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Parasites of *Percophis brasiliensis* (Percophidae) benefited from fishery regulations: Indicators of success for marine protected areas?

Paola E. Braicovich[1] [iD] | Manuel M. Irigoitia[1] [iD] | Nelson D. Bovcon[2] [iD] |
Juan T. Timi[1] [iD]

[1]Laboratorio de Ictioparasitología, Instituto de Investigaciones Marinas y Costeras, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata- Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

[2]Laboratorio de Investigación en Hidrobiología, Facultad de Ciencias Naturales y Ciencias de la Salud, Universidad Nacional de la Patagonia San Juan Bosco, Trelew, Chubut, Argentina

Correspondence
Paola E. Braicovich, Laboratorio de Ictioparasitología, Instituto de Investigaciones Marinas y Costeras, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata – Consejo Nacional de Investigaciones Científicas y Técnicas, Funes 3350, (7600) Mar del Plata, Argentina.
Email: braicovi@mdp.edu.ar

Abstract

1. Fishing is the greatest source of anthropogenic impact on global marine resources and the ecosystems supporting them. The decline of many fish stocks has led to the need to apply control and protection measures to promote the recovery of these resources.

2. In the Argentine Sea, a multispecies coastal fishery in the El Rincón region has displayed signs of overexploitation since the beginning of the century. Consequently, temporal and spatial protection measures were implemented in 2004.

3. In previous studies, an independent stock of *Percophis brasiliensis* in El Rincón was identified based on the parasite communities of fish caught in 2005. However, no subsequent studies using parasite communities have been performed since the protective fishery closure measures were applied.

4. To evaluate parasites as indicators of temporal change in the El Rincón stock of *P. brasiliensis* after the implementation of these protection measures, a sample from 2018 was compared with that from the previous study, as well as with three other samples. Two of the latter (Argentine Common Fishing Zone and San Matías Gulf) corresponded to previously identified independent stocks in the Argentine biogeographical province and the third was a new sample from the Magellanic Province in southern Patagonian waters.

5. The structure and composition of parasite assemblages of the El Rincón stock of *P. brasiliensis* differed significantly in 2018, after several years of protective measures. The increased loads observed in several parasite species constitute a promising signal of successful ecosystem recovery. A discrete stock in the Magellanic Province was also identified, providing insights into the population structure of *P. brasiliensis* along its distributional range, with applications for the sustainable management of this resource.

KEYWORDS
biological indicators, fisheries, parasite assemblages, *Percophis brasiliensis*, protection measures

1 | INTRODUCTION

Fisheries comprise the greatest anthropogenic impact on global marine resources (Watson et al., 2013). The 20th century saw the decline of many fish stocks (van Gemert & Andersen, 2018), threatened by continuous depletion of populations and an increasing risk of species extinction, ecosystem regime shifts and even the loss of the overall integrity of marine ecosystems (Mullon, Fréon, & Cury, 2005; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Pikitch, 2012). A battery of measurements have been applied worldwide in an attempt to counteract these effects and promote the recovery of the resources, namely harvest regulations, changes in gear selectivity and implementation of spatial and temporal closures at different scales or the creation of marine reserves (de Bruyn, Murua, & Aranda, 2013; Edgar et al., 2014; Roberts, Hawkins, & Gelly, 2005; van Gemert & Andersen, 2018). Although the benefits of these alternatives are highly heterogeneous (Costello et al., 2016), increases in spawning stocks of exploited species are the most frequently reported effects of reserves being fully or partially closed to fishing (Gell & Roberts, 2002), resulting in the increased abundance, average size and biomass of protected animals, as well as increased diversity (Halpern, 2003).

Fisheries affect not only targeted stocks, but also entire communities of organisms. This includes fish parasites, which are impacted by reduced host abundance and food web complexity, which affect their transmission efficiency, population density and assemblage species richness (Wood & Lafferty, 2015). Understanding how parasite assemblages respond to protection measures may therefore help to evaluate the degree of effectiveness of fisheries management measures (Isbert et al., 2018).

The coastal region of the Argentine Sea, El Rincón (38° 30′–41° 30′ S), is a semi-enclosed area that generates its own oceanographic features, where locally modified waters create frontal zones with important biological properties (Acha, Mianzán, Guerrero, Favero, & Bava, 2004), providing breeding grounds and zones of concentration for juveniles of several fish species by promoting the retention of larvae (Acha, Orduna, Rodrigues, Militelli, & Braverman, 2012; Carozza et al., 2004). Coastal fisheries had developed and increased markedly in this region, showing signs of overexploitation by the end of the last century (Ruarte, Rico, & Lagos, 2017). Consequently, as of 2004, an area of this region was closed during the reproductive season of most economically relevant fish species (October to February) as a protection measure. Restrictions were later progressively extended on both temporal and spatial scales, reaching a maximum in 2010, which resulted in decreased landings in subsequent years (Fernández Aráoz, Lagos, & Carozza, 2014). Several species in the area showed a recovery of biomass between 2009 and 2012 (Ruarte et al., 2017), but no further evaluation has been carried out, although more than a decade has passed since the implementation of the restrictions.

The Brazilian flathead, *Percophis brasiliensis*, is one of the main resources in the multispecies demersal fishery operating in the northern Argentine Sea, including the region of El Rincón, where there is an independent stock of this species (Rico, Lagos, Rodríguez, & Lorenzo, 2018). The El Rincón stock has been distinguished based on population parameters, otolith microchemistry and parasites (Avigliano, Sáez, Rico, & Volpedo, 2015; Braicovich & Timi, 2008; Rico et al., 2018; Rodrígues, Rico, Militelli, Osovnikar, & Maggioni, 2010). The study of parasites as markers for host population discrimination by Braicovich and Timi (2008) was conducted on flatheads caught in El Rincón in 2005, shortly after the application of fishing restrictions. A recovery in the biomass of several fish species, including *P. brasiliensis*, was recorded after the implementation of protection measurements, with data recorded until 2012 (Ruarte et al., 2017). The present parasite assemblages of flatheads from El Rincón could shed additional light on the the effectiveness of the management measures applied. To that end, the present study includes a comparison of parasites from *P. brasiliensis* caught at El Rincón in 2018 with those caught in 2005, as well as with neighbouring stocks in the Argentine Common Fishing Zone and in San Matías Gulf (Braicovich & Timi, 2008).

In the Argentine Sea, all studies on the population structure of *P. brasiliensis* were carried out in waters off Buenos Aires Province and San Matías Gulf (Rico et al., 2018). The first region belongs to the Argentine biogeographical province, and the second has been assigned to the Argentine or the Magellanic Province (Balech & Ehrlich, 2008; Menni, Jaureguizar, Stehmann, & Lucifora, 2010; Miloslavich et al., 2011), constituting an ecotonal region. However, *P. brasiliensis* has a broader distribution, reaching the San Jorge Gulf in Patagonian waters (47°S; Cousseau & Perrotta, 2013), which has characteristics typical of the Magellanic Province. In waters off Buenos Aires province, this species performs seasonal latitudial and bathymetric migrations (Barretto, Sáez, Rico, & Jaureguizar, 2011); however, there is no information on the stock composition in southern Patagonian waters or the possible migration from lower latitudes towards that region.

Fish inhabiting the Magellanic Province harbour parasite assemblages characteristic of that region, which are different enough from those in the Argentine Province to successfully discriminate stocks of several fish species (Cantatore & Timi, 2015; Lanfranchi et al., 2016, 2018). Consequently, it is likely that at least one different stock of *P. brasiliensis* exists in Patagonian waters. In the present paper, samples caught in the Magellanic region were included in comparisons to analyse for the first time the population structure of this species in that region. The aim of this work was, therefore, two-fold: (1) to evaluate how parasite communities of *P. brasiliensis* changed in response to measures promoting the recovery of the resource; and (2) to test the hypothesis that a different stock of *P. brasiliensis* exists in Magellanic waters.

2 | METHODS

Seventy-five specimens of *P. brasiliensis*, distributed in three samples from two localities in the Argentine Sea, belonging to two biogeographical provinces, were examined for metazoan parasites (Figure 1, Table 1). Fish were obtained from research cruises and commercial catches and deep-frozen in individual plastic bags at −18°C until

FIGURE 1 Map showing sampling sites and zoogeographical provinces. MDP, Mar del Plata; ER1, El Rincón 2005; ER2, El Rincón 2018; SMG, San Matías Gulf; RA1, Rawson 2016; RA2, Rawson 2017; striped region, protected area
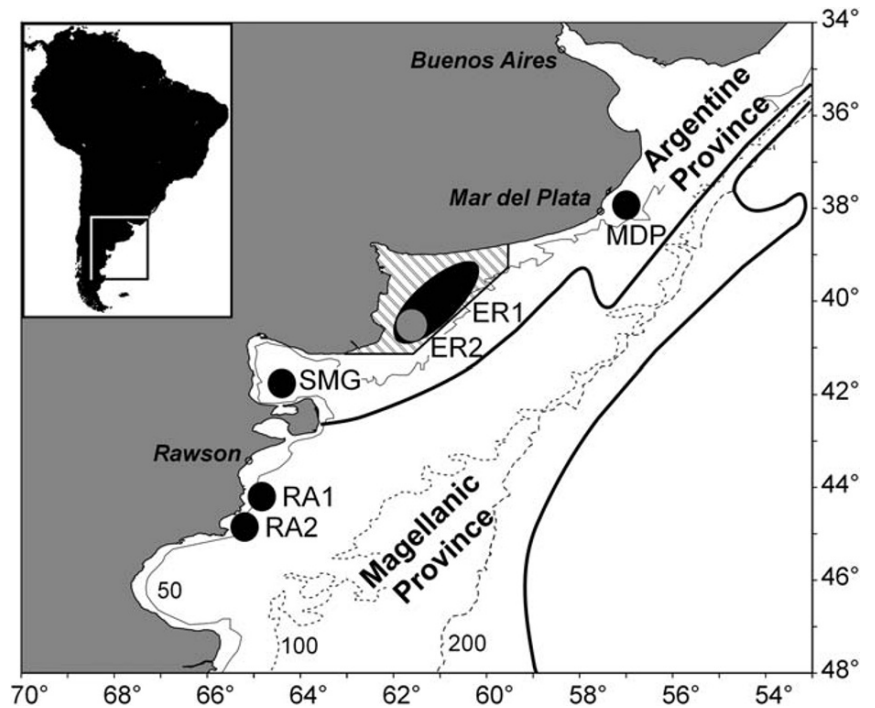
TABLE 1 Composition of samples of *Percophis brasiliensis* in six localities of the Argentine Sea (ordered by latitude)

Sample	Sample code	N	Latitude/longitude	Date	Total length ± SD (range) (cm)	Biogeographical province	Source
Mar del Plata	MDP	51	38° S; 57° W	10/2005	56.4 ± 6.5 (44.0–71.0)	Argentine	Braicovich & Timi, 2010
El Rincón 2005	ER1	51	39–41° S; 60–62° W	10/2005	50.0 ± 3.7 (45.0–58.0)	Argentine	Braicovich & Timi, 2008
El Rincón 2018	ER2	40	40°57′ S; 61°37′ W	10/2018	49.2 ± 3.3 (43.8–58.0)	Argentine	Present study
San Matías Gulf	SMG	32	41°40′–42°10′ S; 63°50′–65°00′ W	01/2006	52.9 ± 6.7 (41.0–66.0)	Ecotone	Braicovich & Timi, 2008
Rawson 2016	RA1	23	43°47′ S; 65°00′ W	10/2016	54.7 ± 3.3 (48.5–62.0)	Magellanic	Present study
Rawson 2017	RA2	12	43°52′ S; 65°30′ W	03–04/2017	55.9 ± 5.8 (45.0–63.5)	Magellanic	Present study

Note: N, number of fish examined.

examination. After thawing, the total length was measured (TL, cm) and each fish was processed as in Braicovich and Timi (2008, 2010).

In order to evaluate possible changes in parasite populations after the implementation of protection measures in El Rincón (ER), previously published data for 51 flatheads caught in 2005 (Braicovich & Timi, 2008) were included. Additionally, to reveal recurrent distributional patterns, two samples from neighbouring localities were included in the analyses for comparative purposes: one from Mar del Plata coast and one from San Matías Gulf, captured in 2005–2006 (Braicovich & Timi, 2008, 2010). The datasets, totalling 209 examined fish, are summarized in Table 1.

The total length of fish was compared across samples by a one-way permutational multivariate analysis of variance (PERMANOVA;

Anderson, Gorley, & Clarke, 2008) on the Euclidean distances (1 × 6 factorial design, 'sample' as a fixed factor), testing for main effects after 9,999 permutations and subsequent *post-hoc* pairwise comparisons. Following Anderson et al. (2008), an unrestricted permutation of raw data was used.

Prevalence and mean abundance for each parasite species in each locality were calculated following Bush, Lafferty, Lotz, and Shostak (1997); long-lived larval parasites were selected for all subsequent analyses since these parasite species are persistent for long periods or even for the entire life of hosts, and therefore are more reliable for comparisons (Braicovich, Pantoja, Pereira, Luque, & Timi, 2017). Indeed, as long-lived parasites live in the body cavity or encysted in tissues, no seasonal variability in the parasite loads is

expected for these larvae; therefore, their burdens and community structure remain stable throughour host migratory routes (Timi & MacKenzie, 2015).

Owing to the large differences in parasite abundance across parasite species, data were square-root transformed prior to multivariate analyses to down-weight the importance of very abundant species, such that less dominant species also played a role in determining similarity among samples (Clarke & Gorley, 2015). A Bray–Curtis similarity matrix was computed at infra-community level (*sensu* Bush et al., 1997) for the long-lived parasite assemblages and was subjected to multivariate analyses.

In order to visualize possible temporal and geographic patterns in the composition of parasite assemblages across the samples, non-metric multidimensional scaling (nMDS) of the similarity matrix was performed between all infra-communities and their centroid differences were visualized by means of bootstrap averaging based on repeated resampling (with replacement, 90 iterations) from the original dataset (Clarke & Gorley, 2015). Average values were then visualized in an nMDS using as many dimensions as needed to closely match the original distance matrix (correlation coefficient of $\rho = 0.99$) and the fit of the nMDS ordinations was quantified by a stress value.

Differences between infra-communities among samples were examined in more detail using canonical analysis of principal coordinates (CAP) (Anderson et al., 2008; Anderson & Willis, 2003) on the same similarity matrix. The potential for over-parameterization was prevented by choosing the number of PCO axes (m) that maximized a leave-one-out allocation success to groups (Anderson & Robinson, 2003). To test for differences between infra-communities among the samples, a permutation 'trace' test (sum of squared canonical eigenvalues) was applied and a P-value was obtained after 9,999 permutations.

Since MDS and CAP analyses do not take into account possible biases introduced by differences in host size, the structure of long-lived parasite infra-communities was compared between samples (1 × 6 factorial design, samples as fixed factors) by means of a one-way permutational multivariate analysis of variance (PERMANOVA), with host size as a covariable and testing for main effects after 9,999 permutations and subsequent *post-hoc* pair-wise comparisons. Following Anderson et al. (2008), a permutation of residuals with a reduced model was used as the method of permutation. A sequential sum of squares (type I) was applied because host size was introduced as a covariable (ANCOVA model).

For those species with prevalence >10%, in at least one of the samples (component species; Bush, Aho, & Kennedy, 1990), χ^2 analysis was used to test for significant differences in prevalence between samples from ER captured in different years (Zar, 1999). General linear models were applied to test differences in the abundance of parasites (response variable) owing to the capture year and the total length of host (explanatory variables). *Terranova* sp. and *Pseudoterranova cattani* were excluded from the analysis because they were absent in one of the two samples. In these comparative analyses, an adult parasite, *Moravecia argentinensis*, was included because it inhabits the blood vessels and is the unique strictly specific parasite of

P. brasilianus with prevalence >10%. A negative binomial error distribution was used owing to the discrete nature of the data (counts) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), employing the MASS package (Ripley et al., 2019). The significance of each explanatory variable on the models produced was assessed through Anova tables for Various Statistical Models employing a χ^2 test, in CAR package (Fox et al., 2016). The analyses were performed in R software version 3.6.1 (r-project.org).

Finally, a nMDS was performed using the Bray–Curtis similarity index on prevalence data to visualize possible geographic patterns in the composition of parasite assemblages across the six samples at the component community level (*sensu* Bush et al., 1997). Hierarchical agglomerative clustering was applied to the component communities using group-average linking, and resemblance levels were overlaid on the nMDS plot (Clarke & Gorley, 2015).

3 | RESULTS

Twenty-four parasite taxa were found in samples of *P. brasiliensis* (Table 2), 13 of which were long-lived larval stages that accounted for 92.4% of parasites found. Larval stages of nematodes *Pseudoterranova cattani* and *Hysterothylacium aduncum* were recorded for the first time in this host, in samples from ER2 and RA.

Significant differences in fish length across samples (Table 3) were due to the smaller flatheads from ER1 and ER2 relative to all other samples (all $P_{perm} < 0.01$). Fish from ER1 and ER2 did not differ in size ($P_{perm} > 0.01$), nor were there differences in size among fish from the remaining samples (all $P_{perm} > 0.01$).

The bootstrap-average-based nMDS ordination of long-lived parasites (Figure 2) showed a pattern of separation between infra-communities from different samples, with a low level of stress (0.08). Indeed, the parasite assemblages from the four sites were mostly distributed along the first axis with both samples from ER being situated apart from each other, while those from RA constituted a rather homogeneous group.

A similar pattern of samples discrimination was revealed by the CAP analysis (Figure 3a), which showed significant differences amongst the samples ($tr = 2.20$, $P < 0.01$). The selected orthonormal principal coordinates (PCO) axes ($m = 7$) described 98.3% of the variation in the data cloud, with 82.8% correct allocations of infra-communities into the pre-established groups, and a misclassification error of 17.2%. Cross-validation of the results (Table 4) showed that higher percentages of correctly allocated infra-communities occurred in MDP and ER2, whereas those from RA2 showed lower proportions of correct allocations, owing mainly to misclassification of RA2 hosts in RA1. Indeed, the two first canonical axes resulting from the CAP separated the samples mainly along the first axis and a strong association between the multivariate data 'cloud' and the hypothesis of group differences as indicated by the reasonably large size of their canonical correlations ($d_1 = 0.94$ and $d_2 = 0.76$). In that sense, both samples from the Magellanic Province (RA1 and RA2) were located at the left of the biplot, being characterized by the abundances of

TABLE 2 Taxonomic composition, microhabitat, prevalence and mean abundance of parasites of *P. brasiliensis* in six samples from four zones of the Argentine Sea

	Site	MDP P	MDP MA ± SD	ER1 P	ER1 MA ± SD	ER2 P	ER2 MA ± SD	SMG P	SMG MA ± SD	RA1 P	RA1 MA ± SD	RA2 P	RA2 MA ± SD
Digenea													
Cardicola ambrosioi	BV	2.0	0.02 ± 0.1	2.0	0.02 ± 0.1	5.0	0.1 ± 0.5	0.0	–	0.0	–	8.3	0.3 ± 1.6
Ectenurus virgulus	ST	3.9	0.06 ± 0.3	0.0	–	0.0	–	0.0	–	0.0	–	0.0	–
Lecithochirium microstomum	ST	13.7	0.4 ± 1.5	9.8	0.2 ± 1.1	0.0	–	6.2	0.2 ± 0.7	0.0	–	0.0	–
Lecithocladium cristatum	ST	3.9	0.6 ± 3.6	0.0	–	0.0	–	6.2	0.1 ± 0.2	0.0	–	0.0	–
Prosorhynchus sp. [a]	GI	11.8	0.2 ± 6.0	3.9	0.04 ± 0.2	2.5	0.03 ± 0.2	0.0	–	0.0	–	0.0	–
Cestoda													
Scolex polymorphus	IN	74.5	76.7 ± 101.6	51.0	32.6 ± 59.9	67.5	98.2 ± 180.7	65.6	27.7 ± 36.8	8.7	0.02 ± 0.4	8.3	0.9 ± 0.9
Grillotia carvajalregorum [a]	ME	100	957.9 ± 949.0	100	364.5 ± 222.3	100	914.4 ± 586.0	100	142.3 ± 191.1	100	33.9 ± 28.3	100	48.4 ± 87.3
Callitetrarhynchus gracilis [a]	ME	33.3	0.5 ± 1.4	9.8	0.1 ± 0.4	0.0	–	3.1	0.03 ± 0.2	0.0	–	0.0	–
Tentaculariidae gen. sp. [a]	ME	39.2	2.0 ± 8.8	41.2	3.5 ± 16.9	85.0	9.6 ± 23.4	6.2	0.06 ± 0.2	4.3	0.04 ± 0.2	25.0	0.4 ± 0.9
Pseudophyllidea plerocercoid [a]	ME	3.9	0.04 ± 0.2	9.8	0.1 ± 0.3	25.0	1.0 ± 3.7	0.0	–	0.0	–	0.0	–
Nematoda													
Anisakis simplex s.l. [a]	ME	43.1	1.3 ± 2.5	98	16.5 ± 13.3	97.5	10.9 ± 10.5	53.1	8.7 ± 26.2	100	48.1 ± 39.4	83.3	132.9 ± 151.7
Contracaecum sp. [a]	ME	0.0	–	7.8	0.4 ± 1.5	95.0	7.0 ± 4.1	15.6	0.2 ± 0.4	87.0	0.02 ± 0.4	41.7	1.3 ± 2.0
Hysterothylacium sp. [a]	ME	100	75.6 ± 104.7	70.6	2.7 ± 4.3	85.0	4.4 ± 4.0	9.4	0.2 ± 0.5	26.1	0.6 ± 1.3	25.0	0.3 ± 0.7
Hysterothylacium aduncum (A)	ST; IN	3.9	0.2 ± 1.4	3.9	0.1 ± 0.4	22.5	4.4 ± 15.6	0.0	–	4.3	0.04 ± 0.03	0.0	–
Hysterothylacium aduncum [a] (L)	ME	0.0	–	0.0	–	2.5	0.03 ± 0.2	0.0	0.0	21.7	0.5 ± 1.1	8.3	0.08 ± 0.3
Pseudoterranova cattani [a]	ME	0.0	–	0.0	–	17.5	0.4 ± 0.7	0.0	–	4.3	0.04 ± 0.03	0.0	–
Terranova galeocerdonis [a]	ME	5.9	0.1 ± 0.6	11.8	0.2 ± 0.6	0.0	–	0.0	–	0.0	–	0.0	–
Moravecia argentinensis	BV	52.0	1.1 ± 1.5	45.1	0.7 ± 1.0	47.5	1.2 ± 1.8	6.2	0.06 ± 0.2	52.2	0.04 ± 0.8	50.0	1.3 ± 0.3
Ascarophis marina	ST	0.0	–	0.0	–	1.0	0.05 ± 0.2	3.1	0.03 ± 0.2	0.0	–	0.0	–
Acanthocephala													
Corynosoma australe [a]	ME	100	170.1 ± 135.7	96.1	24.5 ± 29.1	97.5	41.9 ± 65.7	75.0	5.5 ± 10.2	73.9	3.7 ± 4.5	91.7	10.3 ± 11.0
Corynosoma cetaceum [a]	ME	64.7	3.3 ± 5.7	56.9	3.9 ± 8.9	55.0	1.7 ± 2.5	25.0	1.9 ± 6.4	0.0	–	0.0	–
Isopoda													
Gnathiidea gen. sp.	GI	15.7	0.2 ± 0.5	9.8	0.2 ± 0.5	0.0		3.1	0.0 ± 0.1	0.0	–	0.0	–
Copepoda													
Trifur tortuosus	GI	0.0	–	0.0	–	0.0	–	3.1	0.03 ± 0.2	0.0	–	0.0	–
Hirudinea													
Hirudinean	GI	0.0	–	1.9	0.02 ± 0.1	0.0	–	0.0	–	0.0	–	0.0	–

[a] Long-lived parasites.

Abbreviations: A, adult; BV, blood vessels; GI, gills; IN, intestine; L, larval stage; ME, mesenteries; ST, stomach.

TABLE 3 PERMANOVA results of comparisons of host total length and infra-community structure of long-lived parasites of *P. brasiliensis* across six samples from four zones of the Argentine Sea

Response variable	Source	d.f.	SS	MS	Pseudo F	P (perm)
Fish total length	Sample	5	1,900.4	380.07	14.564	0.0001
Euclidean distance	Residual	203	5,297.6	26.096		
	Total	208	7,197.9			
Infracommunity structure	Host size	1	3,311.4	3,311.4	6.7381	0.0028
Bray–Curtis similarity	Sample	5	$1.4251e^{05}$	28,502	57.997	0.0001
	Host size × sample	5	29,660	5,932.1	12.071	0.0001
	Residual	197	96,814	491.44		
	Total	208	$2.723e^{05}$			

Note: P-values obtained after 9,999 permutations.

Abbreviations: d.f., degrees of freedom; MS, mean squares; SS, sum of square.
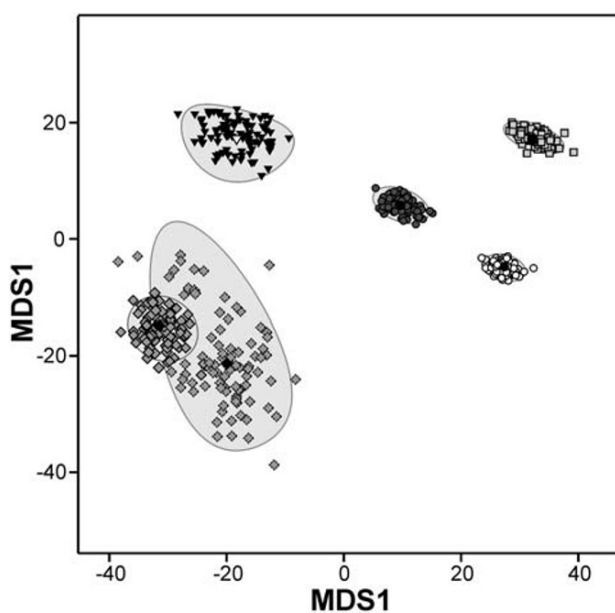
FIGURE 2 Non-metric multi-dimensional scaling plot of bootstrap averages (90 repetitions) of parasite infra-communities in six samples of long-lived parasites of *Percophis brasiliensis* from the south-western Atlantic based on Bray–Curtis dissimilarity of square root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. Black symbols and white triangle represent the overall centroids across all repetitions. Grey areas represent 95% confidence regions. Squares, Mar del Plata; grey circles, El Rincón 1; white circles, El Rincón 2; solid border rhombuses, Rawson 1; dotted border rhombuses, Rawson 2; triangles, San Matías Gulf

(Table 3). However, the sample also had a significant effect independent of this, and pair-wise tests between host samples after accounting for host size showed differences between most pairs ($P_{(perm)}$ < 0.01), with the exception of those from RA1 and RA2 ($P_{(perm)}$ > 0.01). Differences in the multivariate dispersions can be partially responsible for such a lack of pattern since PERMDISP results were highly significant ($F_{5,\ 203}$ = 16.842 $P_{(permdisp)}$ < 0.01), owing to comparisons involving samples from ER1 and RA2 (all $P_{(perm)}$ < 0.01).

Comparisons of parasite prevalence between both samples from ER showed that *Contracaecum* sp., *P. cattani* and Tentaculariidae gen. sp. differed significantly (all *P* < 0.01), with higher prevalence in samples captured from ER in 2018, compared with those from 2005. The general linear model analyses showed that the year of capture was important in explaining the abundance for most parasite species compared (Table 5), while host size partially explained the variation in abundances for *C. australe*, *G. carvajarlregorum*, *Hysterothylacium* sp. and *A. simplex* s.l. No significant interaction between capture year and host size was observed for any species. For all those species differing in parasite abundance, the values were higher in fish captured in 2018. For the rest of the species, including *Moravecia argentinensis*, no significant differences were found (all *P* > 0.01).

At the level of component communities, the nMDS and cluster analyses carried out for abundances showed a similar pattern to that for infra-communities (Figure 4). Indeed, two groups were clearly separated, one composed of the samples caught in the Argentine Province (MDP, ER1 and ER2) and the other by samples from the Magellanic Province (SMG, RA1 and RA2) with high similarity (65%).

Anisakis simplex s.l. (Figures 3a,b) and *Contracaecum* sp. (Figures 3a,c), whereas those from the Argentine Province were at the right and related to a group of indicator species composed mainly of the larval acanthocephalan *Corynosoma australe* (Figures 3a,d), the cestode *Grillotia carvajalregorum* (Figures 3a,e) and the nematode *Hysterothylacium* sp. (Figures 3a,f), the latter species mostly associated with flatheads caught at ER in 2018.

The resemblance of long-lived parasite infra-communities was influenced by host size, which also interacted with sample origin

4 | DISCUSSION

The parasite fauna of *P. brasiliensis* is probably one of the best known in the south-western Atlantic (Braicovich et al., 2017; Braicovich & Timi, 2008, 2010). In new samples collected 13 years after prior work, and from the southern distribution area, two new parasites were recorded, yielding a total of 38 species of parasites known for this host.

Marine reserves aim to restore balanced ecosystems to protect resources and habitats (Wootton et al., 2012). After implementing

FIGURE 3 (a) Canonical analysis of principal co-ordinates (CAP) bi-plot based on Bray–Curtis dissimilarities on square-root abundance data of long-lived parasites of *P. brasiliensis* in six samples in the south-western Atlantic. Vectors represent Pearson's correlations ($r > 0.4$) of the abundance of individual parasite species with the CAP axes. Squares, Mar del Plata; grey circles, El Rincón 1; white circles, El Rincón 2; solid border rhombuses, Rawson 1; dotted border rhombuses, Rawson 2; triangles, San Matías Gulf. AS, *Anisakis simplex* s.l.; CA, *Corynosoma australe*; CC, *Corynosoma cetaceum*; CO, *Contracaecum* sp.; GC, *Grillotia carvajalregorum*; HY, *Hysterothylacium* sp. (b–f) Circle diameters scaled according to the square-rooted abundance for the five main indicator species for stock discrimination in each individual fish. (b) *A. simplex* s.l.; (c) *Contacaecum* sp.; (d) *C. australe*; (e) *G. carvajalregorum*; (f) *Hysterothylacium* sp. Circle colours as for (a)
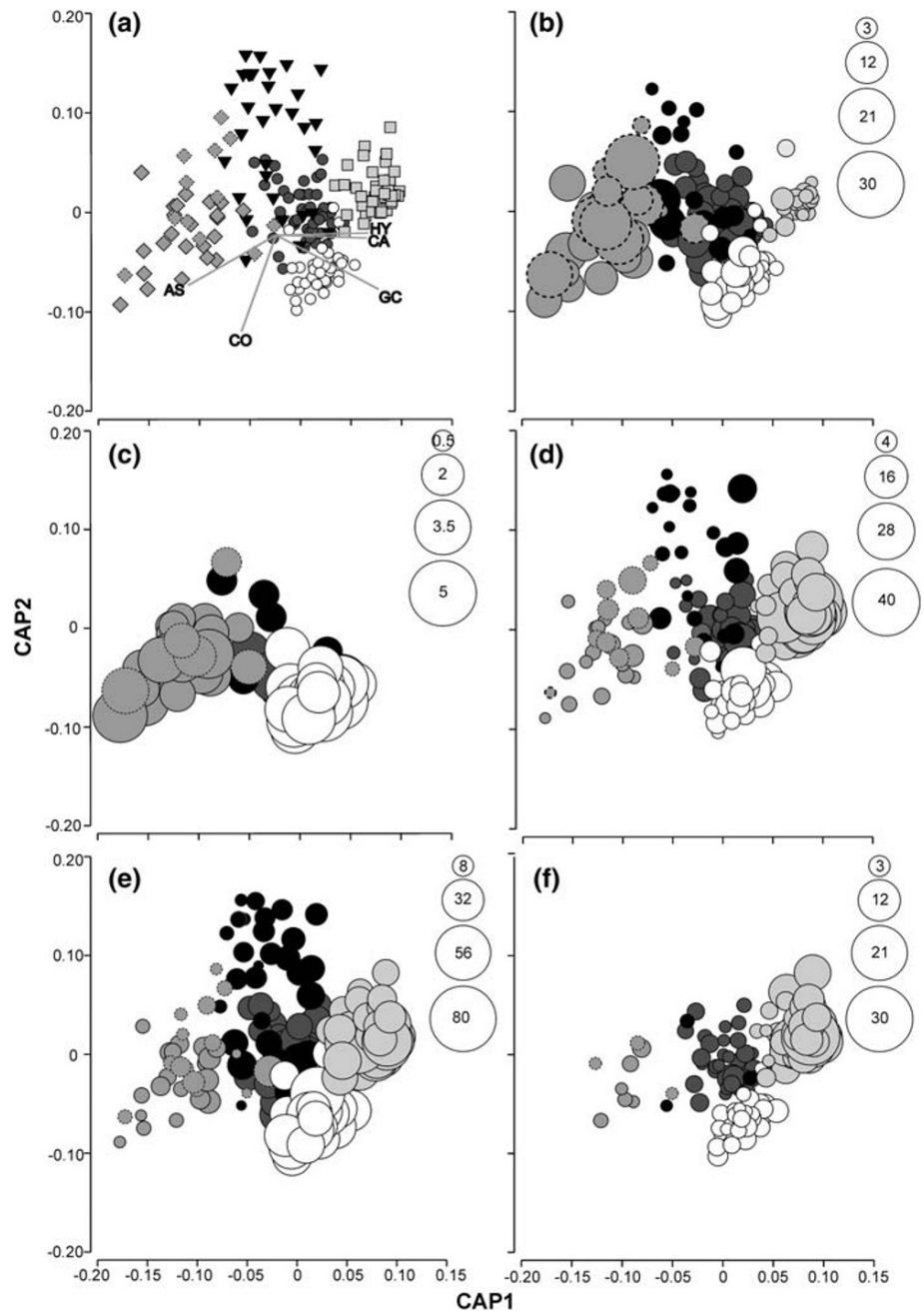

TABLE 4 Results of the cross validation of principal co-ordinates analysis (CAP) (leave-one-out allocation of individual fish to one of six samples)

Sample	MDP	ER1	ER2	SMG	RA1	RA2	Total	Correctly classified (%)
MDP	**47**	3	1	0	0	0	51	92.2
ER1	0	**42**	5	4	0	0	51	82.4
ER2	0	3	**37**	0	0	0	40	92.5
SMG	0	6	2	**22**	1	1	32	68.8
RA1	0	0	0	1	**20**	2	23	87.0
RA2	0	1	1	2	3	**5**	12	41.7

Note: Rows correspond to number of fish parasite infra-communities allocated to each group, including (at far right) the percentage correctly classified in their actual sample.

Abbreviations: ER1, El Rincón 2005; ER2, El Rincón 2018; MDP, Mar del Plata; RA1, Rawson 2016; RA2, Rawson 2017; SMG, San Matías Gulf.

TABLE 5 Results of the general linear models comparing between abundances of individual parasites from El Rincón corresponding to 2005 and 2018

Parasite species	Year		Size host		Interaction (year/size host)	
	χ^2	P	χ^2	P	χ^2	P
Corynosoma australe	6.54	=0.01	56.83	<0.01	1.64	>0.01
Corynosoma cetaceum	5.28	>0.01	0.30	>0.01	1.41	>0.01
Grillotia carvajalregorum	69.92	<0.01	21.13	<0.01	5.19	>0.01
Tentaculariidae gen. sp.	6.09	>0.01	0.51	>0.01	0.00	>0.01
Hysterothylacium sp.	12.63	<0.01	26.07	<0.01	3.44	>0.01
Anisakis simplex s.l.	4.21	>0.05	34.28	<0.01	0.00	>0.01
Pseudophyllidea plerocercoid	11.24	<0.01	0.74	>0.01	0.70	>0.01
Contracaecum sp.	177.5	<0.01	0.12	>0.01	3.24	>0.01
Moravecia argentiensis	4.29	>0.01	5.36	>0.01	0.32	>0.01
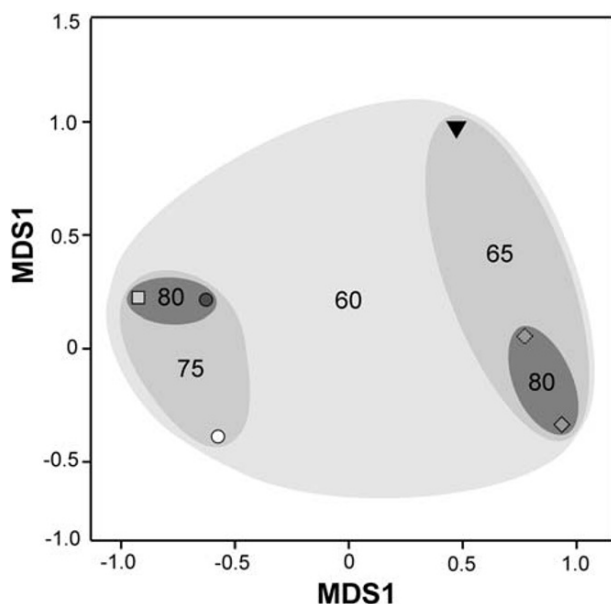
FIGURE 4 Non-metric multi-dimensional scaling plot of mean abundance (Bray–Curtis dissimilarity) of long-lived parasites in six samples of *P. brasiliensis* in the south-western Atlantic. Results of hierarchical agglomerative clustering are overlaid on the non-metric multi-dimensional scaling plot with similarity levels represented by a grey scale, with its value given as a number inside each grey area. Square, Mar del Plata; grey circle, El Rincón 1; white circle, El Rincón 2; rhombus, Rawson 1; rhombus dotted line, Rawson 2; triangle, San Matías Gulf

appropriate reforms, changes can happen quickly, with recovery of the average fishery estimated to take less than 10 years (Costello et al., 2016). Since fishing can reduce the transmission of parasites through reduction of both fish densities and food web complexity (Wood, Lafferty, & Micheli, 2010), considerable changes in the composition of parasite assemblages are likely in increasingly fished ecosystems (Wood & Lafferty, 2015), whose extent and direction depend on parasite life history and host fishing status (Wood & Lafferty, 2015; Wood, Sandin, Zgliczynski, Guerra, & Micheli, 2014). A primary effect of marine reserves is increased density of exploited

populations, which facilitates parasite transmission (McCallum, Gerber, & Jani, 2005), and a reversal of such changes in parasite burdens should therefore be expected in effectively restored fisheries.

Indeed, most previous research has recorded higher parasite species richness, diversity and abundance in protected areas (Bartoli, Gibson, & Bray, 2005; Lafferty, Shaw, & Kuris, 2008; Loot, Aldana, & Navarrete, 2005; Sasal, Desdevises, Durieux, Lenfant, & Romans, 2004; Sasal, Faliex, & Morand, 1996; Wood et al., 2013), although other studies found no clearcut differences in assemblage structure (Ternengo, Levron, Mouillot, & Marchand, 2009) or opposite trends of abundance across parasite species (Isbert et al., 2018; Marzoug, Boutiba, Kostadinova, & Perez-del-Olmo, 2012). These effects on parasite communities have been used as indirect evidence on how fisheries can affect parasites (Wood & Lafferty, 2015) in a small number of studies (Isbert et al., 2018). However, probably because all these studies were carried out by comparison between fished and protected areas, little mention has been made of the potential of parasites as indicators of the success of protected areas in recovering ecosystems (but see Isbert et al., 2018), which should include data from before and after protection measures. To the best of our knowledge, this is the first study comparing the structure of parasite communities before and after the implementation of fishery regulations in the marine environment.

As expected, results from the present study include a significant change in the structure and composition of parasite assemblages, which is a consequence of increased loads for several species. We acknowledge that, by comparing two samples, one before and the other after the implementation of protection measures, other causes of the observed variability may be overlooked. These include those related to small-scale spatial changes in parasitism, since samples were caught at different sites within the protected area, and those related to natural short- and long- term temporal oscillations or trends. However, we consider capture site and the extent of the area sampled within ER to be of little relevance as sources of variability for parasite burdens of *P. brasiliensis*. Indeed, parasite assemblages in this host are homogeneous in both composition and structure in comparisons of a single stock at much larger spatial scales (Braicovich & Timi, 2008) and

it is well established that a single stock of *P. brasiliensis* inhabits ER (Avigliano et al., 2015; Braicovich & Timi, 2008; Rico et al., 2018; Rodrígues et al., 2010). Additionally, both samples from Rawson examined in the present study were separated by a similar distance as in ER but showed no differences in parasite community structure.

Temporal patterns in parasite population and community structure can be affected by environmental characteristics and host biology associated with annual or seasonal changes (Poulin, 2006). However, in this case, changes related to short-term or seasonal causes were avoided by restricting comparative analyses to larval parasites, all of them living in the body cavity or internal tissues. Members of this guild are persistent for long periods or even for the entire life of hosts (Braicovich et al., 2017; Lester & MacKenzie, 2009; Timi & MacKenzie, 2015), and consequently, seasonality is not expected to occur. Furthermore, both samples from ER (2005 and 2018) were caught during the same season (October), further reducing any expected influence of seasonality. Additionally, the parasite communities of *P. brasiliensis* in a neighbouring region (Braicovich & Timi, 2010) were stable in both composition and community structure throughout the year. Indeed, other studies on temporal repeatability of community structure of the same guild (mostly the same species) of parasites in fishes from the northern Argentinean Sea have demonstrated a high degree of short-term monthly, seasonal or interannual stability (Braicovich, Luque, & Timi, 2012; Braicovich & Timi, 2010; Rossin & Timi, 2010; Timi, Lanfranchi, & Etchegoin, 2009). As a further example, both samples from Rawson, although taken during two consecutive years, were stable and showed no differences during this interval, providing further evidence of the persistence of larval parasite communities in *P. brasiliensis*.

Nonetheless, unmeasured variables, such as climate-driven changes in oceanography or regional changes in coastal pollution, cannot be discounted as sources of observed variability. These changes affect parasites in a variety of ways, either increasing or decreasing levels of parasitism and modifying parasite community structure, depending upon both the nature of the stressor and the group of parasites considered (Lafferty, 1997; Sures, Nachev, Selbach, & Marcogliese, 2017). However, negative effects on parasite populations and species richness are typically observed for pollutants (Blanar, Munkittrick, Houlahan, MacLatchy, & Marcogliese, 2009; Vidal-Martínez, Pech, Sures, Purucker, & Poulin, 2010) and, although global warming can promote developmental rates and transmission success on a local scale, yielding higher local abundance of certain parasites (Poulin & Mouritsen, 2006), other components of global change, such as increases in ocean acidification or ultraviolet radiation and their interactions, can result in the opposite trend (MacLeod, 2017; Studer & Poulin, 2013), leading to decreases in parasitism (Carlson et al., 2017; Cizauskas et al., 2017). In the present study, all parasite species differing significantly in prevalence and/or abundance showed increased values of these parameters in 2018 compared with 2005. Furthermore, *P. cattani* and *Terranova* sp. were only present in samples from 2018. This pattern, which was recurrent across a variety of parasite taxa, such as cestodes, nematodes and acanthocephalans, is unlikely to result from environmental stressors, such as pollution and global change, which, as reviewed above, are expected to have mixed effects, rather than homogeneous positive effects on infection levels. Therefore, in line with previous observations of increased parasitism in marine reserves relative to exploited areas, the effect of protection measures remains as the more plausible explanation for the observed changes in parasite communities of *P. brasiliensis* in El Rincón.

Interestingly, the changes observed are unlikely to be related to an increase in the abundance or density of *P. brasiliensis* populations. An increase in host density would favour the transmission and population size of parasites specific to that host. However, *M. argentinensis*, the strictly specific parasite of *P. brasiliensis*, did not show changes in their population parameters in El Rincón. The other specific parasite, *Cardicola ambrosioi*, also living in blood vessels, showed similarly low values of prevalence and abundance in both periods. All parasites that showed increased burdens are generalist larval stages, with life-cycles involving invertebrate and vertebrate hosts. It is assumed that generalist parasites should be less susceptible than specialists to change after the implementation of protection measures (Isbert et al., 2018). However, increased loads of generalist larval parasites could reflect the restoration of ecosystem functioning via increased biodiversity and species density (Lester et al., 2009; Lubchenco, Palumbi, Gaines, & Andelman, 2003) of both intermediate and definitive hosts. Indeed, several of the species with increased burdens in *P. brasiliensis* have elasmobranchs as definitive hosts, whose populations may have benefitted from fishing restrictions. However, since chondrichthyans are characterized by a low growth rate, high age and size at maturity, extensive period of gestation and small number of large offspring, they display very low population growth rates (Dulvy et al., 2008, 2014; Stevens, Bonfil, Dulvy, & Walker, 2000). Unfortunately, no data on this subject are available, but given the short time since the implementation of protection measures at El Rincón zone, an increase in shark and ray populations seems less plausible as a cause of the increased parasitism observed.

Parasites of *P. brasiliensis* parasitizing marine mammals as adults, i.e. *C. australe* and *P. cattani*, both maturing in pinnipeds (Sardella et al., 2005; Timi et al., 2014), could also respond to factors not directly related to the flathead fishery. The increased burdens of these two parasites can be explained by the gradual recovery of populations of one of their definitive hosts, the sea lion, *Otaria flavescens*, whose resurgence took place as a consequence of the prohibition of marine mammal harvesting in Argentina in 1974, after a long period of heavy exploitation that threatened extirpation (Grandi, Dans, & Crespo, 2015). Populations of fur seals, *Arctocephalus australis*, along South American coasts have also increased during recent years, probably owing to the same conservation policies (Crespo et al., 2015).

In contrast, limitations on bottom-trawl fisheries are expected to have a higher impact on the abundance of bottom invertebrate communities, with consequently strong effects on generalist larval parasites. Bottom trawling reduces benthic invertebrate abundance, biomass and diversity (Sciberras et al., 2018), selecting for communities dominated by organisms with short life-histories (Hiddink et al., 2018; van Denderen et al., 2015). However, because

of their shorter generation times, many invertebrates are able to withstand disturbance of the seabed and display higher recovery rates (Duplisea, Jennings, Warr, & Dinmore, 2002; Hiddink et al., 2018). The restoration of community production, trophic structure and function is therefore expected to be faster for invertebrates than for vertebrates. Since most of the parasites of *P. brasiliensis* showing changes in abundance are trophically transmitted and use crustaceans as intermediate hosts, the observed variations in El Rincón are possibly related to recovery at these lower levels of the food chain. In fact, greater transmission rates of parasites to fish owing to higher prey biomass will increase parasite population density in definitive hosts, even if their densities remain stable.

The stability of the population parameters of host-specific parasites suggests that no changes in the population size of *P. brasiliensis* took place during the study period, but the increased levels of parasites with heteroxenous life cycles can be interpreted as a sign of ecosystem recovery. Indeed, the increased prevalence of several species leads to higher species richness at the component community level, which is a characteristic of healthy ecosystems (Hudson, Dobson, & Lafferty, 2006). On the other hand, the higher abundance and diversity of parasites in protected fish populations, owing to an increased host density that facilitates their transmission, persistence and abundance, may potentially produce negative effects on host fitness (Krkošek, 2016; McCallum et al., 2005), leading to unintended health costs for protected wildlife (Gómez & Nichols, 2013). Conservation policies can, therefore, pose serious health risks to wildlife, whose extent depends upon the overcrowding of animals in protected areas, the size of the area and the kind of pathogen (Ezenwa, 2004; Lebarbenchon, Poulin, Gauthier-Clerc, & Thomas, 2007). Despite the increased burdens of some helminth species observed in *P. brasiliensis* caught in 2018, these values are within or below the range of abundances recorded in other populations of this species throughout its distributional range (Braicovich et al., 2017). This suggests that the rate of host population increase should not be affected at the present levels of parasitism. However, given the reductions of host fitness that increases in parasitism can impose which eventually affect the recovery of host populations, changes in the transmission dynamics and their potential detrimental effects should be considered in the cost–benefit analyses of protected areas, to improve their efficacy and management strategies (Wootton et al., 2012).

Indeed, differences in parasitism in fish from exploited vs. protected areas have been used as a sign of the negative impacts of increased host densities, such as induction of unfavourable trophic cascades and disease outbreaks (Lafferty, 2004; Lebarbenchon et al., 2007; Wootton et al., 2012), exposing the need to evaluate parasitism in protected areas.

Other aspects of marine protected areas under constant evaluation are the success and performance of their different indicators (Claudet & Guidetti, 2010; Giakoumi et al., 2018; Humphreys & Herbert, 2018; Kockel, Ban, Costa, & Dearden, 2020), including biological ones (Gladstone, 2002; Pelletier et al., 2005; Pelletier, Claudet, Ferraris, Benedetti-Cecchi, & García-Charton, 2008). Parasites

have proven to be suitable indicators for many aspects of the biology of their hosts, as well as sensitive indicators of changing conditions in aquatic systems (Blanar et al., 2009; Marcogliese, 2005; Sures et al., 2017). Indeed, they meet most of the the recommended criteria for suitable indicators in several branches of environmental sciences related to environmental impact analysis and evaluation of restoration processes (Bellinger & Sigee, 2010; Gibbons, Pearthree, Cloutier, & Ehlenz, 2020; Pander & Geist, 2013; Roni, Hall, Drenner, & Arterburn, 2019; Sures et al., 2017). Their value as indicators of the occurrence and magnitude of these changes relies on several characteristics of parasitism. First, parasites are ubiquitous components of ecosystems, comprise a noteworthy proportion of world biodiversity exploiting all kinds of organisms (Dobson, Lafferty, Kuris, Hechinger, & Jetz, 2008; Poulin & Morand, 2000) and achieving substantial biomass, abundance and productivity in some ecosystems (Kuris et al., 2008). Consequently, they are widespread and abundant in the biota, easy to identify and inexpensive to sample, especially if large host samples are being analysed. Second, by having shorter generation times, parasites can reflect changes in ecosystem conditions faster than their hosts. Third, parasites display a significant diversity of life cycles, transmission strategies and specificity, providing a battery of tools for the detection and interpretation of ongoing changes in the biology of their hosts. The replacement of the use of single biological indicators by more holistic ecological ones, simultaneously addressing communities, multiple life stages and habitat properties is often recommended (Pander & Geist, 2013). Thus, analyses of parasite assemblages combine evidence of multiple lineages and life cycle stages, which is expected to be more efficient and robust in capturing recurrent patterns in overall biodiversity than individual taxa, especially for heteroxenous species that integrate the different chains of food webs. Fourth, since each host harbours a discrete community that can be completely recorded and quantified, parasite assemblages provide spatial and temporal replication for appropriate and robust statistical comparisons of restoration effectiveness. Finally, whereas specific parasites can provide evidence on the population parameters of their specific hosts, non-specific parasites, such as those analysed in this paper, allow corroboration, by means of analyses across host species, of any trend that can be interpreted as indicative of a restoration success from a more reliable and integrative perspective.

Marine protected areas are essential tools for reversing the global degradation of ocean life and helping to restore the complexity of ecosystems through a chain of ecological effects (Sala & Giakoumi, 2018). Parasites, as integral components of such webs, provide, therefore, a cost-effective, reliable and robust set of bioindicators for a better and more precise monitoring of the success and effectiveness of protection measures.

Percophis brasiliensis is one of the main resources for the coastal fisheries in Argentina and its population parameters are currently monitored owing to increasing catch levels (Rico et al., 2018). However, evaluation efforts are concentrated in northern waters, north of 39° S (Rico et al., 2018), with no information on the status of this resource in southern regions. The significant differences between parasite assemblages observed in flatheads caught at Rawson, in

waters belonging to the Magellanic Province, and those from lower latitudes in the Argentine Province, indicate that a discrete stock of *P. brasiliensis* inhabits the southern region. Previous studies on population parameters have determined the existence of two stocks of this species in the Argentine Sea, one in the Argentine–Uruguayan Common Fishing Zone, north of 39° S and a second in El Rincón (Rico et al., 2018; Rico & Sáez, 2010; Sáez, Rico, Despós, & Casagrande, 2011). Although flatheads from El Rincón and San Matías gulf have been considered as members of a single stock based on the chemical composition of otoliths (Avigliano et al., 2015), they have been distinguished as different on the basis of reproductive (Rodrígues et al., 2010) and parasitological evidence (Braicovich & Timi, 2008). Consequently, this study reports the existence of a fourth stock in north Patagonian waters, whose identification provides insights into the population structure, applicable to the development of the sustainable management of this resource.

Parasites of *P. brasiliensis* have also been used as indicators of zoogeographical units in the south-west Atlantic, throughout the entire distribution of the species in the Argentine Province, from Rio de Janeiro in Brazil to San Matías Gulf in Argentina (Braicovich et al., 2017). In the northern Argentine Sea, flathead parasite assemblages are characterized by high burdens of a group of non-specific larval parasites (Braicovich et al., 2017), a pattern recurrent in all regional fish species studied, especially when compared with parasite communities in the Magellanic province (Cantatore & Timi, 2015). The present study is the first assessment of parasite community structure in flatheads from the Magellanic Province, and shows the same trend as all previous studies. Indeed, in the present work, a significant decrease in parasite loads for typical species of the Argentine Province, such as *G. carvajalregorum*, *C. australe*, *C. cetaceum* and *Hysterothylacium* sp. was observed in both samples from Rawson, whereas the opposite trend was evident for the anisakids *Anisakis simplex* s.l., *P. cattani*, *H. aduncum* and *Contracaecum* sp., which are commonly found at higher loads in the colder north Patagonian waters of the Magellanic Province (Cantatore & Timi, 2015; Lanfranchi et al., 2018; Timi et al., 2014).

Spatial variability of fish parasites has been largely used as a tool for stock assessment and, to lesser extent, for biogeographical purposes or for evaluating the effect of fisheries on marine resources. Although temporal varibility in parasite burdens has been successfully used to understand a variety of environmental problems (Sures et al., 2017), it has received less attention from a fisheries perspective. The observed changes in parasite assemblages of *P. brasiliensis* after the implementation of protection measures reveal that their responsiveness to anthropogenic disturbances might be advantageous not only to detect environmental problems, but also for monitoring the success of protection measurements implemented to promote the recovery of the resources.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

ORCID

Paola E. Braicovich https://orcid.org/0000-0002-2501-3452
Manuel M. Irigoitia https://orcid.org/0000-0003-2193-6775
Nelson D. Bovcon https://orcid.org/0000-0002-3786-406X
Juan T. Timi https://orcid.org/0000-0003-3717-0030

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