



Are different parasite guilds of *Pagrus pagrus* equally suitable sources of information on host zoogeography?

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Abstract

Metazoan parasite assemblages of *Pagrus pagrus* inhabiting the southwestern Atlantic were analysed with the aim of identifying the existence of different stocks and to comparatively assess the value of different parasite guilds as indicators of zoogeographical regions. A total of 186 fish was examined. Samples were obtained from three Brazilian and one Argentine localities, distributed in three different biogeographic districts of the Argentine Zoogeographical Province. *Pagrus pagrus* harboured 26 metazoan parasite species distributed in three guilds, ectoparasites (10 species), long-lived larval endoparasites and short-lived gastrointestinal endoparasites (eight species each). Prevalence and abundance values of the former two guilds allowed analysing them comparatively to assess their value as biological indicators of both host population structure and zoogeography. Results of analyses on long-lived parasites evidenced the existence of three stocks, one in the regions of Rio de Janeiro and Sao Paulo, other in southern Brazil (Rio Grande do Sul) and a third in northern Argentina (Mar del Plata), responding to the differential environmental conditions characteristic of three zoogeographical ecoregions. Ectoparasite assemblages exhibited significant differences between all pairs of samples, including those considered as a single stock according to data on persistent parasites. Assemblages of long-lived larval parasites are considered as better indicators for stock assessment purposes than ectoparasites, whose population parameters were variable temporally and heterogeneous at small spatial scales. The distributional variability of persistent parasites of *P. pagrus* along large scales provides valuable information to help defining robust biogeographical patterns, applicable to stock identification and fishery management of this species.

Keywords Red porgy · Metazoan parasite assemblages · Biological indicators · Southwestern Atlantic · Argentina · Brazil

Introduction

During the past decades, there has been an explosion of studies documenting broad-scale geographical patterns in biodiversity, seeking to explain them, and exploring their implications. Many of these studies have been prompted by increasing needs to identify the most effective schemes for conservation and sustainable use of natural resources (Gaston 2000). Most of biogeographical research in marine environments has focused on free-living taxa, whereas the biogeography of marine parasites is virtually unknown, especially over large spatial scales (Rohde 2002; Poulin et al. 2011; Reverter et al. 2017). Despite parasites are ubiquitous components of marine communities and have been increasingly used as indicators of host distribution and population structure for fishery purposes (Timi and MacKenzie 2015), very few studies have attempted to use parasites as indicators of zoogeographical regions in the

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marine realm (Rohde 2002). Among these large-scale studies, some have used marine parasites as indicators of ancient dispersal routes and oceanic barriers (Szidat 1955; Hayward 1997; Rohde and Hayward 2000), but other studies based on analyses of several phylogenetically related fish species, of their ectoparasites or based only on presence/absence of data, failed to find a fit of parasite distributions into known zoogeographical regions (Byrnes and Rohde 1992; González and Moreno 2005; Marques et al. 2009). However, studies based on all parasites of *Hippoglossus stenolepis* from the Northeastern Pacific (Blaylock et al. 1998) and on only endoparasites of *Sebastes capensis* from the Southeastern Pacific (González et al. 2006), were able to define zoogeographic regions congruent with those previously established on the basis of the distribution of free living organisms in the Pacific coasts of North and South America. Blaylock et al. (2003) in a similar work on *H. stenolepis* found patterns that agreed only partially with those identified by Blaylock et al. (1998), attributing these differences to the inclusion of short-lived parasite species in the former analysis.

More recently, the potential of fish parasites as sources of information to identify zoogeographical provinces in the southwestern Atlantic Ocean was proposed by Cantatore and Timi (2015), based on data of persistent and low host-specific parasites found in several fish species belonging to different families. Similarly, Pereira et al. (2014), Lanfranchi et al. (2016) and Braicovich et al. (2017) found that such parasites can be used as indicators of ecoregions and of higher levels of biogeographic classifications in the same region. All studies in the southwestern Atlantic restricted their analyses to the guild of long-lived parasites, which persist for long periods or even for the entire life of hosts, diminishing possible effects of short-term temporal variations on parasite loads (Cantatore and Timi 2015; Braicovich et al. 2016). However, the usefulness of other parasite guilds still needs to be addressed, in particular for ectoparasites, which are generally host-specific and develop direct life-cycles.

A way to assess the value of different parasite guilds as biogeographical tags is to analyse their distribution in the same set of hosts comparatively, which would require the different guilds to be present at considerable burdens. Among teleost species surveyed for parasites in the southwestern Atlantic, *Pagrus pagrus* has been shown to harbour high ectoparasite loads in terms of species richness and abundance, as well as a number long-lived and little-specific larvae (Soares and Luque 2015), previously identified as markers of zoogeographical units for other fish species. *Pagrus pagrus* is a valuable species that attains a maximum size of 54 cm, whose size and age of sexual maturity are 23 cm and 3 years, respectively (Cousseau and Perrotta 2013). Along its distribution range in the South West Atlantic, commercial landings of *P. pagrus* attain several thousand metric tonnes, and this resource is more abundant in some areas where its fishing is

more intense: on hard bottoms along Cabo Frio in Rio de Janeiro State and on biotrititic shelf bottoms south of Rio Grande in Brazil (Ávila-da-Silva and Haimovici 2006) and associated to biotrititic bottoms and mussel banks south of Mar del Plata, in Argentina (Cousseau and Perrotta 2013). Consequently, this host provides an excellent system for comparative studies of distributions of parasite guilds and for assessing their relative value as biological indicators.

The aim of this work is, therefore, twofold: (1) to comparatively assess the value of different parasite guilds as indicators of zoogeographical regions in the southwestern Atlantic, and based in their parasite guilds (2) to identify the existence of different stocks of *P. pagrus* in this region.

Materials and methods

Fish and parasite sampling

A total of 186 specimens of *Pagrus pagrus*, distributed in four samples from different localities in the southwestern Atlantic, were examined for metazoan parasites (Fig. 1, Table 1). All fish were obtained from commercial catches and deep frozen in individual plastic bags until examination.

According to their geographic location, samples were assigned to different biogeographic ecoregions of the Warm Temperate South West Atlantic Zoogeographical Province (Spalding et al. 2007): Those from Rio de Janeiro and Sao Paulo belong to the ecoregion South Eastern Brazil; the samples from Rio Grande do Sul correspond to the ecoregion Rio Grande, and the samples from Mar del Plata belong to the ecoregion Uruguay-Buenos Aires Shelf (Spalding et al. 2007).

Fish were either kept fresh or deep frozen in plastic bags at $-18\text{ }^{\circ}\text{C}$ until examination. After thawing, the total length was measured (TL, cm). Parasites were recovered from the body surface, gills, pores of cephalic sensory system, branchial and body cavities, and viscera (stomach, intestine, liver, gonads and mesenteries) after examination under a stereoscopic microscope.

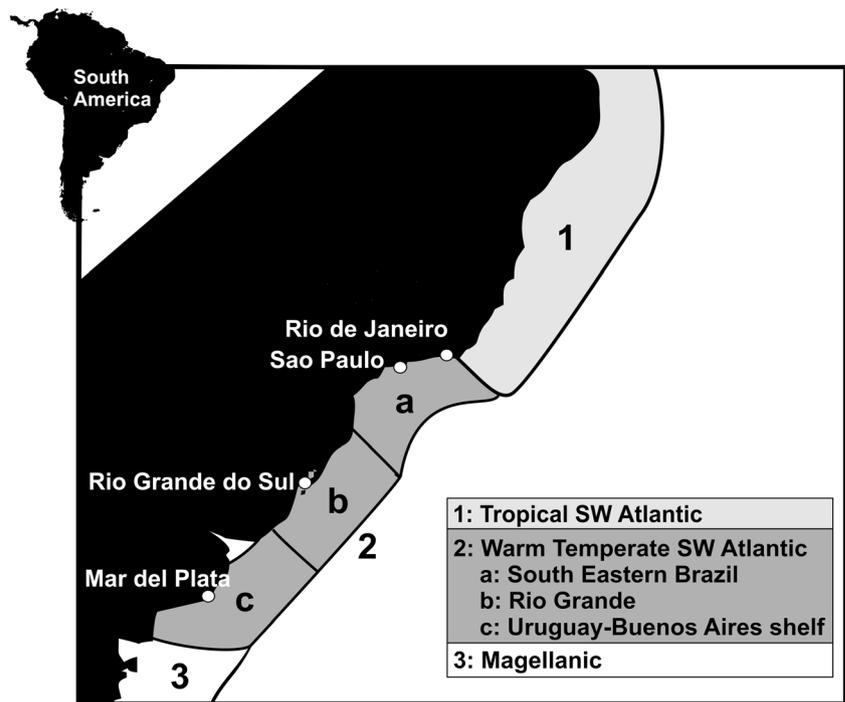
Population and community descriptors

Prevalence and mean abundance for each parasite species in each locality were calculated following Bush et al. (1997). Parasites were grouped in three guilds, ectoparasites, long-lived endoparasites (larval species found in tissues or body cavity) and short-lived endoparasites (adult and larval stages living in the gut).

Similarity analysis

Similarity in parasite species composition was computed at infracommunity and component community levels. Bray-

Fig. 1 Study area, sampling localities and biogeographical provinces and ecoregions adapted from Spalding et al. (2007)



Curtis similarity indices (Magurran 1988) were calculated on parasite abundance between all possible pairs of hosts (infracommunities) from different zones for each parasite guild. As large numbers of fish were not parasitized in some samples, depending on the parasite guild, zero-adjusted Bray-Curtis similarity matrices were used (Clarke et al. 2006). At the level of component communities, Bray-Curtis similarity indices were calculated on values of both prevalence and mean abundance between all possible pairs of samples. Due to the large differences in parasite loads across parasite species, data were square root-transformed previous all analyses in order to down-weight the importance of very prevalent/abundant species so that the less dominant species played some role in determining similarity among samples (Clarke and Gorley 2015).

In order to assess whether or not the geographic origin of the samples can be differentiated based on the abundance values of their parasites, non-metric multi-dimensional scaling (nMDS) of the Bray-Curtis similarity matrix was performed between all infracommunities of each guild, and their centroid differences were visualised by means of bootstrap averaging

(Clarke and Gorley 2015), which is based on repeated resampling (with replacement, 50 iterations) from the original dataset; the average values are then visualised in a nMDS using as many dimensions as needed to closely match the original distance matrix (correlation coefficient of $\rho = 0.99$). The fit of the MDS ordinations was quantified by a value of stress.

Differentiation of group centroids was further tested using a one-way permutational multivariate analysis of the variance (PERMANOVA, Anderson et al. 2008), introducing host size as a covariable (ANCOVA model). The structures of parasite infracommunities between samples (1×4 factorial design, 'sample' as fixed factor) were compared, testing for main effects after 9999 permutations and subsequent pair-wise post hoc pair-wise comparisons. Following Anderson et al. (2008), a permutation of residuals under a reduced model was used as method of permutation. A sequential sum of squares (Type I SS) was applied because host length was introduced as a covariable, and the samples were unbalanced (different numbers of fish examined by sample). Because PERMANOVA is sensitive to differences in multivariate dispersion between

Table 1 Composition of samples of *Pagrus pagrus* in four localities, ordered by increasing latitude, of the southwestern Atlantic

Locality	Locality code	Latitude and longitude of landing port	Date of capture	<i>n</i>	Total length \pm SD (range) (cm)
Rio de Janeiro	RJ	22° 50' S, 41° 58' W	09/2014	37	26.9 \pm 6.0 (20.0–38.0)
Sao Paulo	SP	23° 26' S, 45° 02' W	07/2012	61	32.0 \pm 1.8 (29.0–36.0)
Rio Grande do Sul	RS	32° 28' S, 51° 56' W	08/2015	50	32.0 \pm 6.6 (24.0–45.3)
Mar del Plata	MP	38° 20' S, 56° 40' W	03/2016	38	39.1 \pm 4.6 (33.0–50.5)

groups (sensu homogeneity of variances, which can inflate type I error even when centroids have identical locations), the same models were tested for differences in dispersion using the routine PERMDISP (Anderson et al. 2008). Dispersions were measured as distance to the centroid, and each term in the analysis was tested using 9999 permutations.

PERMANOVA analyses, based on Euclidean distances were used to compare the fish total length across samples (1×4 factorial design, 'sample' as fixed factor), testing for main effects after 9999 permutations and subsequent pair-wise post hoc pair-wise comparisons using an unrestricted permutation of raw data as method of permutation (Anderson et al. 2008).

At the component community level, non-metric multi-dimensional scaling analyses (nMDS) (Clarke and Gorley 2015) were performed using the Bray-Curtis similarity index on both prevalence and mean abundance data to visualise possible geographic patterns in the composition of parasite assemblages across the samples. Only those parasite species at prevalence higher than 10% in at least one of the samples were included in the analyses. A hierarchical agglomerative clustering was applied to the component communities using group-average linking, and resemblance levels were overlaid on the MDS plot (Clarke and Gorley 2015).

All similarity and distance measures, as well as MDS and clustering analyses, were implemented in PERMANOVA+ for PRIMER package (Anderson et al. 2008).

Results

General results

Fish from Rio de Janeiro (RJ) and Mar del Plata (MP) were considerably smaller and larger, respectively, than those of central regions (Table 1). Indeed, mean host lengths were significantly different between samples (Table 2), with most pairs of samples being significantly different with each other ($P < 0.01$) with the exception of Sao Paulo (SP) and Rio Grande do Sul (RS) ($P > 0.05$).

The parasite fauna of *P. pagrus* comprised 26 parasite species, most of them (23 species) present in MP, whereas lower species richness were observed in Brazilian samples, 14 in RJ, 10 in SP and 13 RS. Among them, ectoparasites were the most species-rich guild in all localities, being represented by similar values (8–10 species) across samples (Fig. 2a), whereas the lowest number of species was observed for short-lived parasites. On the other hand, hosts from MP harboured the richest component communities for all the guilds. A similar picture was observed regarding infracommunity species richness (Fig. 2b), although, in this case ectoparasites mean species richness was considerably higher in MP.

The mean number of species of long-lived endoparasites was extremely low in all samples, resulting of the low prevalence shown for most species across samples (Table 3). The only taxon found at high prevalence was the cestode species complex *Scolex polymorphus* found only in MP. Due to the impossibility of identifying these larval cestodes at specific level, as well as the fact that most hosts were devoid of short-lived endoparasites, members of this guild were excluded from subsequent analyses, which therefore were based on a set of 18 species. Although half of these species were present in all localities, being most of them ectoparasites, parasite burdens, in terms of prevalence and mean abundance, varied among the component communities from the considered zones (Table 3).

Similarity analyses

The bootstrap-average-based nMDS ordination (Fig. 3a) of long-lived parasites showed an apparent pattern of separation between samples, with a low level of stress (0.04). Indeed, the parasite assemblages from MP were clearly separated from those from Brazil, with RJ and SP apparently composing a single group. A similar picture was observed when short-lived ectoparasites were analysed (stress level = 0.02) (Fig. 3b). However, in this case, infracommunities from RJ resulted equidistant from the other two Brazilian samples.

The results of PERMANOVA analyses, for both long-lived endoparasites and ectoparasites, showed a significant effect of host length on the multivariate parasite abundance, and an interaction between the host length and locality were observed (Table 2), indicating that the nature of the relationship between the covariate and the multivariate response differed within different levels of the factor. Furthermore, taking into account the variations among samples due to fish size, significant variability was detected among the parasite assemblages. Pair-wise tests agreed in general with bootstrap-average-based nMDS ordinations. Indeed, most pairs of samples differed significantly ($P < 0.01$), with the exception of RJ and SP ($P > 0.05$) for abundance of long-lived parasites, whereas all samples of ectoparasites differed significantly from each other ($P < 0.01$).

Some of these differences can be attributed to differences in the multivariate dispersions of parasite infracommunities in terms of their deviations from centroids, because the PERMDISP results were significant for both guilds ($F_{3,180} = 23.63$ and $F_{3,180} = 189.61$ for long-lived parasites and ectoparasites, respectively; both P (perm) < 0.001). Indeed, the pair-wise test showed significant differences in the multivariate dispersions for all those comparisons involving RS (all P (perm) < 0.01) that was the locality with higher deviations from centroids for both guilds.

The MDS and cluster analyses of prevalence data when long-lived parasites were considered revealed an apparent

Table 2 One-factor PERMANOVA results comparing total length of *Pagrus pagrus* and square root-transformed abundance, with host total length as covariable, of two guilds of its parasites across four localities in the southwestern Atlantic. *P* values obtained after 9999 permutations

Response variable	Source	d.f.	SS	MS	Pseudo <i>F</i>	<i>P</i> (<i>perm</i>)
Fish total length (Euclidean distance)	Locality	3	2794.9	931.64	38.641	< 0.001
	Residual	180	4339.8	24.11		
	Total	183	7134.7			
Long-lived endoparasites (Bray-Curtis dissimilarity)	Host size	1	70695	70695	87.343	< 0.001
	Locality	3	66250	22083	27.284	< 0.001
	Host size × locality	3	25465	8488.40	10.487	< 0.001
	Residual	176	1.42e ⁵	809.39		
	Total	183	3.05e ⁵			
Ectoparasites (Bray-Curtis dissimilarity)	Host size	1	34508	34508	32.145	< 0.001
	Locality	3	1.4088e ⁵	46959	43.745	< 0.001
	Host size × locality	3	12366	4122	3.840	< 0.001
	Residual	176	1.8893e ⁵	1073.5		
	Total	183	3.7668e ⁵			

pattern of separation between samples (Fig. 4a). Despite samples being equidistant in the bidimensional space, cluster analyses identified two groups clearly separated, one composed by the two samples caught in the northern region of the study area (RJ and SP) and the other by southern samples (RS and MP) with high similarity (66 and 68%, respectively). *Corynosoma australe* and *Grillotia carvajalregorum* were related to both southern samples and *Anisakis simplex s.l.* and

Hysterothylacium sp. to both RJ and MP, finally *Raphidascaris* sp. to fish from RJ. A similar pattern was obtained for mean abundances (Fig. 4b), although with a higher similarity between northern samples (80%) and lower similarity between southern localities (56%). In this case, *C. australe*, *G. carvajalregorum* and *Hysterothylacium* spp. were, as expected for their mean abundances, strongly associated to MP. In the case of ectoparasites, prevalence (Fig. 4c) and mean abundance (Fig. 4d) showed different patterns. Indeed, regarding prevalence, RJ and RS were more similar to each other (79%) in relation to the rest, whereas SP and MP branched successively at decreasing similarity (72 and 65%, respectively). Most species were associated to MP, whereas Gnathiidae gen. sp., *Echinopelma brasiliensis* and *Encotyllabe spari* were related to RS, RJ and SP, respectively. On the other hand, the most similar localities in terms of mean abundances were RJ and SP (64%), with SP and MP branching successively at 55 and 44%. In all MDS, analyses stress level = 0 indicated community compositions substantially different from random.

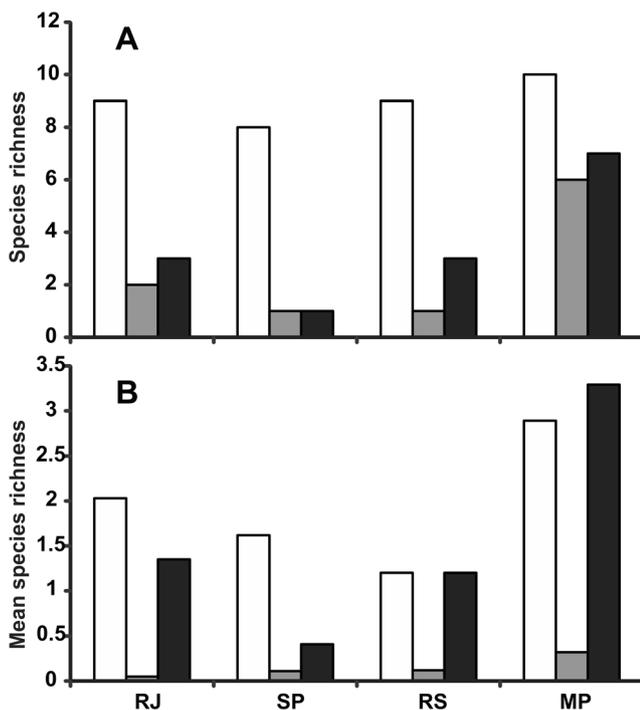


Fig. 2 Species richness of three parasite guilds of *Pagrus pagrus* in four samples along the Atlantic coasts of South America. **a** Component community species richness and **b** mean infracommunity species richness. White bars: ectoparasites; grey bars: short-lived endoparasites; black bars: long-lived endoparasites. RJ Rio de Janeiro, SP Sao Paulo, RS Rio Grande do Sul, MP Mar del Plata

Discussion

The high species richness observed in the whole sample is in agreement with that found in previous studies on parasite communities of *P. pagrus* (Paraguassú et al. 2002; Soares and Luque 2015; Soares et al. 2014). However, the number of parasite species varied across guilds, being that short-lived endoparasites the least represented, as observed in previous works (Paraguassú et al. 2002; Soares and Luque 2015; Soares et al. 2014). This fact can be due to the low trophic level and a bentophagous diet of *P. pagrus* composed mainly by invertebrates and low trophic level fishes, such as anchovy (Manooch 1977; Capitoli and Haimovici 1993), characteristics that result in poor-species assemblages of trophically

Table 3 Prevalence (P) and Mean abundance (MA) of parasites of *Pagrus pagrus* in four samples from the southwestern Atlantic coasts

Parasite	Guild	Stage	Rio de Janeiro		Sao Paulo		Rio Grande do Sul		Mar del Plata	
			P	MA (range)	P	MA (range)	P	MA (range)	P	MA (range)
Monogenea										
<i>Encyrtillabe spari</i>	Ec	Adult	75.68	2.30 (0–10)	100	8.88 (0–32)	4.00	0.04 (0–1)	2.63	0.03 (0–1)
<i>Anoplodiscus longivaginatus</i>	Ec	Adult	5.40	0.19 (0–4)	11.47	0.20 (0–4)	6.00	0.08 (0–2)	23.68	0.74 (0–13)
<i>Echinopelma brasiliensis</i>	Ec	Adult	13.51	0.14 (0–1)	29.51	0.46 (0–4)	20.00	0.36 (0–4)	5.26	0.05 (0–1)
<i>Lamellodiscus baeri</i>	Ec	Adult	5.40	0.08 (0–2)	18.03	1.11 (0–30)	8.00	0.22 (0–8)	97.37	22.03 (0–60)
<i>Polyabroides multispinosus</i>	Ec	Adult	5.40	0.05 (0–1)	1.64	0.02 (0–1)	8.00	0.10 (0–2)	15.79	0.55 (0–10)
Digenea										
<i>Parahemionus merus</i>	Se	Adult	2.70	0.03 (0–1)	9.84	0.46 (0–11)	12.00	0.14 (0–2)	–	–
<i>Aponurus laguncula</i>	Se	Adult	–	–	–	–	–	–	7.89	0.08 (0–1)
<i>Lecithochirium microstomum</i>	Se	Adult	–	–	–	–	–	–	7.89	0.08 (0–1)
<i>Ectenurus vigultus</i>	Se	Adult	–	–	–	–	–	–	2.63	0.05 (0–2)
<i>Pachycreadium gastrocoylum</i>	Se	Adult	–	–	–	–	–	–	10.53	0.66 (0–15)
<i>Otodistomum</i> sp.	Le	Metacercaria	–	–	–	–	–	–	7.89	0.08 (0–1)
Cestoda										
<i>Grillotia carvajalregorum</i>	Le	Plerocercus	–	–	–	–	12.00	8.10 (0–327)	89.47	127.18 (0–1026)
<i>Scotex polymorphus</i>	Se	Plerocercoid	–	–	–	–	–	–	52.63	3920.29 (0–11,546)
Acanthocephala										
<i>Corynosoma australe</i>	Le	Juvenile	–	–	–	–	36.00	36.34 (0–648)	100	200.10 (8–1165)
Nematoda										
<i>Hysterothylacium</i> sp.	Le	Larva III	89.19	22.32 (0–142)	93.44	24.44 (0–150)	72.00	34.12 (0–347)	100	118.37 (3–443)
<i>Raphidascaris</i> sp.	Le	Larva III	29.73	2.54 (0–26)	–	–	–	–	–	–
<i>Anisakis simplex</i> s.l.	Le	Larva III	16.22	0.27 (0–3)	–	–	–	–	23.78	0.47 (0–4)
<i>Contracaecum</i> sp.	Le	Larva III	–	–	–	–	–	–	5.26	0.16 (0–4)
<i>Terranova</i> sp.	Le	Larva III	–	–	–	–	–	–	2.63	0.03 (0–1)
<i>Cucullamus protrudens</i>	Se	Adult	2.70	0.03 (0–1)	–	–	–	–	–	–
<i>Ascarophis</i> sp.	Se	Larva	–	–	–	–	–	–	2.63	0.03 (0–1)
Copepoda										
<i>Clavellotis pagri</i>	Ec	Adult	16.22	0.24 (0–3)	32.79	0.74 (0–8)	18.00	0.24 (0–3)	36.84	0.95 (0–8)
<i>Lernanthropus caudatus</i>	Ec	Adult	16.22	0.41 (0–6)	8.20	0.16 (0–4)	6.00	0.22 (0–8)	18.42	0.63 (0–6)
<i>Colobomatus pagri</i>	Ec	Adult	43.24	1.16 (0–5)	–	–	14.00	0.22 (0–3)	73.68	1.39 (0–6)
<i>Pseudoeucanthus</i> sp.	Ec	Adult	–	–	–	–	–	–	5.26	0.08 (0–2)
Isopoda										
Gnathiidae gen. sp.	Ec	Praniza	21.62	0.32 (0–3)	9.84	0.79 (0–19)	36.00	5.22 (0–48)	10.53	0.11 (0–1)

Ec ectoparasites; Le long-lived endoparasites; Se short-lived endoparasites

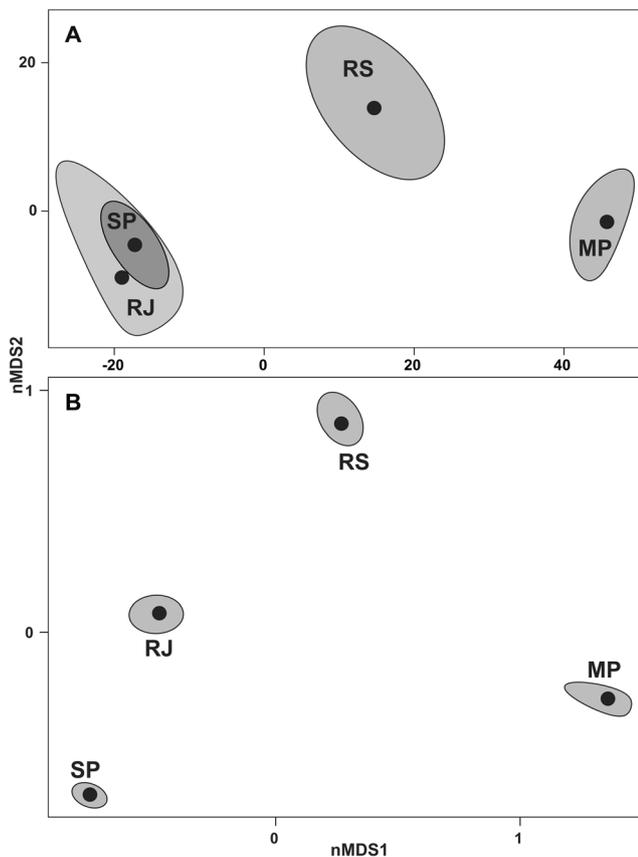


Fig. 3 Non-metric multi-dimensional scaling (nMDS) plot of bootstrap averages (50 repetitions) of parasite infracommunities in four samples of *Pagrus pagrus* from the South West Atlantic based on Bray-Curtis similarity of square root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. **a** Long-lived parasites and **b** ectoparasites. Black circles represent the overall centroids across all repetitions. Boundary lines represent 95% confidence regions. RJ Rio de Janeiro, SP Sao Paulo, RS Rio Grande do Sul, MP Mar del Plata

transmitted parasites (George-Nascimento 1987; Valtonen et al. 2010). Long-lived endoparasites, on the other hand, persist for long periods or for the entire host life, accumulating in fish and consequently reaching higher values of species richness.

Species richness of both ectoparasites and long-lived endoparasites varied across samples, attaining the maximum value in MP. This could be due to the significantly larger size of fish in this locality, since higher hosts often harbour higher parasite burdens (Poulin 2004); nevertheless, mean infracommunity species richness of both guilds was larger in hosts from RJ than in the other two Brazilian localities, in spite of their significantly smaller size in this locality. Therefore, parasite community structure and their similarities are also determined by other factors, including biological and environmental drivers of parasite diversity.

Results of bootstrap averaging and PERMANOVA analyses evidenced that factors other than host length play a role in structuring parasite assemblages, by showing similarities and

differences not related to fish size, especially the second analysis, which “corrects” the effect of that variable. The observed differences could result from a combination of factors acting differentially on the structure of parasite guilds. In marine environments, major determinants of geographic variations in assemblage structure are environmental conditions, mainly the temperature and salinity profiles (Esch and Fernández 1993), through its effect on life cycles of the different parasite species and their hosts (Cantatore and Timi 2015). In addition, geographical variations of parasitism will depend on the presence of suitable hosts for all the developmental stages (MacKenzie and Abaunza 1998), as well as on their densities and population size (Bagge et al. 2004). Short-term temporal variability in physical conditions is also relevant in driving population parameters of short-lived species, many of which, and probably most of them, will survive in or on the host for much less than the fish’s life span (Lester and MacKenzie 2009).

In the present study, both long-lived endoparasites and short-lived ectoparasites showed significant differences between samples, differing only the results of comparisons between RJ and SP, whose assemblages were of similar structure for the former, but different for the latter. Based on a general consensus that the most important criterion for an effective parasite marker of host distribution is its long residence time in the fish (Lester and MacKenzie 2009; Cantatore and Timi 2015; Braicovich et al. 2016), results obtained for persistent parasites are more reliable in terms of host stock structure. Therefore, comparisons between assemblages of this guild suggest the existence of three stocks of *P. pagrus* in the four localities surveyed, with fish from RJ and SP constituting a single unit.

On the other hand, ectoparasite assemblages exhibited significant differences between all pairs of localities, including the couple RJ-SP considered a single stock according to data on persistent parasites. These differences could be due to short-term environmental variability in population attributes of each parasite species, but also in population attributes of *P. pagrus* at each locality. Indeed, most ectoparasites of *P. pagrus* are host-specific and monoxenous, and their population dynamics could respond to host density, population size or age structure at each locality. These demographic and life history traits are highly variable even at small spatial scales for this host species (DeVries 2006), due to their high site fidelity (Grimes et al. 1982), and their consequent exposition to unique suites of environmental factors after recruitment to a given patch of habitat (DeVries 2006), mostly restricted to hard bottoms (Labropoulou et al. 1999). Considering that samples were caught in different years, the variability observed for ectoparasites could also be influenced by long-term temporal changes in these factors.

Due to their specificity and monoxenous life cycles, ectoparasites tend to occur along most the distribution range of their hosts, whereas members of the guild of long-lived endoparasites are heteroxenous and trophically transmitted their

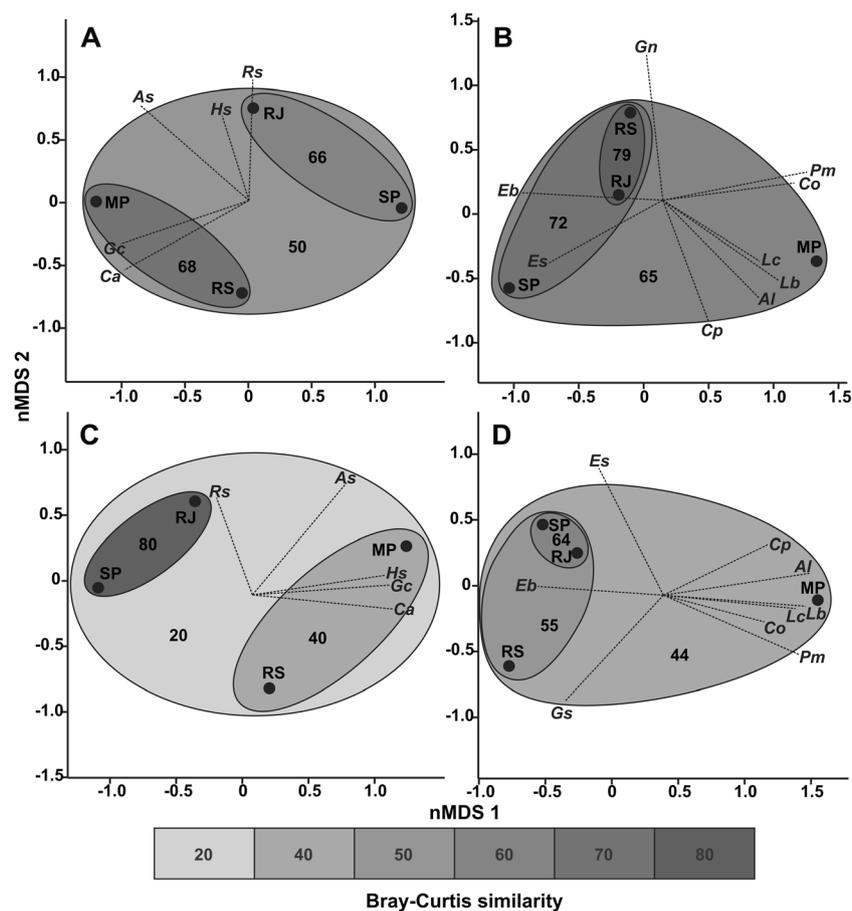


Fig. 4 Non-metric multi-dimensional scaling (nMDS) plot and cluster analyses of four component communities (Bray-Curtis similarity) of parasites of *Pagrus pagrus* in the South West Atlantic. **a** Prevalence of long-lived parasites; **b** prevalence of ectoparasites; **c** mean abundance of long-lived parasites and **d** mean abundance of ectoparasites. Results of a hierarchical agglomerative clustering are overlaid on the nMDS plot with similarity levels represented by a grey scale, with its value given as a number inside each grey area. Vectors represent Pearson's correlations

of prevalence of individual parasite species with the nMDS axes. Localities: RJ Rio de Janeiro, SP Sao Paulo, RS Rio Grande do Sul, MP Mar del Plata. Parasite species: Al *Anoplolepis longivaginata*; As *Anisakis simplex* s.l.; Ca *Corynosoma australe*; Co *Colobomatus pagri*; Cp *Clavellotis pagri*; Eb *Echinopelma brasiliensis*; Es *Encotyllabe spari*; Gc *Grillotia carvajalregorum*; Gn Gnathiidae gen. sp.; Hs *Hysterothylacium* sp.; Lb *Lamellodiscus baeri*; Lc *Lernanthropus caudatus*; Pm *Polyabroides multispinosus*; Rs *Raphidascaris* sp.

distributions depending consequently upon those of their intermediate and definitive hosts. These other hosts include invertebrates and fish for larval stages and elasmobranchs, predatory teleosts and marine mammals and birds for adults, many of them displaying high vagility and homogenising the distribution of larval stages over large areas. As a result, assemblages of long-lived larval parasites constitute better indicators for stock assessment purposes than ectoparasites, whose population parameters are not only variable temporally but heterogeneous at small spatial scales.

Due to their long periods of persistence in the host, an additional advantage of long-lived parasites as markers is the temporal stability of their assemblages, even at interannual scales, as shown by the similitude between samples RJ and SP, captured 2 years apart. Therefore, the influence of long-term temporal variability in parasite burdens, if any, is surpassed by the effect of spatial variability. Indeed, parasite communities of

P. pagrus have proven to be stable along long periods of time in Brazilian waters (Soares et al. 2014), whereas in Argentine waters, the long-lived species found in *P. pagrus* have proved to be stable at seasonal and interannual scales in other fish species (Braicovich and Timi 2010; Timi et al. 2005).

The degree of geographic population differentiation in Atlantic populations of *P. pagrus* has been evaluated with genetic markers. Using mitochondrial DNA and microsatellite markers, Ball et al. (2007) found deep differences between large areas, such as western and eastern North Atlantic and Brazil, but little or no significant regional geographic variation within them. Similarly, only limited or no genetic evidence for a separation between adjacent regions has been reported, i.e. in the Atlantic-Mediterranean divide (Bargelloni et al. 2003) and the Argentine Sea (Porrini et al. 2015). Despite the sedentary habits of adult *P. pagrus*, the relatively long-lived pelagic stages of larvae and occasional

adult movements are sufficient for genetic homogeneity within regions (Ball et al. 2007). However, life history parameters such as growth, size and size at maturity have shown differences between *P. pagrus* from the Atlantic and the Gulf of Mexico (Hood and Johnson 2000); similarly, body shape characterisation has evidenced two significantly different morphotypes between two regions in the Argentine Sea (Porrini et al. 2015), evidencing that genetic homogeneity within large areas should not be used to imply that populations or stocks of *P. pagrus* should be managed as single groups (Ball et al. 2007). The use of parasite tags constitutes, therefore, a useful tool to provide evidence for stock identification of this species in the southwestern Atlantic, supporting that the fisheries along Mar del Plata, Southern Brazil and Rio de Janeiro occur over distinct populational units that can be managed independently and that overfishing or recovery on any of these regions has no significant effects on the fish abundance of the other regions in the short term.

Analyses of results from a biogeographical perspective indicate that localities where the three stocks of *P. pagrus* were identified by their long-lived parasites belong to the three ecoregions of the Tropical Temperate South West Atlantic Province, supporting the biogeographical scheme proposed by Spalding et al. (2007), such has been observed for other coastal fishes in the region (Pereira et al. 2014; Braicovich et al. 2017). Indeed, as observed in these previous works for other fish species, samples from SP were more similar to those from MP than to those from southern Brazilian coasts. On the other hand, the heterogeneity in ectoparasites burdens strongly suggests that members of this guild should be avoided as indicators of zoogeographical studies, especially taking into account their variability at local scales.

In conclusion, the distributional variability of persistent parasites along large scales, but not of short-lived ectoparasites, provides valuable information to help defining robust biogeographical patterns, whose identification has become an urgent requirement for systematic conservation planning (Whittaker et al. 2005), especially in marine ecosystems, largely affected by fisheries and other anthropogenic disturbances (Lourie and Vincent 2004; Shears et al. 2008; Muller-Karger et al. 2017).

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Compliance with ethical standards

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

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Human and animal rights This article does not contain any studies with human participants. All fish and invertebrate specimen were collected in accordance with the guidelines of the state and federal collection permits granted for this study.

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