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New invasive predator reduces the abundance of native prey in a cold-temperate marine fouling community

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Abstract

1. Invasive species threaten the conservation of marine environments, and urgent management strategies are needed to prevent their introduction, establishment and spread. Specifically, marine invasive predators destabilize ecological interactions and alter community structure and function. However, most of the evidence showing the effect of these predators is restricted to a few species and regions, while for others the information remains scarce.

2. This study experimentally evaluated the ecological effects of the sea slug *Pleurobranchaea maculata*, a recently introduced invasive predator, on the fouling communities of a cold-temperate port in the South-western Atlantic.

3. The results show that increasing predation pressure reduces significantly the abundance of sea anemones, which are among the preferred prey items.

4. This study reveals new evidence to help better understand the effects of *P. maculata* on the biological communities of a recently invaded region. Furthermore, it provides the first experimental evidence supporting the hypothesis that marine invasive predators can induce a significant decrease in the abundance of native species in benthic communities of cold-temperate marine environments in the South-western Atlantic.

KEYWORDS
ecological effects, experimental ecology, non-native species, *Pleurobranchaea maculata*, predator–prey interactions, South-western Atlantic

1 | INTRODUCTION

Biological invasions represent a serious threat to the conservation of marine ecosystems (Molnar et al., 2008; Díaz et al., 2019), and urgent management strategies are needed to prevent and minimize their impacts (Thresher & Kuris, 2004; Giakoumi et al., 2019). Species introductions are occurring at an alarming rate (Bax et al., 2003; Seebens, Gastner & Blasius, 2013; Schwindt et al., 2020), and the fact that global commerce relies on shipping for over 70% of the total value of international trade (OMI, 2018; Jägerbrand et al., 2019) suggests that this trend will increase dramatically in the next few decades (Sardain, Sardain & Leung, 2019). In the South-western Atlantic, the number of marine non-native species has experienced a 4.5-fold increase since the beginning of this century (Schwindt et al., 2020), but understanding of their ecological effects remains limited, as well as being geographically and taxonomically biased (Schwindt & Bortolus, 2017). A more extensive awareness of the ecological effects caused by invasive species is crucial to allow environmental managers to effectively take action in the prevention, control and mitigation of biological invasions (Cassey et al., 2018; Schwindt et al., 2020).

TABLE 1 Summary of the observed or expected predatory or competitive effects produced by marine invasive predators in the South-western Atlantic. Details are given in terms of the studied predator, the type of ecological interaction (P, predation; CE, competition by exploitation; CI, competition by interference), the main affected taxa, the evidence of the interaction and its type (E, experimental; O, observational; I, inferred) and the expected or observed effects of each interaction

Predator	Type of interaction	Affected taxa	Evidence of interaction	Evidence type	Ecological effect expected or observed by the interaction	Reference[†]
Arthropoda						
Charybdis hellerii (A. Milne Edwards, 1867)	P	Crustaceans, molluscs and macroalgae	Presence of various prey items in stomach content	O	Potential change in prey abundance or community composition	Sant'Anna et al., 2015
	CE	Native crabs	Share similar prey items	I	Potential decrease in the abundance or displacement of native crabs	Sant'Anna et al., 2015
Mollusca						
Rapana venosa (Valenciennes, 1846)	P	Native bivalves	Consumption of prey in predator–prey experiments	E	Potential decrease in the abundance of bivalves	Giberto, Schiariti & Bremec, 2011
	P	Native bivalves	Reduce abundance of prey populations	O	Decrease in the abundance of bivalves	Carranza et al., 2010
	P	Native bivalves	Associated spatial distribution with prey	O	Potential decrease in the abundance of bivalve population	Giberto et al., 2006
Pleurobranchaea maculata (Quoy & Gaimard, 1832)	P	Macroalgae and invertebrates	Presence of various prey items in stomach content	O	Potential change in prey abundance or community composition	Bökenhans et al., 2019 Battini et al., 2021
	P	Marine invertebrates	Consumption of prey in predator–prey experiments	E	Potential decrease in the abundance of prey	Battini et al., 2021
Chordata						
Actinopterygii						
Oncorhynchus tshawytscha (Walbaum, 1792)	P	Native fish and squids	Consumption inferred by stable isotopes analyses	I	Potential decrease in the abundance of prey	Ciancio et al., 2008
Oncorhynchus mykiss (Walbaum, 1792)	P	Zooplankton	Consumption inferred by stable isotopes analyses	I	Potential decrease in the abundance of prey	Ciancio et al., 2008
Salmo trutta Linnaeus, 1758	P	Native fish and squids	Consumption inferred by stable isotopes analyses	I	Potential decrease in the abundance of prey	Ciancio et al., 2008
Chromis limbata (Valenciennes, 1833)	CI	Native fish	Competition for shelter with native fish	I	Potential displacement of native fish	Anderson et al., 2017 Anderson et al., 2020
Mammalia						
Neovison vison (Schreber, 1777) [‡]	P	Marine fish and invertebrates	Remains of prey in scats	O	Potential effect on abundance of prey	Gomez et al., 2010 Valenzuela et al., 2013 Schüttler, Cárcamo & Rozzi, 2008
	CE	Native otter	Share similar prey items	O	Potential effect on the abundance or displacement of native otter	Gomez et al., 2010
Lycalopex griseus (Gray, 1837) [‡]	P	Marine fish and invertebrates	Remains of prey in scats	O	Potential effect on abundance of prey	Gomez et al., 2010 Carlton & Hodder, 2003
	CE	Native fox	Share similar prey items	O	Potential effect on the abundance or displacement of fox	Gomez et al., 2010

[†]The references were obtained by a systematic review in ASFA (Aquatic Sciences and Fisheries Abstracts) and Google scholar databases by searching journal articles that mentioned at least one of these terms: invasive, exotic, alien, invader, introduced, non-indigenous or non-native (and all related terms); in combination with predator (and related) and marine, sea, coast, ocean, estuarine or brackish (and related). We selected only the studies that mentioned South-western Atlantic, SWA, Argentina, Uruguay or Brazil (and related terms) and we excluded those articles mentioning 'freshwater' (n = 110). Relevant articles were selected from the original results screening the title and abstract if necessary (n = 11). Additional records (n = 3) were extracted from relevant references within these articles. All of the references (n = 14) were examined in detail to extract the predator identity and taxonomic belonging, the type of ecological interaction and the affected taxa, the evidence and type of evidence supporting each interaction, and the expected or observed ecological effects derived from each reported interaction.

[‡]Even though these are not strictly marine species, marine taxa compose an important part of their diet in the South-western Atlantic, and were therefore included in the revision (Carlton & Hodder, 2003).

Invasive predators can cause a significant decline in native prey populations (Grosholz et al., 2000; Ross et al., 2004; Tyrrell, Guarino & Harris, 2006; Letnic et al., 2009; Doherty et al., 2016), disrupting ecological interactions (Jensen, McDonald & Armstrong, 2002; Walsh, Carpenter & Vander Zanden, 2016; Erós et al., 2020) and altering the dynamics of entire communities (Whitlow, Rice & Sweeney, 2003; Gilbey, Attrill & Coleman, 2008; De Rivera, Grosholz & Ruiz, 2011; Garbary et al., 2014; Freeman, Frischeisen & Blakeslee, 2016; Jormalainen et al., 2016). These predators often have a greater effect on native prey than their native counterparts (Salo et al., 2007; Paolucci, MacIsaac & Ricciardi, 2013; Twardochleb, Olden & Larson, 2013), probably owing to the absence of a common eco-evolutionary history (Carthey & Banks, 2014; Papacostas & Freestone, 2019). The ecological effects produced by invasive predators in the marine environment have received much less attention than those in terrestrial ecosystems (Rilov, 2009), especially in regions like the South-western Atlantic, where knowledge is scarce and restricted to a few species (Table 1). While most of the evidence shows that marine invasive predators lead to a decline in the abundance of one or more prey species, more complex effects including other interactions such as competition or trophic cascades have also been reported (McDonald, Jensen & Armstrong, 2001; Jormalainen et al., 2016; Lord, 2017). Thus, the evidence implies that the ecological effects that marine invasive predators exert on populations, communities and ecosystems can be very significant.

The grey side-gilled sea slug *Pleurobranchaea maculata* (Quoy & Gaimard, 1832), which is native to New Zealand, was recently detected in the South-western Atlantic (Farías, Obenat & Goya, 2015; Farías et al., 2016). This invasive predator has rapidly spread along the coast and can potentially spread to other regions worldwide (Battini et al., 2019). It has become locally abundant within coastal Argentine Patagonia and as a generalist predator it feeds on anemones, polychaetes, hydroids, tunicates and other invertebrates (Battini et al., 2021). Despite the fact that the diet of this species has been studied in detail in both its native and invaded ranges (Ottaway, 1977; Khor et al., 2014; Taylor et al., 2015; Bökenhans et al., 2019; Battini et al., 2021), it remains unclear how it affects the structure and composition of the ecological communities. Thus, the aim of this study was to experimentally evaluate the effect that different intensities of predation by *P. maculata* have on species abundance, composition and diversity of marine fouling communities. The predictions that emerge from this study are that the greater intensities of predation will: (i) lead to a decline in the abundance of some taxonomic groups that are recognized as potential prey of *P. maculata*, and as a consequence (ii) alter the composition and diversity of the entire fouling community. The results of this work will provide science-based evidence that will allow decision makers and environmental managers to improve early actions and prevent negative impacts of marine invasive species.
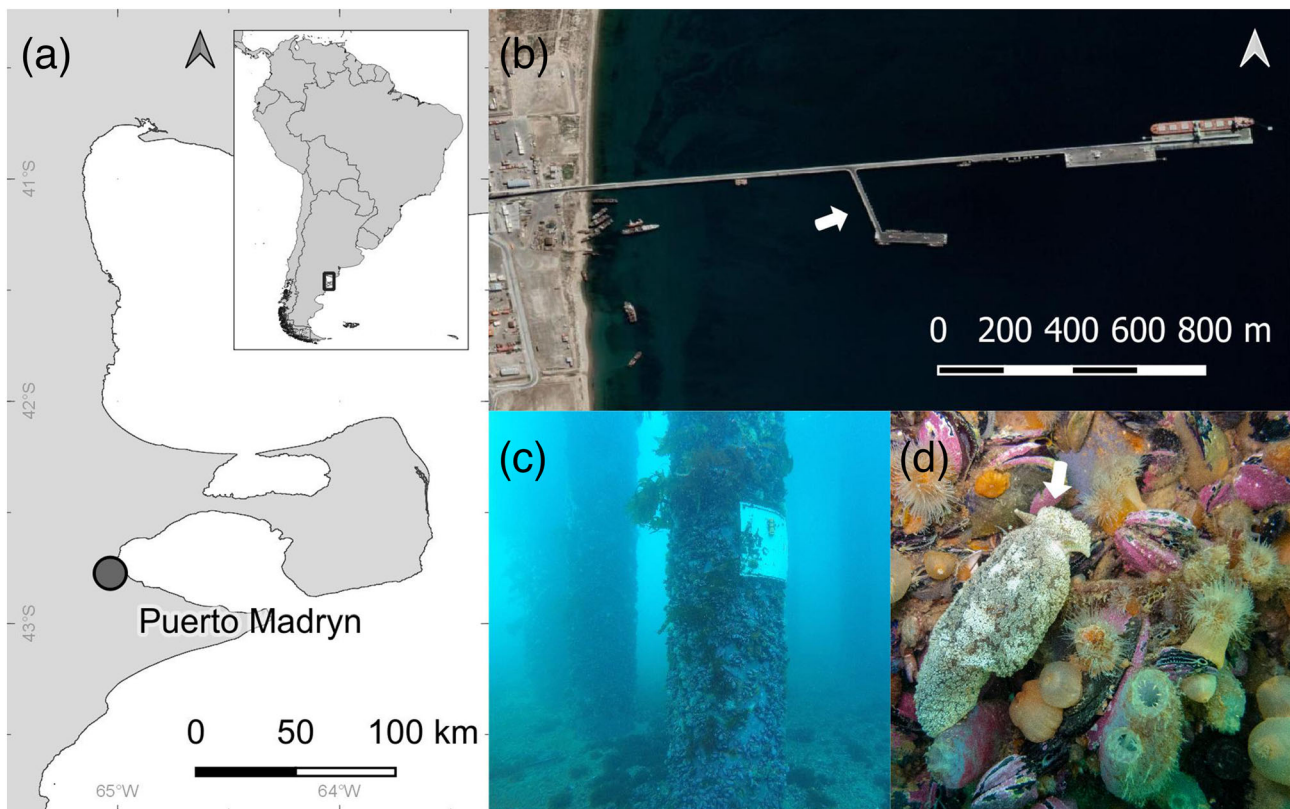

FIGURE 1 (a) Map showing the location of Puerto Madryn (PM) city. (b) Storni port in PM, which serves as one of the two main ports of the region (Schwindt et al., 2014), showing the area where panels were deployed (white arrow). Underwater view of (c) the pilings of the port and (d) its associated diverse fouling community invaded by *Pleurobranchaea maculata* (white arrow)

2 | MATERIALS AND METHODS

2.1 | Study area

The Nuevo Gulf (42°S, 64°W) is a relatively small and enclosed gulf located in northern Argentine Patagonia with calm and protected waters (Figure 1a). Sea temperature varies from 8°C in winter to 21°C in summer, with an annual mean of 14.3°C, and salinity remains relatively constant with a mean value of 34 PSU (Giachetti et al., 2019). The port area is composed of two coastal natural ports, which are the most active ports in the region, both in terms of ship activity and commercial loadings (Schwindt et al., 2014). This has probably led to the introduction of the increasing number of non-native species that have been reported in the area (Orensanz et al., 2002; Castro et al., 2020; Schwindt et al., 2020). The Storni port (Figure 1b) submerged structure is composed of a series of concrete pilings (Figure 1c) that harbour rich and diverse fouling communities (Figure 1d; Giachetti et al., 2019). These communities are represented mainly by bivalves (*Aulacomya atra* and *Mytilus* spp.), anthozoans (*Corynactis carnea* Studer, 1879, *Actinothoe lobata* (=*Metridium senile lobatum*) (Carlgren, 1899) and *Anthothoe chilensis* (Lesson, 1830)) and ascidians (*Asterocarpa humilis* (Heller, 1878), *Ascidiella aspersa* (Müller, 1776) and *Ciona robusta* (Hoshino & Tokioka, 1967)), which create a complex three-dimensional structure that harbours various species of native and introduced gastropods, decapods, polychaetes and echinoderms, among others (Giachetti et al., 2019). The main macropredators are benthic generalist species such as the echinoderms *Arbacia dufresnii* (Blainville, 1825) and *Allostichaster capensis* (Perrier, 1875), the crab *Leucippa pentagona* H. Milne Edwards, 1834, the snail *Tegula patagonica* (d'Orbigny, 1835), the small fish *Helcogrammoides cunninghami* (Smitt, 1898) and the sea slug *P. maculata* (Giachetti et al., 2019; Giachetti et al., 2020). The latter represents one of the most abundant macropredators within the port area, where it concentrates mainly over the pilings (see Supporting Information). The abundance of *P. maculata* in this area showed a seasonal pattern with higher values in winter, reaching densities of up to almost seven individuals per square metre, and lower in the summer (see Supporting Information).

2.2 | Experimental design

2.2.1 | Development of experimental fouling communities in the field

In order to test the effect of *P. maculata* on the fouling communities of the port, experimental fouling communities were developed in the absence of macropredators. To this end, 15 × 15 cm acrylic panels were deployed on the pilings of the port, 2 m below the mean low tide level. The exposed faces of these panels were sanded in order to enhance the ability of fouling organisms to adhere to them (following Giachetti et al., 2019; Giachetti et al., 2020). Each panel was covered with a 7 cm high plastic cage (1.5 × 1.5 cm mesh; Figure 2a) that prevented access to *P. maculata*, sea urchins, sea stars, crabs, small fish and other macropredators. The panels were attached to large rectangular fishing nets, which were tied around the pilings (Figure 2a) before the beginning of the summer (December 2016). To minimize any potential effects owing to differences in depth and orientation of the panels, they were placed on three adjacent pilings (approximately 10 m apart from each other) in an array that consisted of three
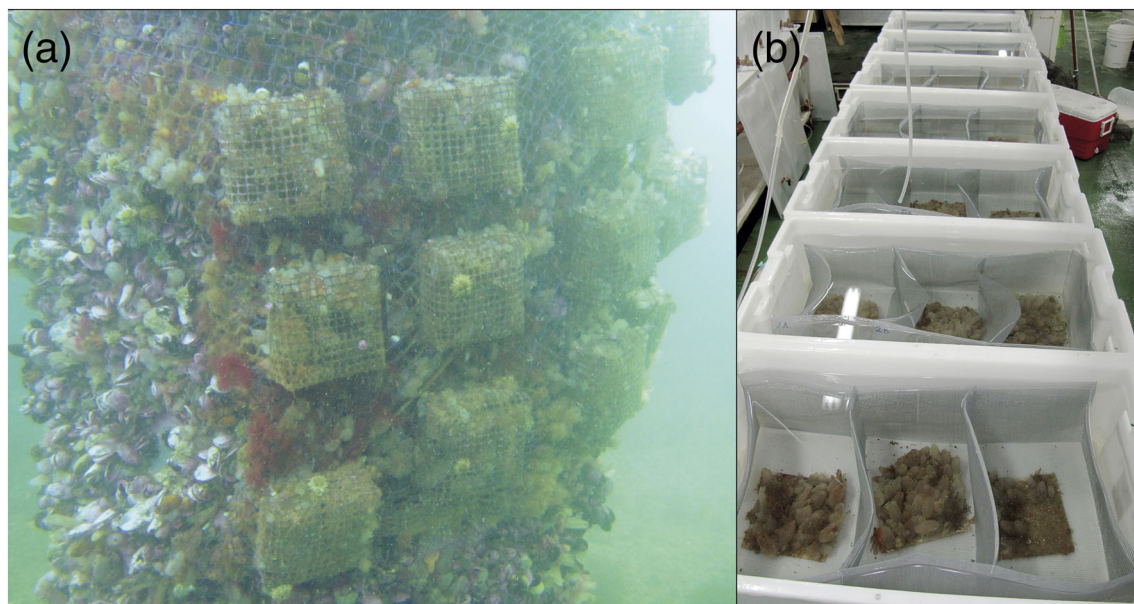

FIGURE 2 (a) Experimental panels deployed on a piling of the Storni port (Puerto Madryn), with plastic cages to prevent the entrance of benthic macropredators. (b) Experimental panels arranged in the aquarium, before predators were added (container covers were removed in order to take the picture)

vertical × four horizontal rows of panels (n = 36), separated by approximately 10–15 cm. After being submerged for 5 months, (May 2016), when most of the panels were totally covered with fouling organisms, they were removed and sealed in individual plastic bags, and carefully transported in insulated containers to the CENPAT Aquarium for further experiments (Figure 2b).

2.2.2 | Preparation of the predators

Ten days before the beginning of the experiment, 72 individuals of *P. maculata* were collected in the port area and transported to the aquarium. Individuals were isolated from each other and acclimated to the aquarium conditions for a week. During this period, they were fed on fresh dead open mussels (*Mytilus* spp. or *Perumytilus* sp.) every 2 days. After that period, sea slugs were starved for another 4 days prior to the experiment. Finally, before the experiment started, all of the individuals were measured to detect potential differences in predator size between treatments. A standardized procedure while conducting the measurements was used to avoid artefacts owing to uneven contraction or relaxation (Battini, 2020). Predator length was compared between treatments using a one-way ANOVA with 'Treatment' as a fixed factor. No differences in predator length (mean length, 73.6 ± 9.9 mm; range, 54–99 mm) between treatments were detected prior to the experiment ($F_{1, 70} = 0.036$, $P = 0.85$).

2.2.3 | Aquarium experiments

The experiment was performed in rectangular 100 L containers (n = 12) with permanent air supply and periodic (every 2–3 days) partial (50%) water renewal. Containers were divided into three equal compartments using a plastic mesh (0.1 × 0.1 cm) that allowed water exchange while preventing mobile invertebrates from moving from one compartment to another (Figure 2b). Following a random blocks design, each compartment was randomly assigned to one of the following treatments: P1, low predation pressure (one panel with one sea slug); P5, high predation pressure (one panel with five sea slugs); or C, control (one panel without sea slugs). In order to minimize the initial differences between panels within each container (block), panels were visually inspected and selected according to their species cover and composition, so that each container received three panels that were as similar as possible to each other. No attempt was made to measure the species cover using more accurate techniques in order to minimize manipulation time and prevent potential damage to the community. After 3 weeks, the experiment was ended before organisms, especially filter feeders such as ascidians, started to die. To measure the cover of colonial organisms, a 2 cm grid was placed on the top of the panel and used to estimate the area occupied by each species; all solitary organisms were counted to estimate their density. All of the taxa were identified to the lowest taxonomic level possible using specific keys, guides and reference material from the IBIOMAR invertebrate collection (CNP-INV), and by consulting expert taxonomists (see Acknowledgements section). Additionally, a voucher specimen of each taxon was deposited in the IBIOMAR collection to ensure taxonomic repeatability (Bortolus, 2008; Bortolus, 2012). For each panel, species richness (total number of taxa) and diversity of solitary and colonial organisms (Shannon–Wiener index) were estimated.

2.2.4 | Statistical analysis

To assess the effect of predation over the abundance of the different taxonomic groups, generalized linear mixed-effect models were fitted with 'treatment' as a fixed factor and 'container' as a random factor (blocks). In the case of solitary taxa (anthozoans, polychaetes, bivalves, decapods ophiuroids and solitary ascidians), for which there were count data, models were fitted using a Poisson distribution through package 'lme4' (Bates et al., 2019) in R (R Core Team, 2020). For some groups (bivalves and solitary ascidians), preliminary data examination suggested that residuals were highly over-dispersed, so models were fitted using a 'Conway–Maxwell Poisson' distribution through the package glmmTMB (Magnusson et al., 2019). For anthozoans, preliminary data analysis suggested that residuals were not homoscedastic owing to the high number of zeros in the dataset. Therefore, for this group, models were fitted using a zero-inflated approach through the package 'pscl' (Jackman, 2017). These models split the response variable into presence/absence data, which were fitted using a binomial function, and the count data, which were modelled using a negative binomial function (Zeileis, Kleiber & Jackman, 2008). In the case of colonial groups (sponges, bryozoans and colonial ascidians), for which there were cover data, models were fitted using a normal distribution through the package 'nlme' (Pinheiro et al., 2018).

To compare the composition of assemblages of solitary and colonial taxa among the different treatments, a two-dimensional non-metric multidimensional scaling ordination was performed, based on the triangular matrix derived from the Bray–Curtis similarity index. Additionally, permutational multivariate analyses of variance (PERMANOVA) tests were performed for both solitary and colonial organisms based on a Bray–Curtis similarity matrix using 'treatment' as a fixed factor and 'container' as a nesting random factor. Prior to these analyses, cover data for colonial organisms and abundance data for solitary organisms were square-root transformed to decrease the influence of dominant species (Clarke & Warwick, 2001). These analyses were performed using package 'vegan' v. 2.5–6 (Oksanen et al., 2019). To compare species richness among treatments, generalized mixed models with 'treatment' as a fixed effect and 'container' as a random effect (blocks) were fitted using package 'glmmTMB' v. 1.0.0 (Magnusson et al., 2019). Models were fitted using a 'Conway–Maxwell Poisson' distribution because initial exploratory analyses suggested that the data were underdispersed when using a Poisson distribution. To compare the diversity of solitary and colonial species, the Shannon–Wiener index was computed for each panel and then fitted to linear mixed models with

TABLE 2 List of the taxa, corresponding functional group (FF, filter feeders; D, detritivores/grazers; P, predators and O, omnivorous) and mean density (individuals per m^2) of fouling communities after 3 weeks of exposure to different intensities of predation by *Pleurobranchaea maculata* (C, control, no predators; P1, one predator, low predator intensity; P5, five predators, high predator intensity). For colonial taxa (†), abundance is expressed as cover (cm^2). Non-native species are indicated with an ‡ and cryptogenic with (‡) following Schwindt et al., 2020

Taxonomic group	Species/taxon	Feeding type	Experimental community		
			C	P1	P5
PORIFERA					
	Porifera indet.†	FF	34.8 ± 49.6	23.9 ± 29.6	43 ± 43.2
Calcarea	*Sycon* sp.†	FF	0.8 ± 1.7	1.9 ± 3	1.5 ± 2.2
CNIDARIA					
Anthozoa	*Actinothoe lobata*	FF	29.6 ± 54.7	25.9 ± 40	3.7 ± 12.8
PLATYHELMINTHES					
Polycladida	*Phrikoceros mopsus*	P	7.4 ± 17.3	3.7 ± 12.8	0 ± 0
ANNELIDA					
Polychaeta	Cirratulidae	D	51.9 ± 75.4	66.7 ± 102.9	70.4 ± 72.1
	Eunicidae	P	7.4 ± 17.3	3.7 ± 12.8	0 ± 0
	Polynoidae	P	48.1 ± 55.1	48.1 ± 55.1	29.6 ± 28.9
	Nereididae	P	18.5 ± 35.2	11.1 ± 27.6	18.5 ± 29.7
	Phyllodocidae	P	0 ± 0	7.4 ± 25.7	7.4 ± 17.3
	Terebellidae	D	14.8 ± 28.9	3.7 ± 12.8	0 ± 0
MOLLUSCA					
Bivalvia	*Aequipecten tehuelchus*	FF	0 ± 0	0.7 ± 2.6	0 ± 0
	Aulacomya atra	FF	22.2 ± 55.3	25.9 ± 35.2	37 ± 49.5
	Mytilus spp.	FF	18.5 ± 40	11.1 ± 27.6	18.5 ± 29.7
Gastropoda	*Tegula patagonica*	H	11.1 ± 20.1	3.7 ± 12.8	0 ± 0
	Trophon geversianus	P	0 ± 0	0 ± 0	3.7 ± 12.8
ARTHROPODA					
Cirripedia	*Amphibalanus improvisus*	FF	7.4 ± 17.3	0 ± 0	7.4 ± 17.3
	‡*Balanus glandula*	FF	0 ± 0	0 ± 0	3.7 ± 12.8
Amphipoda	‡*Monocorophium acherusicum*	FF-D	0 ± 0	0 ± 0	3.7 ± 12.8
Decapoda	*Halicarcinus planatus*	O-D	40.7 ± 40	59.3 ± 66.6	66.7 ± 69.6
	Pachycheles chubutensis	FF	259.3 ± 176.6	433.3 ± 173.8	363 ± 224.1
Pycnogonida	Pycnogonida indet.	P	3.7 ± 12.8	0 ± 0	0 ± 0
BRYOZOA					
Bryozoa	‡*Bugula neritina*†	FF	87.6 ± 80.5	103 ± 92.1	134.3 ± 139.1
	‡*Bugulina flabellata*†	FF	18.9 ± 20	19.3 ± 28.9	5.6 ± 7.1
	Cheilostomatida†a	FF	2.2 ± 7.7	0 ± 0	0 ± 0
ECHINODERMATA					
Ophiuroidea	*Amphipholis squamata*	P	25.9 ± 35.2	55.6 ± 68.7	33.3 ± 50.6
	Ophiactis asperula	P	0 ± 0	0 ± 0	3.7 ± 12.8
CHORDATA					
Ascidiacea	‡*Ascidiella aspersa*	FF	3014.8 ± 1,353	3074.1 ± 593.2	2855.6 ± 1265.5
	(‡)*Asterocarpa humilis*	FF	207.4 ± 175.1	233.3 ± 209.4	277.8 ± 191.5
	‡*Ciona robusta*	FF	681.5 ± 474.7	944.4 ± 431	518.5 ± 245.1
	(‡)*Corella eumyota*	FF	0 ± 0	7.4 ± 17.3	11.1 ± 27.6
	‡*Molgula manhattensis*	FF	485.2 ± 723	270.4 ± 198.3	507.4 ± 447.8
	‡*Botryllus schlosseri*†	FF	45 ± 63.4	36.7 ± 61.5	23 ± 27
	‡*Diplosoma listerianum*†	FF	0.9 ± 3.2	0 ± 0	0 ± 0
	‡*Lyssoclinum fragile*†	FF	1.5 ± 2.9	13.1 ± 18.5	7.2 ± 19

aThis taxon includes *Membranipora isabelleana* (species complex) and *Exochella* sp., which are grouped because they were not distinguished during laboratory processing.

similar 'treatment' and 'container' factors using the package 'nlme' (Pinheiro et al., 2018). All analyses were performed in R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

At the end of the experimental period, the fouling communities overall comprised 38 different taxa (Table 2), including 11 non-native, one cryptogenic and one potentially non-native species (*Eulalia* cf. *clavigera*) that required greater taxonomic resolution to confirm the identification. At the greatest predation intensity, the abundance of the sea anemone *A. lobata* was significantly reduced compared with the other treatments (Table 3, Figure 3a). This group showed very low overall abundance, and it was necessary to use a zero-inflated model in order to analyse the data. This model showed that in panels that had at least one individual of *A. lobata*, the mean abundance was significantly reduced by 95% (from an average of 1.6 individuals per panel to just 0.1 in the treatment with a high density of predators; Table 3). For the rest of the groups, the greatest predation intensity was not associated with a significant reduction in their abundance (Figure 3a) or cover (Figure 3b). Some groups previously reported as potential prey of *P. maculata*, such as polychaetes and flatworms, did not show a significant response to increased predation intensity. However, both flatworms and larger (>1 cm) polychaetes (belonging to Polynoidae, Terebellidae and Eunicidae families), were almost absent from the treatment with a high density of predators and they reached a maximum abundance when predators were absent (Table 2). Smaller polychaetes (belonging to Cirratulidae, Nereididae and Phyllodocidae) did not show this trend, and were homogenously abundant across predation intensities (Table 2). Finally, decapods showed significant differences among predation intensities (Figure 3a), mainly driven by the abundance of *Pachycheles chubutensis* Boschi, 1963 and *Halicarcinus planatus* (Fabricius, 1775)

TABLE 3 Analysis of deviance estimators based on type II Wald χ^2 tests for the fixed effect term predation intensity (C, control, no predators; P1, one predator per panel, low predation intensity; P5, five predators per panel, high predation intensity) for the linear and generalized linear mixed-effects (LME and GLME respectively) and zero-inflated (ZI) models for each taxonomic group. Significant differences at an $\alpha = 0.05$ are highlighted in bold

Taxon	Model	χ^2	d.f.	P-Value
Porifera	LME	1.449	2	0.485
Anthozoa	**ZI**	**7.905**	**2**	**0.029**
Polychaeta	GLME	0.066	2	0.968
Bivalvia	GLME	0.505	2	0.777
Decapoda	**GLME**	**12.714**	**2**	**0.002**
Bryozoa	LME	0.677	2	0.713
Ophiuroidea	GLME	2.955	2	0.223
Solitary Ascidiacea	GLME	0.800	2	0.671
Colonial Ascidiacea	LME	0.848	2	0.655

(Table 2). However, differences were heterogeneous at the species level, with *H. planatus* being more abundant in treatment P5 while *P. chubutensis* was more abundant in P1.

Predation by *P. maculata* did not have a significant effect on the structure of the community, as indicated by both the non-metric multidimensional scaling and the PERMANOVA tests for solitary ($F_{2, 33} = 1.142$, $P = 0.246$) or colonial taxa ($F_{2, 33} = 0.822$, $P = 0.713$) among treatments (Figure 4a). The experimental communities were dominated by solitary ascidians, among which the invasives *Ascidiella aspersa* and *Ciona robusta*, and the cryptogenic *Asterocarpa humilis* were the most frequent species (Table 2). Among mobile species, the most abundant was the native crab *Pachycheles chubutensis* (Table 2). The average total richness was 14 ± 2 taxa (ranging 10–18 taxa); when considering only native species, richness was considerably lower (average, 6 ± 2 taxa; range, 2–10 taxa) (Figure 4b). No significant differences were found among treatments considering all taxa (Type II Wald $\chi^2 = 0.758$, $P = 0.685$) or just native species (Type II Wald $\chi^2 = 0.341$, $P = 0.843$; Figure 3b). Diversity, measured as the Shannon–Wiener index, of solitary and colonial organisms averaged 1.30 ± 0.21 and 0.857 ± 0.371, respectively, and was also unaffected by predation (Type II Wald $\chi^2 = 1.38$, $P = 0.501$ and Type II Wald $\chi^2 = 0.058$, $P = 0.971$ respectively; Figure 4c).

4 | DISCUSSION

This study provides the first experimental evidence showing that predation by the invasive sea slug *P. maculata* may lead to a significant reduction in the abundance of native prey, among which sea anemones, polychaetes and flatworms showed the highest vulnerability. Sea anemones have been consistently reported as the preferred prey of *P. maculata* (Ottaway, 1977; Willan, 1984; Salvitti et al., 2017; Bökenhans et al., 2019). Polychaetes and flatworms were also previously reported among the main prey of *P. maculata* (Salvitti et al., 2017; Bökenhans et al., 2019; Battini et al., 2021), and although the effect on these groups was not statistically significant, the absence of individuals at the end of the experiment in the treatment with greatest predation intensity suggests that they are also vulnerable to predation by *P. maculata*. Decapods showed significant differences among treatments but these were not associated with greater predation intensity. These species are not among the main prey items of *P. maculata* (Bökenhans et al., 2019; Battini et al., 2021) and differences were heterogeneous at the species level, suggesting that they were not driven by predation. Also, as these species are not predators, differences in their abundance most probably did not affect the abundance of other species in the community. Indeed, no macropredators other than *P. maculata* were found on the plates, with the exception of very small and scarce generalist species (such as some polychaetes, pycnogonids, brittlestars and flatworms; see Table 2). Hence, even though different types of predators can produce multiple effects on the fouling communities (Giachetti et al., 2020; Leclerc, Viard & Brante, 2020), it is unlikely that their presence on the plates produced any bias in these results.
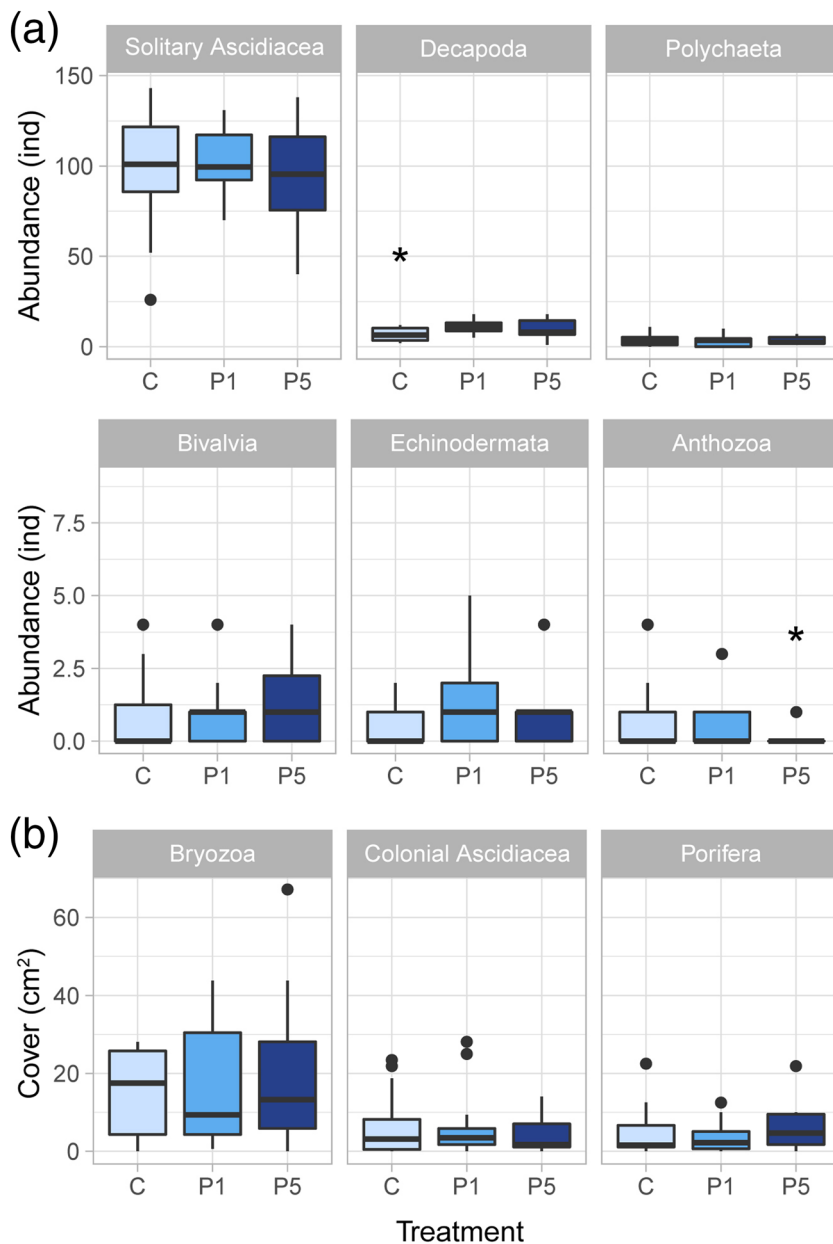
FIGURE 3 Effect of the different predation treatments (C, control, no predators; P1, low predator intensity, one predator per panel; P5, high predator intensity, five predators per panel) on (a) the abundance of solitary taxonomic groups and (b) the cover of colonial groups. Significant difference between one treatment and the others is denoted by an asterisk. Groups showing very low abundances or cover (see Table 2) are not shown. The boxplots show the median, first and third quartiles as the middle line, lower and upper hinges, respectively, whereas whiskers and points represent values within and beyond 1.5 times the inter-quartile range and each hinge, respectively

Novel predator–prey interactions between native prey, such as sea anemones, and *P. maculata* may have favoured the establishment of this invasive sea slug in the South-western Atlantic (Battini et al., 2021). The prey naivety framework (Carthey & Banks, 2014; Anton et al., 2020) predicts that the ecological effects of invasive predators largely depend on the degree of novelty compared with the native predators, with which prey species share an eco-evolutionary history (Ricciardi & Atkinson, 2004; Sih et al., 2010; Lepori et al., 2012). In the coastal areas of the South-western Atlantic, few species have been reported to feed on sea anemones, many of which are also sea slugs (García-Matucheski & Muniain, 2011; Garese et al., 2012). In this regard, sea anemones possess specialized anti-predator defences that include body contraction, active escape through detachment and locomotion, and increased body size (Kramer & Francis, 2004). In particular, acontiate anemones such as *A. lobata*

can effectively avoid predation by sea slugs through the extrusion of mesenterial filaments (acontia) (Östman et al., 2010), which launch hundreds of nematocysts that fire on contact with predators (Edmunds et al., 1976; Kramer & Francis, 2004). Previous laboratory experiments showed that *A. lobata* can induce an aversive behaviour in *P. maculata* after acontia are extruded, although this is not sufficient to prevent predation (Battini, 2020). Moreover, the available evidence suggests that other species of native sea anemones that inhabit fouling and natural rocky communities, such as *C. carnea*, *Parabunodactis imperfecta* and *A. chilensis*, are also efficiently preyed upon by *P. maculata* (Bökenhans et al., 2019; Battini et al., 2021). The lack of effective strategies to avoid predation and the absence of specialized predators in the study area suggest that these sea anemones may be naive to predation by *P. maculata* (Anton et al., 2020). Within this context, the results of this work suggest that
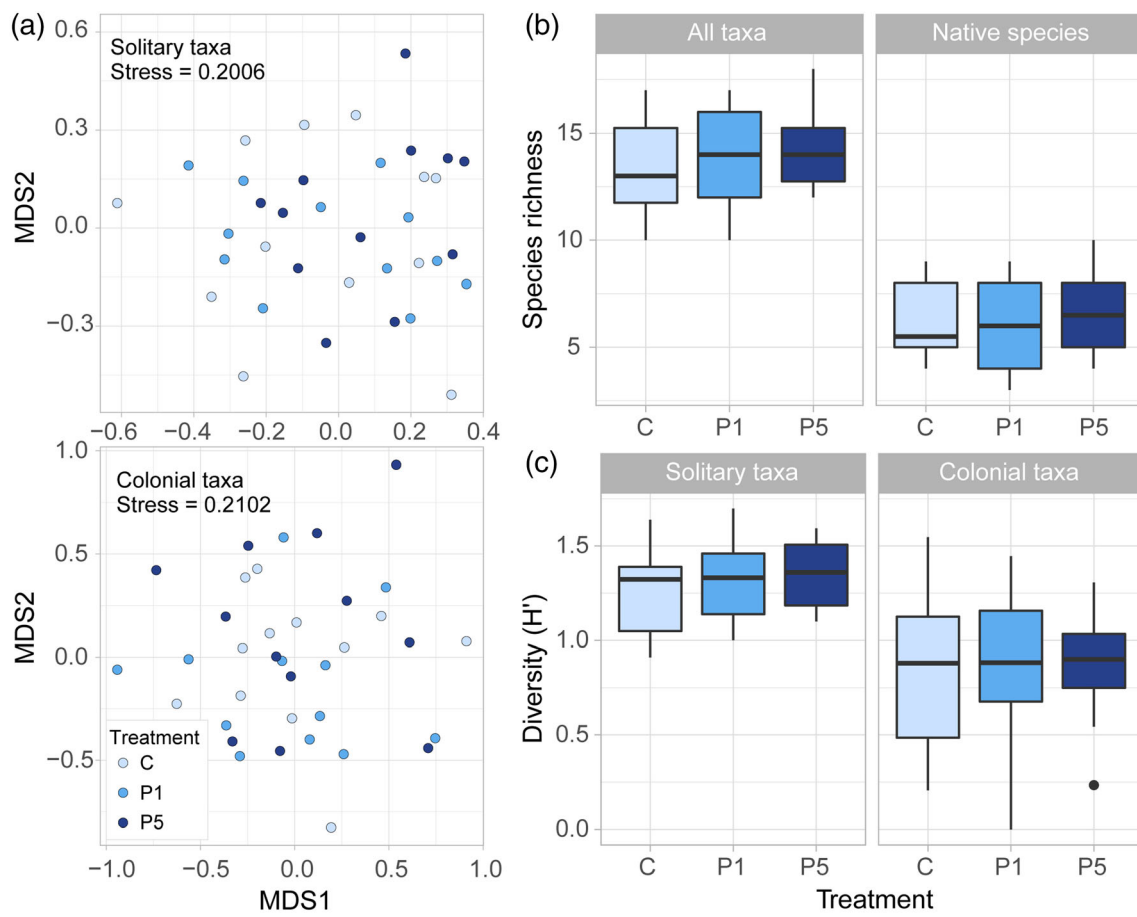
FIGURE 4 Effect of the different predation treatments (C, control, no predators; P1, low predator intensity, one predator per panel; P5, high predator intensity, five predators per panel) on (a) the structure of the community of solitary (above) and colonial (below) taxa, (b) species richness (related to all and to native species only) and (c) the diversity of the community considering solitary and colonial taxa. The boxplots show the median, first and third quartiles as the middle line, lower and upper hinges, respectively, whereas whiskers and points represent values within and beyond 1.5 times the inter-quartile range and each hinge, respectively

the ability to prey upon sea anemones could have played an important role in the invasive success of *P. maculata*. Indeed, the high abundance of sea anemones in the fouling communities could help explain the successful establishment of this invasive sea slug in certain locations of the South-western Atlantic, agreeing with previous findings that artificial structures favour the introduction and spread of invasive species (Glasby et al., 2007; Airoldi et al., 2015; Soares et al., 2020). Moreover, given that food availability can control the abundance of invasive predators (Shiganova, 1998), the high availability of sea anemones (Giachetti et al., 2019) could explain the unusually high densities of *P. maculata* compared with those in its native range (Taylor, Wood & McNabb, 2011; Taylor et al., 2015).

Contrary to the second prediction of this work, there was no direct evidence suggesting that an increasing predation pressure may drive changes in the community composition or diversity. Thus, the predatory effect of *P. maculata* on the abundance of native species was not mirrored at the community level. These results are only partially concurrent with previous findings as they do not reflect the diversity of prey consumed by *P. maculata* (Willan, 1984; Salvitti et al., 2017; Bökenhans et al., 2019; Battini et al., 2021). However,

the composition and diversity of the experimental fouling communities developed on the plates, in the absence of macropredators and in a relatively short time, might differ from those of mature communities naturally occurring on piers and on natural rocky shores. Hence, its extrapolation to natural subtidal communities needs to be performed with caution. Additionally, changes at the community level may require longer exposure times to predation, even at high levels of predation intensity, than those used in this study, as they involve complex and slow processes such as colonization, species replacement, etc. Long time series have revealed that non-native predators can significantly reduce the species richness and diversity of aquatic communities (Yan, Girard & Boudreau, 2002). Given that the introduction of *P. maculata* in the South-western Atlantic is still recent (Farías, Obenat & Goya, 2015; Farías et al., 2016), it may be too early to draw conclusions regarding the absence of community level changes driven by this species, and further monitoring and environmental research are recommended.

Overall, this study constitutes not only the first experimental approach to understanding the effects of a newly introduced marine species along the South-western Atlantic, but also contributes to

understanding the mechanisms underlying its successful introduction. Furthermore, it provides the first evidence that marine invasive predators can potentially drive a significant decrease in the abundance of native prey species in benthic communities of this region (Table 1). Despite the enormous increase in regional research effort focused on marine exotic species within the last few decades (Schwindt & Bortolus, 2017; Fowler et al., 2020), their ecological effects remain largely understudied. Thus, there is an urgent need to address how invasive species can threaten the conservation of the marine environment in the South-western Atlantic (Schwindt & Bortolus, 2017; Schwindt et al., 2018). This information is crucial to support policies to ameliorate further deterioration (Bailey et al., 2020; Fowler et al., 2020), such as raising public awareness to prevent the accidental introduction and spread of invasive species or encouraging the deliberate removal of the target species (Giakoumi et al., 2019). Worldwide, invasive predators have produced severe declines in the abundance of prey populations (Grosholz et al., 2000; Ross et al., 2004; Tyrrell, Guarino & Harris, 2006) and caused profound shifts in the composition, structure and dynamics of native communities (Whitlow, Rice & Sweeney, 2003; De Rivera, Grosholz & Ruiz, 2011; Freeman, Frischeisen & Blakeslee, 2016). Since the management of marine invasive species is particularly challenging and highly costly (Giakoumi et al., 2019), this work highlights the need for more efficient prevention measures in order to avoid further spread of this invasive predator (and others) along the South-western Atlantic. Moreover, it provides novel sound evidence that will allow decision makers and environmental managers to take actions to minimize or prevent the introduction, establishment and spread of marine invasive species throughout the South-western Atlantic and other regions where this species could invade (Battini et al., 2019).

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