × 0.20 m) were collected during 06/02/2016 (autumn), 08/12/2016 (winter), 11/29/2016 (spring) and 02/28/2017 (summer) in MDP port and during 05/10/2016 (autumn), 08/18/2016 (winter), 11/21/2016 (spring) and 02/09/2017 (summer) in PMY port. The marked differences in days between study sites for the autumn sampling (ca. 30 days) are related to the bad weather and maritime conditions in PMY that made impossible to take samples in the port area. In MDP port, sampling units were obtained scraping the fouling community of the floating wooden docks, while in PMY port samples were collected scraping the fouling community of the wharf pilings by SCUBA diving (2 samples from Almirante Storni wharf and 3 from Comandante Piedra Buena wharf). The differences between the sampling techniques are related to the

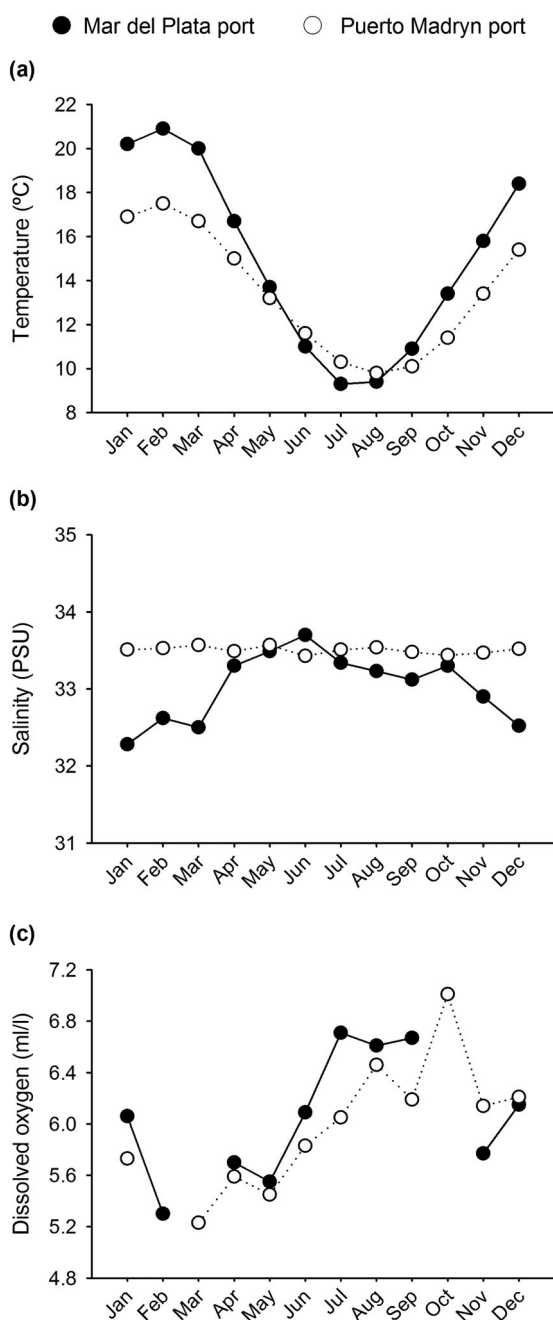


Figure 2. Comparison of historical monthly mean values of environmental variables between Mar del Plata port and Puerto Madryn port. (A) seawater temperature, (B) salinity and (C) dissolved oxygen. Data obtained from: A, Centro Argentino de Datos Oceanográficos, CEADO (records from 1960 to 2019); B–C, Schwindt et al. (2010) (records from 1960 to 2010).

fact that the only way to access to wharf pilings in PMY is by the sea.

In both sites, samples were obtained at 1 m below the low tidal level. Each sample was kept in a separated plastic bag and preserved in ethanol 96%. In the laboratory, samples were washed with running water through a 0.35 mm square mesh sieve. After that, all peracarid specimens were carefully separated, counted and

identified at the lowest taxonomic level using a stereomicroscope and taxonomic guides (Giambiagi 1925; Conlan 1990; Harrison and Ellis 1991; LeCroy 2007). Additionally, organisms were classified as exotic, native and cryptogenic (species that cannot be reliably demonstrated as being either introduced or native; Carlton 1996; Marchini and Cardeccia 2017) following Chapman and Carlton (1991) criteria.

Density values were extrapolated and expressed as individuals/m². Population traits of exotic, native and cryptogenic species were assessed by the following parameters (Rumbold et al. 2015b, 2016; Rumbold 2019): seasonal mean density (individuals/m² ± standard deviation); the percentage of dominance (%D); the proportion of ovigerous females in comparison to total individuals; sex ratio (males/(males + total females)); relative maturity size, calculated as the minimum size of ovigerous females/mean size of ovigerous females; mean fecundity index calculated as brood size/total body length; and the mean reproductive effort expressed as mean egg volume/total body length. To determine the fecundity index or the reproductive effort and total body length, only ovigerous females with stage I embryos were used (Rajagopal et al. 1999). Eggs were considered as ellipsoids and their volume were quantified by the formula $V = 4/3 \pi r_1 r_2^2$, where r_1 is half of the longest dimension of the egg and r_2 is half of the broadest dimension perpendicular to r_1 (Jeong et al. 2009).

Data analysis

To analyse differences in the annual mean of port and ship movements between MDP and PMY ports, a one-way ANOVA was used (Zar 2007). To determine seasonal differences in total peracarid species richness between MDP and PMY port, according to their invasive status (i.e. exotic, native and cryptogenic) and season (i.e. autumn, winter, spring and summer) a three-way ANOVA was used (Zar 2007). To analyse the population dynamics of species within each study site, using as factors population groups (i.e. juveniles, males and females) and seasonality (i.e. autumn, winter, spring and summer) a two-way ANOVA was performed (Zar 2007). In addition, due to the fact that density values of some species were low, no statistical analyzes were carried out to study their population traits. Data was previously logarithmic transformed and a Student–Newman–Keuls (SNK) test was applied when statistically significant differences of means were found. Nonmetric Multidimensional scaling (nMDS) ordinations were used to show the seasonal differences of peracarid assemblages among ports on square-root transformed total density data, to reduce

the influence of very abundant species, with a Bray–Curtis similarity matrix (Clarke and Warwick 1994). A χ^2 -test with Yates correction was applied to examine the deviation of sex ratio from an expected ratio of 1:1. Determination coefficients were calculated for each population to assess the relationship between eggs number or eggs volume and female size. Statistical tests were performed using R statistical software (R Core Team 2017). Significance was assessed at $\alpha = 0.05$ (Zar 2007).

Results

Port activity

The mean port and ship movement for the 2010–2016 period showed significant differences between study sites (in both cases; one-way ANOVA, $P < .001$; Figure 3), being PMY port more active in both conditions (mean port movement: ca. 157×10^4 tn; mean ship entries: 749 ships), compared to MDP port (mean annual port movement: ca. 54×10^4 tn; mean annual ship entries: 485 ships).

Comparison of exotic, native and cryptogenic assemblages between ports

A total of 15 peracarid species were found during the study period (Table I): seven were categorized as exotic, two as native and four as cryptogenic; while two species need more taxonomic studies to establish their correct identification.

Species richness of MDP port registered the highest number of peracarid species (total: 11 spp.) in

comparison to PMY port (total: 8 spp.; Table II). The only species registered in both study sites were the exotic amphipods *Monocorophium acherusicum*, *Jassa marmorata*, the cryptogenic tanaidacean *Tanais dulongii* and isopod *Idotea balthica*. The exotic amphipods *Ericthonius brasiliensis* and *Jassa slatteryi*, the exotic isopods *Sphaeroma serratum*, *Paracerceis sculpta* and *Dynamene edwardsi*, and the cryptogenic amphipods *Caprella equilibra* and *Caprella dilatata* were restricted to MDP port; while the native isopods *Exosphaeroma lanceolatum* and *Cymodoce bentonica*, the undetermined amphipod *Leucothoe cf. spinicarpa* and isopod *Pseudosphaeroma sp.* were only recorded in PMY port.

The species richness of exotic, native and cryptogenic species between ports did not show seasonal variations in each study site (three-way ANOVA, $P > .05$; Table III), but registered significant differences between sites, species status and the interaction between sites and species status (in all cases three-way ANOVA, $P < .001$). In MDP port exotics were dominants (five to six spp.), followed by cryptogenics (three to four spp.) and no native species were recorded (in all cases SNK test, $P < .05$); in PMY port exotics showed the highest species richness (one to two spp.), followed by natives (one to two spp.) and cryptogenics (zero to one spp.; in all cases SNK test, $P < .05$). The interaction of factors (study sites \times species status) revealed that exotic and cryptogenic species were higher in MDP port (total: seven exotics and four cryptogenics) in comparison to PMY port (total: two exotics and two cryptogenic, in all cases SNK test, $P < 0.05$); while in PMY port only two native species were registered.

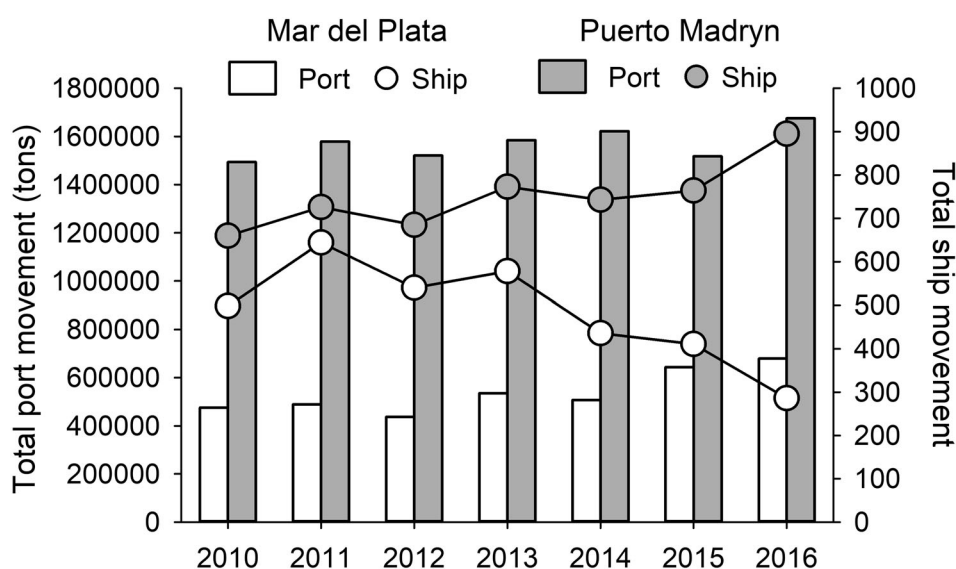


Figure 3. Annual port movement (bars, left y axis) and ship entries (circles, right y axis) between 2010 and 2016 of Mar del Plata and Puerto Madryn ports; data obtained from Subsecretaría de Actividades Portuarias de la Provincia de Buenos Aires (<https://www.gba.gob.ar/produccion>) and Administración Portuaria de Puerto Madryn (APPM; <http://www.appm.com.ar/>), respectively.

Table 1. List of peracarid species registered during the sampled period, their status (E: exotic, N: native, C: cryptogenic, TS: species that need taxonomic study, the date of first collection, their probable native range, their general geographic distribution and their distribution in the southwestern Atlantic.

Taxa	Status	Date of first collection	Reference	Probable native range	General geographic distribution	Distribution in the southwestern Atlantic
Order Amphipoda						
<i>C. dilatata</i> Krøyer, 1843	C	1966	Bastida 1970	Unknown	Europe, SW Atlantic	San Bernardo (36°S) to Puerto Madryn (42°S, Argentina)
<i>C. equilibra</i> Say, 1818	C	1961	McCain 1965	Unknown	Europe, S Africa, Japan, Australia, New Zealand, SW Atlantic	San Bernardo (36°S) to Puerto Madryn (42°S, Argentina)
<i>E. brasiliensis</i> (Dana, 1853)	E	2007	Albano and Obenat 2019 (reported as <i>Erichthonius punctatus</i>)	N Atlantic	Europe, Mediterranean, S Africa, India, Korea, Japan, China, Australia, New Zealand, N and SW Atlantic	Mar del Plata (38°S, Argentina)
<i>J. marmorata</i> Holmes, 1905	E	1968	Alonso de Pina 2005	NE Atlantic	Europe, Mediterranean, W Africa, Japan, China, Australia, New Zealand, E Pacific (Alaska to Chile), NW and SW Atlantic	Uruguay to Puerto Madryn (42°S, Argentina)
<i>J. slatteryi</i> Conlan, 1990	E	2010	Rumbold et al. 2015a	NE Pacific	Europe, S Africa, Japan, Korea, Australia, New Zealand, Pacific (Alaska to Chile), NW and SW Atlantic	Mar del Plata (38°S, Argentina)
<i>Leucothoe</i> cf. <i>spinicarpa</i> (Abildgaard, 1789)	TS	before 1931	Schellenberg 1931 (<i>Leucothoe spinicarpa</i>)	Unknown	<i>Leucothoe spinicarpa</i> was recorded in Europe, Mediterranean, S Africa, India, Japan, Australia, New Zealand, NE Pacific, NW and SW Atlantic, Antarctica	<i>Leucothoe spinicarpa</i> was recorded in Argentine continental shelf, San Antonio Este (40°S), Puerto Madryn (42°S), Tierra del Fuego (54°S, Argentina); Falkland Islands (Malvinas Islands, 51°S)
<i>M. acherusicum</i> (Costa, 1853)	E	before 1969	McCain 1969	N Atlantic	Europe, Mediterranean, SE Africa, India, Korea, Japan, China, Australia, New Zealand, N and SW Atlantic	Mar del Plata (38°S) to Ushuaia (54°S, Argentina)
Order Isopoda						
<i>D. edwardsi</i> (Lucas, 1849)	E	2007	Rumbold et al. 2018a	N Africa/ Europe	Mediterranean, NW Africa, S Africa, SW Atlantic	Mar del Plata (38°S, Argentina)
<i>E. lanceolatum</i> (White, 1843)	N	1921	Giambiagi 1925	SW Atlantic	South Africa, New Zealand, SE Pacific and SW Atlantic	Puerto Madryn (42°S) to Ushuaia (54°S, Argentina); Falkland Islands (Malvinas Islands, 51°S)
<i>I. balthica</i> Fabricius, 1798	C	1964	Bastida 1968 (reported as <i>Idotea</i> sp.)	N Atlantic	Europe, Mediterranean, NW and SW Atlantic	Uruguay to Playa Cangrejales (43°S, Argentina).
<i>P. sculpta</i> (Holmes, 1904)	E	2007	Rumbold et al. 2018a	NE Pacific	Europe, Mediterranean, NW and S Africa, Pakistan, China, Japan, Australia, New Zealand, NE Pacific (including Hawaii), NW and SW Atlantic	Mar del Plata (38°S, Argentina)
<i>Pseudosphaeroma</i> sp. Chilton, 1909	TS	2003	Bruce and Wetzer 2008	SW Atlantic?		Puerto Madryn (42°S) to Cabo dos Bahias (49°S, Argentina)
<i>S. serratum</i> (Fabricius, 1787)	E	1964	Bastida 1968 (reported as <i>Exosphaeroma calcarea</i>)	NE Atlantic	Europe, Mediterranean, SE Africa, Thailand, Australia, SW Atlantic	La Paloma (34°S, Uruguay) to Puerto Madryn (42°S, Argentina)
<i>C. bentonica</i> Loyola e Silva, 1962	N	2005	Schwindt et al. 2014 (reported as <i>C.</i> cf. <i>bentonica</i>)	SW Atlantic	SW Atlantic	Puerto Madryn (42°S, Argentina)
Order Tanaidacea						
<i>T. dulongii</i> (Audouin, 1826)	C	1915	Giambiagi 1922 (reported as <i>T. gallardoi</i>)	Unknown	Europe, Mediterranean, NW Africa, Japan, Australia, NW and SW Atlantic	Mar del Plata (38°S) to Puerto Madryn (42°S, Argentina)

Table II. Seasonal and total mean density (individuals/m²) and dominance (%D) of peracarid species from Mar del Plata port and Madryn port (E: exotic, N: native, C: cryptogenic; TS: species that need taxonomic study; Aut: autumn, Win: winter; Spr: spring; Sum: summer).

Taxa	Mar del Plata port Aut	Puerto Madryn port Win	Spr	Sum	Mean ± SD	%D	Aut	Win	Spr	Sum	Mean ± SD	%D
Order Amphipoda												
<i>C. dilatata</i> (C)	170	55	1340	215	445.00 ± 600.46	6.15						
<i>C. equilibra</i> (C)	80	35	320	720	288.75 ± 313.54	3.99						
<i>E. brasiliensis</i> (E)	80			445	131.25 ± 212.54	1.82						
<i>J. marmorata</i> (E)			1840	105	486.25 ± 903.86	6.73			5	5	2.50 ± 2.89	2.99
<i>J. slatteryi</i> (E)		150	515		166.25 ± 243.01	2.30						
<i>L. cf. spinicarpa</i> (TS)										5	1.25 ± 2.50	1.49
<i>M. acherusicum</i> (E)	3005	665	8845	5225	4435.00 ± 3479.94	61.34	35	30	50	100	53.75 ± 31.98	64.18
Order Isopoda												
<i>C. bentonica</i> (N)										20	5.00 ± 10.00	5.97
<i>D. edwardsi</i> (E)	205	70	60	195	132.50 ± 78.16	1.83						
<i>E. lanceolatum</i> (N)							25	10	30	5	17.50 ± 11.90	20.90
<i>I. balthica</i> (C)			10		2.50 ± 5.00	0.03	5				1.25 ± 2.50	1.49
<i>P. sculpta</i> (E)	180	160	490	605	358.75 ± 223.10	4.96						
<i>Pseudosphaeroma</i> sp. (TS)									5		1.25 ± 2.50	1.49
<i>S. serratum</i> (E)	800	220	765	250	508.75 ± 316.66	7.04						
Order Tanaidacea												
<i>T. dulongii</i> (C)	575	115	70	340	275.00 ± 232.27	3.80		5			1.25 ± 2.50	1.49
Total Peracarida	5095	1470	14255	8100	7230.00 ± 5411.20		65	45	90	135	83.75 ± 38.81	
Species richness	8	8	10	9	11		3	3	4	5	8	

Table III. Results of three-way ANOVA for comparison of peracarid richness between status (exotic, native and cryptogenic) and study sites (MDP port and PMY port); and seasonal variation (autumn, winter, spring and summer) of species richness by their status in each study site (*df*: degrees of freedom).

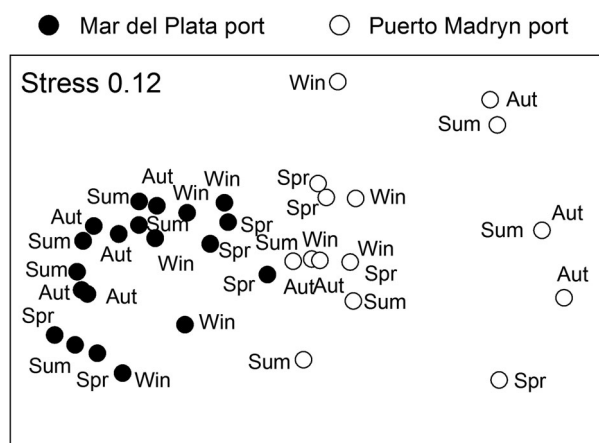
Source of variation	<i>df</i>	<i>F</i>	<i>P</i>
Site	1	64.14	<0.001
Season	3	0.05	0.99
Status	2	71.65	<0.001
Site × Season	3	1.55	0.21
Site × Status	2	42.28	<0.001
Season × Status	6	0.89	0.51
Site × Season × Status	6	1.09	0.37

The nMDS ordination plot of total densities of peracarid species corroborates that samples of MDP port and PMY port showed clear differences in their species assemblages; but in both cases, no pattern of seasonality was observed (Figure 4).

Mar del Plata port: exotic, native and cryptogenic species

Population dynamics

Population dynamics analysis of exotic species showed different patterns. *Monocorophium acherusicum* registered seasonal differences in their density values among seasons and groups (two-way ANOVA, $P < .05$; Table IV; Figure 5A), females showed higher densities (ca. 3000 ind/m²; SNK test, $P < .05$), while males and juveniles did not show significant differences in their

**Figure 4.** Two-dimensional nMDS ordination plot of seasonal peracarid densities of Mar del Plata port and Puerto Madryn port.

values (ca. 450–950 ind/m²; SNK test, $P > .05$); the highest densities of males (ca. 2400 ind/m²), females (ca. 5700 ind/m²) and juveniles (ca. 630 ind/m²) were recorded in autumn and the lowest in winter (males: ca. 140 ind/m²; females: ca. 460 ind/m²; and juveniles: ca. 60 ind/m²; SNK test, $P < .05$). Seasonal density of *D. edwardsi* recorded an interaction among factors (two-way ANOVA, $P < .05$; Figure 5B), males recorded highest densities (ca. 190 ind/m²) than females and juveniles in autumn (ca. 0–15 ind/m²; SNK test, $P < .05$); no significant differences among groups were observed in spring and winter (ca. 0–70 ind/m²; SNK test, $P > .05$); and in summer females and males

Table IV. Results of two-way ANOVA for comparison of densities between seasons (autumn, winter, spring and summer) and groups (males, females and juveniles) from peracarid species of MDP port and PMY port

Study site	Species	Source of Variation	df	F	P
MDP port	<i>M. acherusicum</i>	Season	3	8.53	<0.001
		Group	2	6.73	0.00
		Season × Group	6	0.28	0.94
	<i>C. dilatata</i>	Season	3	1.22	0.31
		Group	2	0.32	0.72
		Season × Group	6	0.34	0.91
	<i>C. equilibra</i>	Season	3	0.37	0.77
		Group	2	0.83	0.44
		Season × Group	6	0.11	1.00
	<i>D. edwardsi</i>	Season	3	3.63	0.02
		Group	2	9.08	<0.001
		Season × Group	6	5.04	<0.001
	<i>P. sculpta</i>	Season	3	1.46	0.24
		Group	2	0.79	0.46
		Season × Group	6	0.19	0.98
<i>S. serratum</i>	Season	3	2.17	0.10	
	Group	2	0.52	0.60	
	Season × Group	6	0.20	0.98	
<i>T. dulongii</i>	Season	3	1.60	0.20	
	Group	2	3.38	0.04	
	Season × Group	6	0.49	0.81	
PMY port	<i>M. acherusicum</i>	Season	3	0.32	0.81
		Group	2	14.18	<0.001
		Season × Group	6	0.54	0.78
	<i>E. lanceolatum</i>	Season	3	0.46	0.71
		Group	2	2.10	0.13
		Season × Group	6	0.31	0.93

recorded similar densities (ca.100), while juveniles were absent (SNK test, $P < .05$). In *P. sculpta* (ca. 360 ind/m²; Figure 5C) and *S. serratum* (ca. 510 ind/m²; Figure 5D) seasonal densities did not show significant differences among seasons and population groups (in both cases, two-way ANOVA, $P > .05$).

In contrast to the species mentioned previously, *J. slatteryi*, *J. marmorata* and *E. brasiliensis* showed a discontinuous seasonal density. In *J. slatteryi*, males, females and juveniles were registered in spring (ca. 10–110 ind/m²; Figure 5E) and summer (ca. 40–320 ind/m²); in *J. marmorata*, all groups were recorded in spring (ca. 150–1500 ind/m²; Figure 5F) and males and females were registered in summer (ca. 35–70 ind/m²); while *E. brasiliensis* showed females and juveniles in autumn (ca. 10–70 ind/m²; Figure 5G), and males, females and juveniles were recorded in summer (ca. 60–250 ind/m²).

In the case of cryptogenic species, the seasonal density of *T. dulongii* recorded significant differences among seasons (two-way ANOVA, $P < .05$; Figure 5H), females densities were higher (ca. 220 ind/m²; SNK test, $P < .05$) than males and juveniles during the whole sampled period (ca. 30 ind/m²; SNK test, $P > .05$). On the other hand, the populations of *C. dilatata* (ca. 440 ind/m²; Figure 5I) and *C. equilibra* (ca. 290 ind/m²; Figure 5J) did not show significant differences among seasons and population groups (in both

cases, two-way ANOVA, $P > .05$); and in *I. balthica*, only males were observed in spring (ca. 10 ind/m²; Figure 5K).

Reproductive traits

In exotic species, ovigerous females were recorded throughout all the seasons only in *M. acherusicum*, registering a mean percentage (respect total individuals) between ca. 19–29% (Table V). In the case of *P. sculpta*, ovigerous females were recorded in autumn, spring and summer, varying between ca. 6–16%. In *S. serratum* were observed in spring and summer, showing a mean percentage ca. 4–16%. The percentage of ovigerous females of *J. slatteryi* varied ca. 17–31% in winter and spring. On the other hand, ovigerous females of *J. marmorata* and *D. edwardsi* were registered only in spring (ca. 25–29%); while *E. brasiliensis* only showed the presence of ovigerous females in summer (ca. 7%). Regarding cryptogenic species, ovigerous females of *T. dulongii* were observed from winter to summer, with a mean percentage ca. 6–14%; in *C. dilatata* were recorded in all seasons, varying between ca. 6–37%; while in *C. equilibra*, ovigerous females were registered in spring and summer ca. 6–27%.

Sex ratio was skewed towards females in most of the analysed populations (ca. 0.10–0.30; in all cases χ^2 -test, $P < .001$; Table V); except in *D. edwardsi* (ca. 0.68; χ^2 -test, $P < .001$) and *I. balthica* (ca. 1; in both cases was male biased); and in *C. equilibra* sex ratio did not differ from the expected 1:1 ratio (χ^2 -test, $P = .42$).

Ovigerous females of *M. acherusicum* registered the lowest values of relative maturity size (0.54); while the rest of the species showed higher values, between 0.64 and 0.90 (Table VI). Correlation analysis showed that fecundity increased with female size in *M. acherusicum* ($r = 0.54$), *J. marmorata* ($r = 0.64$) and *C. dilatata* ($r = 0.79$; in all cases $P < .05$), whereas in the rest of the species analysed, the lower number of ovigerous females did not allow to determine this coefficient. The fecundity index was higher in *D. edwardsi* (31.90 eggs/mm), followed by *P. sculpta* (12.18 eggs/mm), *S. serratum* (5.00 eggs/mm), *T. dulongii* (7.79 eggs/mm), *J. marmorata* (5.68 eggs/mm), *C. dilatata* (4.11 eggs/mm) *E. brasiliensis* (3 eggs/mm) and *M. acherusicum* (2.41 eggs/mm). Reproductive effort showed a positive relationship between the egg volume and the total body length of ovigerous females in *M. acherusicum* ($r = 0.41$), *D. edwardsii* ($r = 0.32$), *E. brasiliensis* ($r = 0.39$), *C. dilatata* ($r = 0.45$) and *T. dulongii* ($r = 0.88$; in all cases $P < .05$). The mean reproductive effort was higher in *T. dulongii* and *E. brasiliensis*

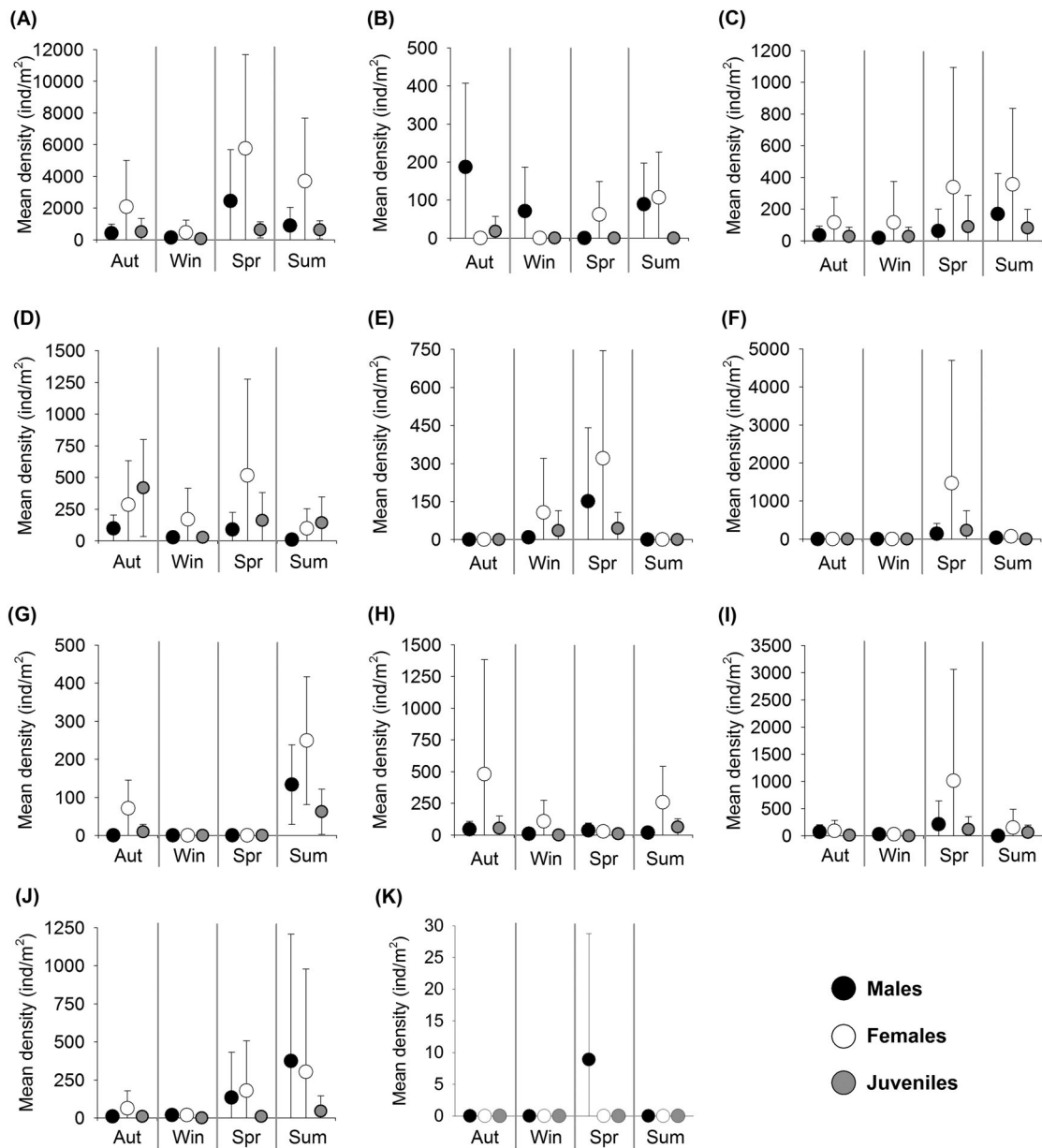


Figure 5. Seasonal variation of total mean density (\pm standard deviation) of males, females and juveniles of exotic and cryptogenic peracarid species recorded in Mar del Plata port: (A) *M. acherusicum*, (B) *D. edwardsii*, (C) *P. sculpta* (D), *S. serratum*, (E) *J. slatteryi*, (F) *J. marmorata* (G) *E. brasiliensis*, (H) *T. dulongii*, (I) *C. dilatata*, (J) *C. equilibra* and (K) *I. balthica*.

($0.01 \text{ mm}^3/\text{mm}$), followed by *C. dilatata* and *J. marmorata* ($0.02 \text{ mm}^3/\text{mm}$), *M. acherusicum* ($0.03 \text{ mm}^3/\text{mm}$), *P. sculpta* and *D. edwardsii* ($0.06 \text{ mm}^3/\text{mm}$) and *S. serratum* ($0.18 \text{ mm}^3/\text{mm}$).

Puerto Madryn port: exotic, native and cryptogenic species

Population dynamics

Regarding exotic species, *M. acherusicum* was the only species that was recorded in all the seasons; the population analysis determined significant differences

between groups (two-way ANOVA, $P < .05$; Table IV; Figure 6A): females registered higher densities than the other groups (ca. $40 \text{ ind}/\text{m}^2$; SNK test, $P < .05$), while males and juveniles did not show significant differences in their density values (ca. $1\text{--}9 \text{ ind}/\text{m}^2$; SNK test, $P > .05$). *Jassa marmorata* registered a discontinuous seasonality and only females were recorded in spring and summer (ca. $5 \text{ ind}/\text{m}^2$; Figure 6B).

Regarding native species, *E. lanceolatum* registered individuals throughout the study period and did not show differences between seasons and groups (two-way ANOVA, $P < .05$; Figure 6C): the mean density of

Table V. Reproductive parameters of peracarid species (%OF: mean percentage of ovigerous females respect total individuals, SR: mean sex ratio) from populations of MDP port and PMY port.

Study site	Species	% OF	SR	χ^2 -test
MDP port	<i>M. acherusicum</i>	23.16	0.30	38.43*
	<i>E. brasiliensis</i>	1.69	0.10	643.66*
	<i>J. marmorata</i>	7.40	0.48	0.66
	<i>J. slatteryi</i>	11.93	0.11	345.02*
	<i>D. edwardsi</i>	6.25	0.27	62.36*
	<i>P. sculpta</i>	8.63	0.25	2194.25*
	<i>S. serratum</i>	5.08	0.24	180.85*
	<i>C. dilatata</i>	19.61	0.17	312.66*
	<i>C. equilibra</i>	8.33	0.19	324.89*
	<i>I. balthica</i>	0.00	1.00	
	<i>T. dulongii</i>	7.22	0.68	32.06*
PMY port	<i>M. acherusicum</i>	19.82	0.03	97.73*
	<i>J. marmorata</i>	0.00	0.00	
	<i>I. balthica</i>	0.00	1.00	
	<i>T. dulongii</i>	0.00	0.00	
	<i>E. lanceolatum</i>	35.00	0.36	2.36
	<i>C. bentonica</i>	0.00	0.50	0.10

* $P < 0.05$.

males and females varied between ca. 6–11 ind/m², and no juveniles were recorded. In the case of *C. bentonica*, females and males were registered only in summer (in both cases ca. 10 ind/m²; Figure 6D). On the other hand, the cryptogenic species *T. dulongii* only showed the presence of females in winter (ca. 5 ind/m²; Figure 6E); while in *I. balthica*, the population was represented only by males in autumn (ca. 5 ind/m²; Figure 6F).

Reproductive traits

In exotic species, ovigerous females of *M. acherusicum* were recorded in all seasons (ranging ca. 10–35%; Table V). In the case of native species, *E. lanceolatum* showed the presence of ovigerous females in autumn and summer (ca. 5–25%) and no ovigerous females were registered for *C. bentonica* and for the cryptogenic species *T. dulongii*.

Sex ratio showed differences between populations: for *J. marmorata*, *M. acherusicum* and *T. dulongii* sex ratio was female biased (ca. 0–0.03; χ^2 -test, $P < .001$); for *I. balthica*, it was skewed toward males (ca. 1); while for *C. bentonica* and *E. lanceolatum* sex ratio did not differ from the expected proportion 1:1 (ca. 0.36–0.50; in both cases χ^2 -test, $P > .05$; Table V).

The mean value of relative maturity size was 0.89 in *M. acherusicum* and 0.95 in *E. lanceolatum* (Table VI). On the other hand, correlation analyses of fecundity index and reproductive effort were not calculated for these species, due to the lower number of ovigerous females recorded. The mean fecundity index and reproductive effort were higher in *E. lanceolatum* (9.78 eggs/mm; 0.13 mm³/mm) than *M. acherusicum* (1.51 eggs/mm; 0.04 mm³/mm).

Table VI. Mean size of ovigerous females, relative maturity (RM), mean number of eggs, fecundity index (FI; mean eggs number/mean ovigerous female size), regression lines and determination coefficient from peracarid species of Mar del Plata port (MDP port) and Puerto Madryn port (PMY port).

Study site	Species	Mean size \pm SD (Range) (mm)	RM	Mean eggs \pm SD (Range) (n°)	FI	n	r	Mean vol \pm SD (Range) (mm ³)	ER	n	r
MDP port	<i>M. acherusicum</i>	3.83 \pm 0.71 (2.06 – 5.31)	0.54	9.24 \pm 5.94 (1 – 25)	2.41	50	0.54	0.1 \pm 0.03 (0.03 – 0.17)	0.03	186	0.41
	<i>J. marmorata</i>	5.35 \pm 1.07 (3.44 – 7.50)	0.64	30.42 \pm 20.25 (7 – 82)	5.68	38	0.64	0.08 \pm 0.02 (0.04 – 0.14)	0.02	160	0.07
	<i>P. sculpta</i>	5.27 \pm 0.44 (4.56 – 6.06)	0.87	64.13 \pm 24.96 (26 – 97)	12.18	8	0.64	0.33 \pm 0.10 (0.10 – 0.56)	0.06	40	0.06
	<i>S. serratum</i>	7.16 \pm 0.74 (5.81 – 8.13)	0.81	35.8 \pm 8.39 (25 – 54)	5.00	10	0.24	1.25 \pm 0.35 (0.68 – 1.90)	0.18	31	0.29
	<i>D. edwardsi</i>	5.13 \pm 0.71 (4.63 – 5.63)	0.90	163.50 \pm 51.62 (127 – 200)	31.90	2		0.28 \pm 0.08 (0.18 – 0.45)	0.06	10	0.32
	<i>E. brasiliensis</i>	5.38 \pm 0.97 (4.69 – 6.06)	0.87	18.5 \pm 10.61 (11 – 26)	3.44	2		0.05 \pm 0.01 (0.03 – 0.07)	0.01	10	0.39
	<i>C. dilatata</i>	7.24 \pm 0.97 (6.06 – 9.00)	0.84	29.74 \pm 13.98 (10 – 67)	4.11	19	0.79	0.16 \pm 0.05 (0.07 – 0.32)	0.02	64	0.45
	<i>T. dulongii</i>	4.14 \pm 1.01 (3.00 – 5.44)	0.72	32.25 \pm 11.50 (18–43)	7.79	4	0.92	0.03 \pm 0.01 (0.02 – 0.06)	0.01	20	0.88
	<i>M. acherusicum</i>	3.43 \pm 0.46 (2.94–4.06)	0.89	5.17 \pm 3.92 (3 – 13)	1.51	6	0.18	2.94 \pm 0.00	0.04	1	
	<i>E. lanceolatum</i>	8.52 \pm 0.64 (8.06 – 9.25)	0.95	83.33 \pm 10.21 (76 – 95)	9.78	3	0.92	1.18 \pm 0.22 (0.73 – 1.50)	0.13	15	0.35

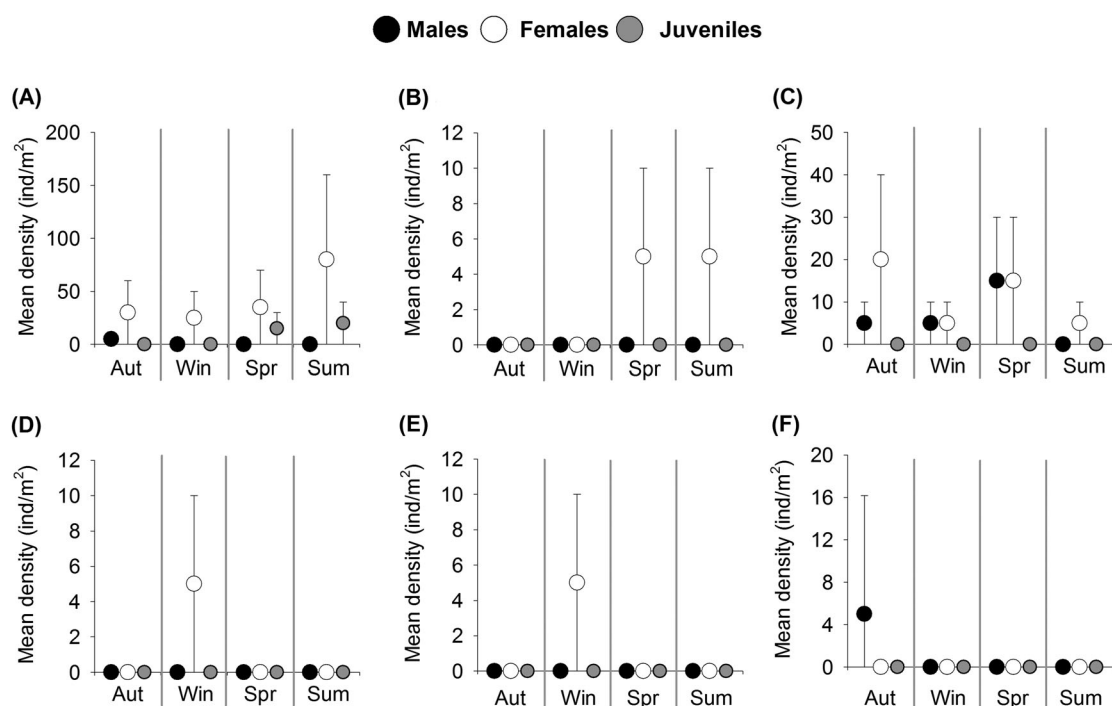


Figure 6. Seasonal variation of total mean density (\pm standard deviation) of males, females and juveniles of exotic, natives and cryptogenic peracarid species recorded in Puerto Madryn port: (A) *M. acherusicum*, (B) *J. marmorata*, (C) *E. lanceolatum*, (D) *C. bentonica*, (E) *T. dulongii* and (F) *I. balthica*.

Discussion

In Argentina, the first studies focused on peracarid diversity in coastal environments started at the beginning of the twentieth century (Giambiagi 1922, 1925; Schellenberg 1931). Most of these works are fragmented and show a poor description. Moreover, several sites have not been surveyed yet, hindering the determination of their distribution (Orensanz et al. 2002). Nevertheless, since the 1960s there has been an increase in the amount of biodiversity studies in artificial marine environments of Argentina (Schwindt and Bortolus 2017; Schwindt et al. 2020), and although many exotic peracarids could have been already established, most first reports of these organisms correspond to this period (see Table II). Furthermore, considering this and previous studies (Olenin et al. 2002; Schwindt et al. 2014; Rumbold et al. 2015a, 2018a; Rumbold 2019; Schwindt et al. 2020), the total number of exotic and cryptogenic peracarid species registered in coastal environments of the Southwestern Atlantic has increased in ca. 50%, only in the last few decades, reflecting that the introduction and further establishment of new exotic species continue nowadays, being one of the main threats to native biodiversity in Southwestern Atlantic (Orensanz et al. 2002; Schwindt and Bortolus 2017; Schwindt et al. 2020).

In port areas, the richness of exotic species increases with the abundance and diversity of artificial materials and the presence of seawalls that reduce the water movement (Glasby et al. 2007; Tyrrell and Byers 2007; Airoidi and Bulleri 2011). MDP port presents a more complex infrastructure, related to the large number of anthropogenic constructions (e.g. seawalls, docks and marinas) that offer a large surface and a variety of artificial materials (e.g. concrete, plastic, steel, wood, among others) for the settlement of the exotic species (Schwindt et al. 2010; Albano and Obenat 2019). Accordingly, this could explain the higher richness and density registered in comparison to PMY port, in which the presence of only two exposed concrete piers, provides a smaller settling area and a poor diversity of artificial substrates for the colonization of exotic organisms (Schwindt et al. 2010, 2014). Additionally, the semi-enclosed area of MDP port offers a more protected site against waves and currents that maximizes the chances of settlement and proliferation of exotic species; while the open area of PMY port is subjected to higher hydrodynamism, offering adverse conditions for the settlement of propagules and a consequent lower exotic species richness (Schwindt et al. 2010; Albano and Obenat 2019).

In general, exotic species that successfully establish in polluted environment (e.g. ports areas) present their

life history traits adapted to a wide range of abiotic stressors (Piola and Johnston 2008; Airoidi and Bulleri 2011). Although, both ports showed similar values in temperature, salinity and dissolved oxygen values; the higher levels of organic matter, organic carbon, hydrocarbons and TBT of MDP port in comparison to PMY port (Massara et al. 2008; de Waisbaum et al. 2010; Albano et al. 2013; Laitano et al. 2015), could explain the absence of native species and the dominance of exotics (e.g. *E. brasiliensis*, *J. marmorata*, *M. acherusicum*, *S. serratum*), probably better adapted to this stressful environment (Lee and Lee 2005; Kalkan et al. 2007; Sánchez-Moyano and García-Asencio 2010; El-Din et al. 2014); meanwhile, the presence of native species in PMY port would be related to more 'healthier' environmental conditions surrounding the port.

Propagule pressure is related to many factors, among which the frequency of ship movements and the port stay length play significant roles in the successful introduction of exotic species (Carlton 1996; Johnston et al. 2009). According to our results, this premise is not fulfilled, because, despite MDP port is not an important port in terms of international shipping (Schwindt et al. 2010) and presents a lower port activity, registered a higher exotic species richness than PMY port, in which, in spite of their international marine traffic (e.g. commercial vessels and cruisers; Schwindt et al. 2010, 2014) and their higher port activity, presented a lower exotic species richness. However, these differences between port activities and exotic species richness can be explained by the fact that MDP port houses one of the most important marine yacht clubs of Argentina receiving a large number of recreational vessels mainly from Brazil (Albano and Obenat 2009, 2019; Schwindt et al. 2010). In several studies, it has been shown that the sailing patterns of recreational vessels characterized by long port stay, low sailing speed, absence of long oceanic transits and long periods between hull cleaning operations, compared to trading vessels and cruisers, increases the chances to gather hull fouling and act as more effective vectors for regional dispersion and introduction of exotic species (Zabin et al. 2014; Ferrario et al. 2017; Martínez-Laiz et al. 2019; Ulman et al. 2019; Castro et al. 2020). Consequently, despite the marked difference in maritime traffic between MDP and PMY port, the dissimilarities in the type of vessels present in both ports would explain the higher richness of exotic species in MDP port. This also suggests that closer surveillance and management strategies focused on recreational vessels are needed, and additionally highlights the role of MDP port as a

potential secondary spread node of exotic species in the Southwestern Atlantic (Rumbold et al. 2018a).

The knowledge of life history traits of exotic species in artificial environments is crucial to understand the factors that determine their successful settlement in a new environment and their potential spread to other areas. On the other hand, the comparison of life history traits between populations of the same species is important to detect genetic and phenotypic differences in response to the environmental conditions of the new invaded habitat (Sakai et al. 2001; Strauss et al. 2006; Smith 2009). The results of this work suggest that the dominant exotic species present reproductive and recruitment periods during several seasons, as occurred with *M. acherusicum* in both ports; and *Dynamene edwardsi*, *P. sculpta* and *S. serratum* in MDP port; indicating that these populations are well-established as it was proposed in previous studies (Kittlein 1991; Rumbold et al. 2016, 2018a). These species are considered among the most successful invasive peracarid species around the world, related to the large number of marine environments that they have invaded and their great capability to adapt to different environmental conditions (Ruiz and Carlton 2003; Galil et al. 2011). On the other hand, the exotic species that registered lower population densities were characterized by reproductive and recruitment periods that were restricted to one season. However, this does not imply that these populations are not well-established in the area, as indicated by previous records of some species in both ports or in nearby marine environments (Kittlein 1991; Rumbold et al. 2016, 2018a, 2018b; Rumbold 2019). Therefore, although reproductive period would appear to be independent of the establishment capacity of exotic species, it has been shown that those species that presents several reproductive and recruitment periods have great invasiveness (Pöckl 2009; Henkel 2014), explaining the wide distribution of *M. acherusicum* in Southwestern Atlantic (Albano et al. 2019).

The lack of native species in MDP port, such as *Apo-hyale grandicornis* reported as *Hyale* sp. by Bastida et al. (1977) in 1973 and *Jassa alonsoae* recorded by Albano and Obenat (2019) in 2007 could be related to the fact that most peracarid species exhibit trophic and habitat overlap. These relate to the similarity in their trophic habits and their use of refuges against predators. Thus, the presence of the newcomers would increase interspecific competition between exotic and native species, altering the structure and composition of native assemblages, either through the disappearance of native species or their displacement to other areas (Piscart et al. 2010; Ros et al. 2014; Beggel et al. 2016;

David et al. 2017). On the contrary, the native species in PMY port (i.e. *E. lanceolatum* and *C. bentonica*) showed lower densities than exotic species, related probably to the discontinuous recruitment period and the lack of ovigerous females. These suggest that environmental conditions became unsuitable for these populations or, alternatively, the presence of exotic species affected somehow the native biodiversity, through interference, exploitation competition or more complex interactions involving other species (Ros et al. 2014; Beggel et al. 2016; David et al. 2017).

The absence or the low number of native ovigerous females, in both ports, impeded us to compare the fecundity values between exotic and native species. However, several authors established that exotic species have higher fecundity values and reach their sexual maturity at smaller sizes compared to native species, resulting in several recruitments and reproductive cycles per season, and explaining their highest densities and dominance in the new invaded environments (Sakai et al. 2001; Smith 2009; Truhlar and Aldridge 2015). Contrary to our expectations, the dominant exotic *M. acherusicum* presented the lowest fecundity index among exotic peracarids from MDP port. In addition, it reached the relative maturity at smaller sizes and registered a lower reproductive effort compared with other exotic species with the highest fecundity values and several reproductive and recruitment periods (e.g. *P. sculpta*, *D. edwardsi*, *S. serratum*). This could be an indicative that this species expends a lower amount of energy in the production of gametes and therefore, presents a more efficient distribution of resources, favouring the presence of recruits and ovigerous females during all the year long.

The present study provides important information to increase the knowledge of the current status of exotic and native species, and to understand the biological invasion pattern in Southwestern Atlantic (Schwindt et al. 2020). However, other factors should not be discarded to explain the differences in native and exotic species richness and abundance, such as the sample of mobile fauna without the use of designed nets and the dissimilarities in the habitat structure in each study area; the explanation of the proximal causes of the observed differences would require more field studies and detailed laboratory experiments (e.g. analyzing the species assemblages on different artificial materials; making comparative studies with natural environments; and, studying the effects of environmental variables, the biotic interactions and the genetic variation of the populations) (Sakai et al. 2001; Tyrrell and Byers 2007; Smith 2009; Airoldi and Bulleri 2011).

Monitoring programmes are considered a powerful tool to determine the presence of exotic species in marine environments (Rilov and Crooks 2009; Schwindt et al. 2014; Schwindt and Bortolus 2017). However, the establishment of national systems for the management of biological invasions is essential to reduce new species introductions and to limit their spreading process (Olenin et al. 2011; Ferrario et al. 2017). In this context, we expect that the present work provides essential information to understand the invasion patterns of exotic peracarids in the Southwestern Atlantic and to develop adaptive management legislations to the specific conditions of each port, in order to implement a more efficient system for the management of invasive species at local and regional scales, minimizing the cost and efforts, and preventing their settlement, dispersion and impact on native biodiversity.

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