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Evaluating the usefulness of natural tags for host population structure in chondrichthyans: Parasite assemblages of *Sympterygia bonapartii* (Rajiformes: Arhynchobatidae) in the Southwestern Atlantic



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ABSTRACT

The usefulness of parasite tags for population discrimination of elasmobranch hosts remains largely unexplored. In order to assess the existence of different populations of *Sympterygia bonapartii* in the Southwestern Atlantic using its parasites as biological tags and to evaluate their usefulness as indicators for chondrichthyan hosts, we analysed data on assemblages of both long-lived and short-lived parasites of 193 skates distributed in eight samples caught at different seasons, years, depths and latitudes. A total of 6527 metazoan parasites, belonging to 19 species, was recorded. Only three species were long-lived, being therefore suitable biological tags, and they were used to assess the population structure of *S. bonapartii*. As a result, three host populations were identified (one Bonaerensean and two Patagonian). Distance-based multiple linear regressions (DistLM) evidenced that latitude was the most important predictor of parasite distribution, confirming the value of long-lived species as biological tags. When short-lived parasites were analysed, most samples differed from each other. Furthermore, a bathymetric rather than a latitudinal pattern was observed across samples, which was associated with reproductive migrations displayed by *S. bonapartii*. DistLM analyses showed that depth and year were almost as important as latitude as predictors of parasite distribution. This proves the little value of this guild as indicators of host population structure. Transient parasites could be acceptable to study seasonal migrations of their hosts, but it is recommended to avoid their use as tags for population assessment, either alone or combined with long-lived species. This is especially relevant for elasmobranch hosts, for which the numerical dominance of short-lived species in their parasite assemblages is the rule. Based on these results, and upon a careful selection of suitable species, we recommend using parasites as reliable and robust sources of information that provide significant data for the implementation of management measures that ensure the conservation, recovery and sustainable use of elasmobranchs under exploitation.

1. Introduction

Over the last decades, fishery pressure on chondrichthyans has been steadily increasing. Indeed, according to the official FAO statistics (2011–2014), the average declared value of total world imports was 123,960 tons per year from 2000 to 2011 (Dent and Clarke, 2015). Argentina is one of the largest suppliers of skate and ray meat, occupying the fifth place of chondrichthyan catches at the global level (Dent and Clarke, 2015). In fact, in 2015 Argentina exported 14,958 tons, the skates representing 98% of the total volume (Subsecretaría de Pesca y Acuicultura, 2016). Consequently, the area of the Southwestern Atlantic comprised by coastal waters of southern Brazil, Uruguay and Argentina, is one of the regions with the highest amount of threatened

chondrichthyan species, many of them batoids (Field et al., 2009). Indeed, a decline in the stocks of several species under exploitation has been recorded in Argentina during the last two decades (Massa and Hozbor, 2011).

Chondrichthyans are particularly vulnerable to overfishing due to a series of biological characteristics that result in a low reproductive potential and, consequently, in very low population growth rates, making them intrinsically sensitive to elevated fishing mortality (Dulvy and Forrest, 2010; Dulvy et al., 2014). These features are low growth, high age and size at maturity, extensive period of gestation and scarce number of large offspring (Stevens et al., 2000; Cortés, 2000; Dulvy et al., 2008, 2014; Field et al., 2009). In such kind of vulnerable resources, the implementation of management strategies is peremptory to

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avoid extinctions and promote population recovery and stock identification, involving the recognition of population structure of fishery resources is a necessary first step (Begg and Waldman, 1999; Cadrin et al., 2005).

The smallnose fanskate *Sympterygia bonapartii* Müller & Henle (1841) inhabits coastal and shelf waters from the State of Rio Grande do Sul, in Brazil to southern Argentina (Menni and Stehmann, 2000; Cousseau et al., 2007), being commercially exploited along its whole distribution (Mabragaña et al., 2002; Paesch and Domingo, 2003; Oddone and Velasco, 2004; Basallo and Oddone, 2014). This species was the most abundant rajid in coastal waters, between 34° and 41° S, and the only among several surveyed species showing stable levels of abundance between 1993 and 2005 (Massa and Hozbor, 2011). These results suppose that this species has been affected in a lesser extent than other resources, constituting a suitable model for studying its population structure.

Some previous studies have suggested the possible existence of different populations of *S. bonapartii* along its distribution range. Indeed, Basallo and Oddone (2014) propose the existence of two different populations, one in the coast of Argentina, and a second in the coastal zones of Uruguay and southern Brazil. More recently, Moya et al. (2015) defined specimens caught at the Bahía Blanca estuary (61°30′–62°30′W and 38°45′–39°20′S) as belonging to a “North Patagonian Population”, finding that size at maturity for males was clearly below the size reported by Mabragaña et al. (2002) in the neighbouring area of El Rincón. At present, no information on population structure of *S. bonapartii* is available beyond these weak evidences.

In the present work, we perform a parasitological study to assess the population structure of *S. bonapartii* in a large proportion of its distribution in the Southwestern Atlantic by using parasites as biological indicators. The use of parasite tags is increasingly applied worldwide for fish stock identification (Catalano et al., 2014; Timi and MacKenzie, 2015) and has been successfully applied previously to several fish in the study region (Cantatore and Timi, 2015). Among hundreds of publications on parasite tags, only a minor proportion has been devoted to chondrichthyan hosts (Timi and MacKenzie, 2015). According MacKenzie and Hemmingsen (2015), elasmobranchs are not obvious candidates for using natural tags for stock assessment due to their condition of top predators, which make them unsuitable hosts for long-lived larval parasites. A long residence time in the host is the most important characteristic for an effective parasite marker for stock discrimination (Lester and MacKenzie, 2009; Braicovich et al., 2016). Hence, short-lived parasites have little value for such purposes because they are acquired and lost as hosts move geographically (MacKenzie and Abaunza, 2005) and their temporal variability could be wrongly interpreted as geographical differences in parasite burdens. To the best of our knowledge, a few papers have used parasite tags for population assessment of selacean hosts (Moore, 2001; Yamaguchi et al., 2003; Isbert et al., 2015); therefore the value of parasite as indicators of population structure in chondrichthyans remains largely unexplored, especially taking into account the numerical dominance of short-lived parasites, whose value as natural tags needs to be assessed.

The aim of this study is therefore two-fold: (1) to assess the existence of different populations of *S. bonapartii* in the study area using its parasites as biological indicators and (2) to evaluate the usefulness of short-lived parasites as tags for such kind of studies on chondrichthyan hosts.

2. Materials and methods

2.1. Fish and parasites sampling

The data set comprises the parasite communities of eight samples of *S. bonapartii* from seven localities in the south-western Atlantic (Fig. 1), covering most of its distributional range in the Argentine-Uruguayan Common Fishing Zone (AUCFZ) and the Argentine Sea (Cousseau et al.,

2007) and including a total of 193 fish. Of these, six samples were obtained from the Bonaerensean district of the Argentine zoogeographic province and two from Patagonian gulfs in the Magellan province (Menni et al., 2010). The data sets are summarized in Table 1.

Fish were caught during research cruises or by the commercial fleet in a period of several years (2010–2015), but each sample was caught during periods ranging from a single day to two weeks in different seasons, except summer (Table 1). Data on latitude, and depth were recorded for those specimens caught during research cruises; in the case of commercial catches, the depth was estimated from the region of capture in a bathymetric map.

All skates were deep frozen in plastic bags at -18°C until examination. After thawing, the total length was measured (TL, cm). The total length of skates was compared between samples by means of a one-way ANOVA and a posteriori Tukey tests for unequal samples (Zar, 2004). The body surface, gills, fosal nostrils, branchial and body cavities, viscera (stomach, spiral valve, liver, spleen, heart, gonads and mesenteries), were examined with the aid of a stereoscopic microscope and parasites were recorded and counted.

Prevalence and mean abundance for each parasite species in each sample, as well as species richness and Brillouin's index of diversity (Magurran, 1988) for each infracommunity (sensu Bush et al., 1997) were calculated.

2.2. Similarity analyses at the infracommunity level

Because their proved value as biological tags for host population assessment, the analyses were carried out for long-lived parasites, then analyses were repeated for short-lived parasites (gastrointestinal parasites and ectoparasites) in order to evaluate their performance as biological indicators.

At the infracommunity level, the Bray-Curtis similarity matrices among individual skates were computed on square-root transformed abundance data in order to down-weight the importance of very abundant species so that the less dominant species play 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 multidimensional scaling (nMDS) of the Bray-Curtis similarity matrix was performed between all individual skates and their centroid differences were visualized 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 visualized in a nMDS using as many dimensions as needed to closely match the original distance matrix (correlation coefficient of $\rho = 0.99$; $m = 10$ dimensions).

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 (1×8 factorial design, ‘sample’ as fixed factor) were compared, testing for main effects after 9999 permutations and subsequent post-hoc pairwise 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). Due to the large number of skates found not parasitized by long lived parasites in some samples, the PERMANOVA analysis was based on a zero-adjusted Bray-Curtis similarity matrix (Clarke et al., 2006) for this group of parasites.

Because PERMANOVA is sensitive to differences in multivariate dispersion between 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

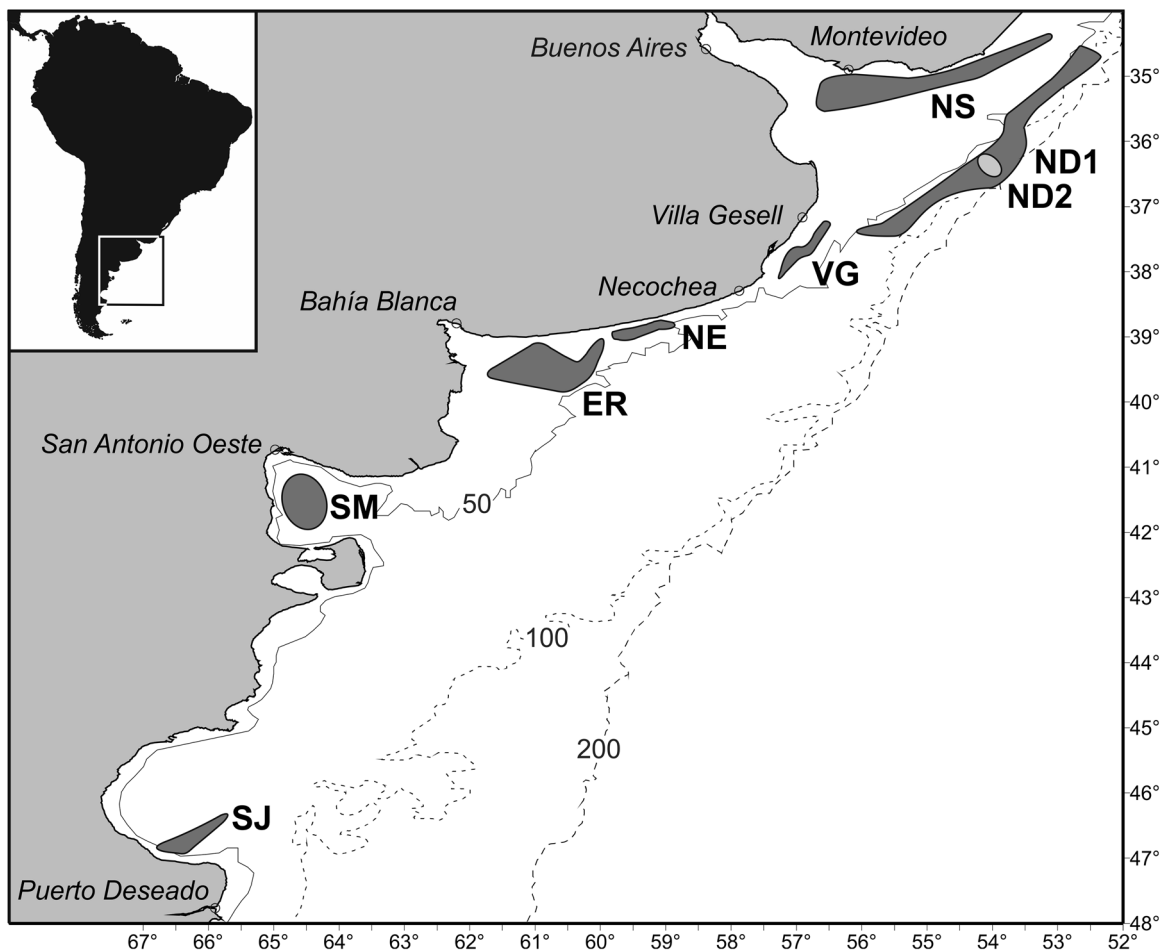


Fig. 1. Map showing the sampling localities (shaded areas) in the southwestern Atlantic Ocean. Locality codes indicated in Table 1.

Table 1
Composition of samples of *Sympterygia bonapartii* from the South West Atlantic coasts, ordered by increasing latitude.

Locality	Locality code	Date	Season	Mean depth (range) m	N	Mean TL \pm SD (range) cm
North shallow	NS	Dec 6–18th, 2013	Spring	22.4 (6–40)	18	64.9 \pm 4.1 (55.0–72.0)
North depth 1	ND1	May 16–28th, 2012	Autumn	83.8 (54–136)	33	56.9 \pm 5.5 (40.5–71.0)
North depth 2	ND2	Nov 28th, 2012	Spring	77.5 (64–100)	8	57.3 \pm 6.7 (48.3–65.0)
Villa Gesell*	VG	Sep 17–24th, 2010	Late winter-spring	30	30	64.5 \pm 4.2 (55.5–72.5)
Necochea*	NE	Nov 23–25th, 2010	Spring	20	44	54.3 \pm 4.3 (38.5–64.0)
El Rincón	ER	Dec 1–2nd, 2011	Spring	16.1 (13–44)	15	49.4 \pm 4.8 (42.0–57.0)
San Matías Gulf*	SM	Aug 14th, 2015	Winter	50	35	62.3 \pm 5.8 (50.0–71.0)
San Jorge Gulf	SJ	Aug 21th, 2012	Winter	52.2 (36–92)	10	58.5 \pm 5.9 (47.5–68.5)

N: number of examined hosts; TL: total length (cm); SD: standard deviation; * commercial catches with depth estimated from the region of capture using a bathymetric map.

distance to the centroid, and each term in the analysis was tested using 9999 permutations.

At the component community level, non-metric multidimensional scaling (nMDS) was also performed using the Bray-Curtis similarity index on prevalence data to visualize possible geographic patterns in the composition of parasite assemblages across the eight samples. A hierarchical agglomerative clustering was applied to the component communities using group-average linking, and resemblance levels were overlaid on the nMDS plot (Clarke and Gorley, 2015).

2.3. Linkage between parasitological data and host/abiotic variables

The relative contribution of host/abiotic variables on assemblage structure was assessed on Bray-Curtis distance matrices of prevalence and mean abundance for long-lived and short-lived parasites as described in the previous section, as well as on averaged Brillouin's index

of diversity and species richness for the eight samples, whose resemblance matrices were calculated based on Euclidean distances (Clarke and Gorley, 2015).

The associations between parasitological data and host/environmental variables were investigated using distance-based multiple linear regression (DistLM) (Anderson et al., 2008) with significance testing based on 9999 permutations.

Predictor variables included in the models were: mean host total length, latitude, depth, and season and year of capture, with the sample from Villa Gesell being assigned to spring. Changes in water temperature have been identified as the main cause of the migratory patterns of *S. bonapartii* in the study region (Mabragaña et al., 2002); unfortunately, no data on water temperature were available from commercial catches nor for some samples from research cruises, therefore this variable was not included in the models. However, water circulation in the south-west Atlantic is characterised by the southern

extension of the Brazil Current (warm and saline water flowing southwards along the continental margin) in the north and the Malvinas Current (cold, low-salinity subantarctic water flowing northwards at the edge of the Argentine shelf) in most of its extent (Piola and Rivas, 1997). The Malvinas Current dominates adjacent shelf waters, producing a latitudinal gradient of temperature which decreases southwards, whereas at the northern limit of the Argentine sea, the effect of the warm Brazil Current is marked (Guerrero and Piola, 1997). Latitudinal gradients in spatial distribution of parasite communities in marine fish are determined by water temperature (Rohde and Heap, 1998; Rohde, 1999), consequently, latitude was considered as a surrogate of the thermal gradient characteristic of the study area (Hoffmann et al., 1997).

Draftsman plots and correlation matrices were used to check for multicollinearity in the predictor variables. Models including all possible combinations of predictor variables were generated using the Best procedure within the DistLM routine. An information theoretic approach based on modified Akaike's Information Criterion (AICc), devised to handle situations where the number of samples (N) is small relative to the number (v) of predictor variables ($N/v < 40$) (Anderson et al., 2008), was used to identify the best model; being those with the lowest AICc considered as the most parsimonious (Symonds and Moussalli, 2011). The difference (Δ_i) between the AICc value of the best model and the AICc value for each of the other models was calculated; models with Δ_i between 0 and 2 are considered as having a substantial level of empirical support, being therefore as good as the best model (Burnham and Anderson, 2002), however as suggested by Richards (2005) models with Δ_i up to 6 should not be discounted, thus all models with $\Delta_i \leq 6$ were retained. For each of selected models, the Akaike weights (w_i) were calculated following Burnham and Anderson (2002) to identify and quantify the uncertainty in model selection and further used to estimate the relative importance of each predictor variable (predictor weight). For each predictor, the Akaike weights of all the models (with $\Delta_i < 6$) that contained that predictor were summed and that values were interpreted as the relative importance of that predictor. Indeed, those predictors occurring consistently in the most likely models have an w_i close to 1, whereas variables that are absent from or are only present in poorly fitting models (high AICc values) have an w_i close to 0 (Symonds and Moussalli, 2011). Also the relative strengths of each candidate model was assessed by calculating the evidence ratio (EvR), which provides a measure of how much more likely the best model is than alternative models (Burnham and Anderson, 2002).

All multivariate analyses were implemented in PERMANOVA+ for PRIMER7 package (Anderson et al., 2008; Clarke and Gorley, 2015).

3. Results

3.1. General results

Mean host length was significantly different between samples ($F_{7,183} = 19.26$; $P < 0.01$), with several pairs of samples being significantly different each other at $P < 0.01$, namely NS-ND1, NS-NE, NS-ER, ND1-VG, ND1-SM, VG-NE, VG-ER, NE-SM, and ER-SM. Other pairs of samples differed at $0.01 < P < 0.05$: ND1-ER and ER-SM.

The parasite fauna of *S. bonapartii* comprised 19 parasite species, 9 of which are new host records (Table 2). A total of 6527 metazoan parasites were counted, with a high proportion of them being represented by adult parasites (5706 specimens) belonging to 9 species of endoparasites and 8 of ectoparasites; a smaller proportion, 821 individuals, was composed by larval stages of 2 species of anisakid nematodes and considered as long-lived parasites inhabiting host tissues. The adult trematode *Otodistomum pristiphori*, a parasite of the coelomic cavity, was also considered as long-lived since it has no possibilities to be lost and specimens dead previous to capture remain identifiable.

Adult endoparasites were constantly dominant across samples from the northern region, but this guild was proportionally less abundant in

both Patagonian gulfs regarding ectoparasites and larval parasites (Fig. 2). The monogenean *Calicotyle macrocotyle*, from the cloaca and spiral valve, was counted as endoparasite.

Parasite burdens, in terms of prevalence and mean abundance, varied among the component communities from the considered zones (Tables 2 and 3). Only *C. macrocotyle* was present in all samples. Many parasites displayed high prevalences in some samples, but mean abundance were generally low. Long-lived parasites, which are more reliable for proper comparisons by diminishing possible effects of temporal variations on parasite loads and allowing the locality effects to be more evident, showed clear geographic patterns. Indeed, prevalence (Fig. 3a) and mean abundance (Fig. 3b) of *O. pristiphori* decreased southwards, whereas *A. simplex s.l.* and *Pseudoterranova sp.* showed the opposite pattern.

When infracommunity indices were analysed, a bathymetric rather than a latitudinal pattern was observed, with those fish caught at deeper waters (below the isobath of 50 m) harbouring more diverse (Fig. 4a) and richer (Fig. 4b) assemblages.

3.2. Similarity analyses

For all subsequent analyses at infracommunity level, skates harbouring no parasites (1 from NE and 1 from ER) were not considered. Some parasite species found at low prevalence in one or two samples (*G. patagonica*, *Piscicapillaria sp.*, *B. corniger* and *A. inflatus*) as well as skin parasites that can be easily lost during fishing and handling, especially in commercial catches, were excluded.

The bootstrap-average-based nMDS ordination (Fig. 5a) of long-lived parasites showed an apparent pattern of separation between samples, with a low level of stress (0.03). Indeed, the parasite assemblages from Patagonian gulfs (SM and SJ) were clearly separated from those in the Bonaerensean region, whereas the latter apparently composed a single group. Indeed their distribution patterns were very similar to the geographical position of catches (see Fig. 1). A better image of sample distribution is obtained by a three-dimensional nMDS (stress level = 0.01) (Supplementary Movie S1), where, however, skates from ER were separated along the third axis. A similar picture was observed when only short-lived parasites were analysed (Fig. 5b), with an acceptable level of stress (0.1). However, in this case, a bathymetric pattern was more evident across Bonaerensean samples, with those from deeper waters (ND1 and ND2) separated from those from shallower waters. Samples distribution in a three-dimensional nMDS (stress level = 0.05), in turn, showed an evident separation between some samples overlapped in Fig. 5b, with NS closer to ER than to VG (Supplementary Movie S2).

The results of PERMANOVA analyses on both long-lived and short-lived species (Table 4) showed a significant effect of host length on the response variables and an interaction between the host length and locality, 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.

In both analyses the pairwise tests agreed in general with bootstrap-average-based nMDS ordinations. Indeed, assemblages of both guilds in both Patagonian samples were significantly different from those in any other sample (Table 5). When only long-lived parasites were analysed (Table 5, above the diagonal), most samples from the Bonaerensean region were similar. Hence, despite no recurrent patterns of similarity were observed (i.e. ND2 was similar to both ND1 and VG, but the latter two samples were significantly different), the six samples from the northern region seem to conform a continuum, with each of them being similar to both closest neighbours. Differences in the multivariate dispersions can be partially responsible of such lack of pattern since PERMDISP results were highly significant ($F_{7,183} = 4.58$, $P(\text{perm}) < 0.001$), involving mainly the sample SM, which had the higher mean

Table 2Developmental stage, site of infection and prevalence of parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts (locality codes as in Table 1).

Parasites	Stage	Site	NS	ND1	ND2	VG	NE	ER	SM	SJ
Monogenea										
<i>Calicotyle macrocotyle</i>	Adult	Cloaca	38.9	63.6	50.0	56.7	84.1	80.0	62.9	90.0
<i>Empurthotrema</i> sp. ^a	Adult	Narine	0.0	60.6	62.5	16.7	0.0	33.3	48.6	50.0
<i>Acanthocotyle</i> sp. ^a	Adult	Skin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0
<i>Rajonchocotyle raiae</i> ^a	Adult	Gills	0.0	60.6	50.0	10.0	13.6	0.0	100	100
Digenea										
<i>Otodistomum pristiophori</i>	Adult	Body cavity	72.2	97.0	75.0	53.3	29.5	13.3	48.6	0.0
Cestoda										
<i>Heteronybelinia mattisi</i>	Adult	Stomach, spiral valve	11.1	15.2	12.5	16.7	11.4	13.3	0.0	30.0
<i>Rhinebothrium chilensis</i>	Adult	Spiral valve	44.4	0.0	0.0	3.3	11.4	40.0	80.0	60.0
<i>Dollfusiiella acuta</i>	Adult	Spiral valve	16.7	45.5	37.5	0.0	0.0	13.3	54.3	0.0
<i>Grillotia patagonica</i> ^a	Adult	Spiral valve	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0
Nematoda										
<i>Proleptus acutus</i>	Adult	Spiral valve	77.8	54.5	75.0	90.0	72.7	60.0	0.0	20.0
<i>Piscicapillaria</i> sp. ^a	Adult	Spiral valve	0.0	0.0	0.0	0.0	2.3	0.0	0.0	20.0
<i>Pseudanisakis argentinensis</i>	Adult	Stomach, spiral valve	0.0	27.3	50.0	23.3	11.4	0.0	71.4	70.0
<i>Anisakis simplex</i> s.l. ^a	Larve	Stomach Wall	0.0	21.2	37.5	10.0	27.3	0.0	85.7	80.0
<i>Pseudoterranova</i> sp. ^a	Larve	Stomach wall	0.0	0.0	0.0	0.0	2.3	6.7	45.7	20.0
Copepoda										
<i>Brianella corniger</i>	Adult	Narine	0.0	3.0	0.0	0.0	2.3	0.0	0.0	0.0
<i>Eudactylina parva</i> ^a	Adult	Gills	50.0	72.7	25.0	46.7	20.5	26.7	28.6	0.0
<i>Kroeyerina sudamericana</i>	Adult	Narine	0.0	6.1	0.0	0.0	9.1	20.0	0.0	0.0
<i>Acanthochondrites inflatus</i> ^a	Juvenile	Gills	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Hirudinea										
Piscicolidae gen. sp.	Adult	Skin	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0

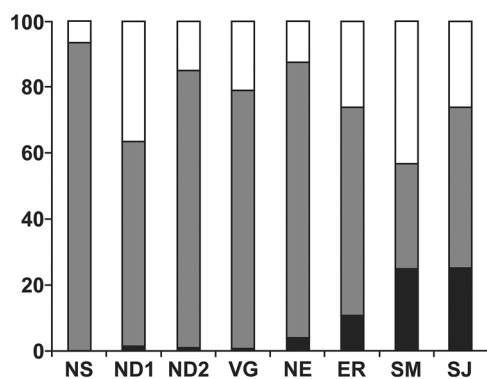
^a New host record.

Fig. 2. Relative abundance of three parasite guilds across eight samples of *Sympterygia bonapartii* in the South West Atlantic. Locality codes indicated in Table 1. White: ectoparasites; gray: adult endoparasites; black: larval endoparasites.

deviation from the centroid (3.23 ± 2.25).

When short-lived parasites were considered, the number of similar pairs of samples in the Bonaerensean region decreased, and a pattern related to depth was more evident. In this case, NS was no longer similar to those caught at similar latitudes (ND1 and ND2), but remained similar to ER. Other similarities in common with long-lived parasites were VG-NE and NE-ER; on the other hand NS-ER and ND2-ER were also similar. Again, PERMDISP results were highly significant ($F_{7,183} = 3.76$, $P(\text{perm}) < 0.01$), involving SM and SJ, which showed the lowest mean deviations from the centroid (33.90 ± 1.48 and 34.39 ± 1.77 , respectively).

The nMDS and cluster analyses to the component communities (prevalence data) when long-lived parasites were considered revealed an apparent pattern of separation between samples following a latitudinal sequence (Fig. 6a), with a low stress level (0.03) indicating a community composition substantially different from random. Two groups were clearly separated, one composed by the two samples caught in Patagonian waters with high similarity (71.43%) and the other by all samples from the Bonaerensean district, among them ER

branched first at low similarity level (19.30%), followed by NE (45%) and by a group of highly similar samples (69.78%). As expected by their prevalences (Fig. 3), *O. pristiophori* was related to Bonaerensean samples and both larval anisakids to the Patagonian localities.

In the case of short-lived parasites, and as observed for infra-communities, a bathymetric rather than a latitudinal pattern was evident (Fig. 6b), also with a low stress level (0.03). A higher similarity was observed among all samples (34.74%) but northern samples from deep waters (ND1 and ND2) grouped with Patagonian samples. The rest of Bonaerensean samples branched in two groups, apparently more related to the depth or the season of capture than to the geographic origin. Indeed, one group included those samples from shallower waters caught on late spring (December), namely NS and ER, and the other containing the central Bonaerensean localities (VG-NE). Most short-lived parasite species were related to skates caught in deeper waters, on the other hand *Proleptus acutus* and the copepods *Kroeyerina sudamericana* and *Eudactylina parva* were indicative of shallow waters. *Rhinebothrium chilensis* showed not a clear pattern, reaching the highest prevalences in the extremes the study area NS and SM-SJ.

3.3. Linkage between parasitological data and host/abiotic variables

Draftsman plots and correlation matrices showed not multicollinearity in the predictor variables and all variables were included in the models.

The results of the DistLM on the assemblage structure of long-lived parasites showed that for both prevalence and mean abundance the best model included only latitude as predictor variable (explaining 52.9% and 59.3% of the total variation of data, respectively, Table 6). In the case of prevalence values, the w_i indicated that PL1 has a 32.1% chance of being the best model and EvR showed that this model was more than twice more likely to be the best approximating model than the subsequent ones. Indeed, latitude was included in all models with $\Delta_i < 2$ (Table 6) and its predictor weight among models with $\Delta_i < 6$ indicated that this variable had the highest probability of being a component of the best model (Table 7). Regarding mean abundance, the w_i indicated

Table 3
Mean abundance (range) of parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts (locality codes as in Table 1).

Parasites	NS	ND1	ND2	VG	NE	ER	SM	SJ
Monogenea								
<i>Calicotyle macrocotyle</i>	2.56 (0–20)	2.39 (0–10)	4.88 (0–19)	2.13 (0–8)	3.59 (0–23)	5.40 (0–16)	2.66 (0–17)	1.80 (0–4)
<i>Empurthotrema</i> sp.	–	2.24 (0–14)	1.25 (0–4)	0.53 (0–5)	–	0–3 (0–9)	1.83 (0–13)	0.70 (0–2)
<i>Acanthocotyle</i> sp.	–	–	–	–	–	–	–	0.10 (0–1)
<i>Rajonchocotyle raiae</i>	–	5.09 (0–27)	2.75 (0–9)	0.10 (0–1)	0.38 (0–5)	–	28.37 (1–162)	9.30 (1–30)
Digenea								
<i>Otodistomum pristiophori</i>	8.94 (0–36)	9.58 (0–41)	12.25 (0–36)	2.43 (0–11)	1.36 (0–37)	0.47 (0–6)	3.69 (0–33)	–
Cestoda								
<i>Heteronybelinia mattisi</i>	0.39 (0–6)	0.55 (0–12)	0.26 (0–5)	0.55 (0–4)	0.27 (0–7)	0.27(0–3)	–	0.40 (0–2)
<i>Rhinebothrium chilensis</i>	17.00 (0–129)	–	–	0.03 (0–1)	0.16 (0–2)	1.13 (0–6)	5.89 (0–24)	14.00 (0–96)
<i>Dollfusiella acuta</i>	0.22 (0–2)	1.79 (0–14)	3.25 (0–19)	–	–	0.27 (0–3)	5.77 (0–53)	–
<i>Grillotia patagonica</i>	–	–	–	–	–	–	–	0.40 (0–4)
Nematoda								
<i>Proleptus acutus</i>	5.72 (0–38)	4.36 (0–28)	7.75 (0–40)	13.57 (0–64)	2.70 (0–26)	2.40 (0–16)	–	0.30 (0–2)
<i>Piscicapillaria</i> sp.	–	–	–	–	0.02 (0–1)	–	–	0.30 (0–2)
<i>Pseudanisakis</i> sp.	–	1.52 (0–14)	3.50 (0–13)	0.63 (0–7)	0.34 (0–7)	–	6.37 (0–28)	1.60 (0–6)
<i>Anisakis simplex</i> s.l.	–	0.42 (0–4)	0.38 (0–1)	0.10 (0–1)	0.36 (0–2)	–	17.89 (0–99)	9.10 (0–51)
<i>Pseudoterranova</i> sp.	–	–	–	–	0.02 (0–1)	1.64 (0–25)	1.06 (0–8)	0.50 (0–3)
Copepoda								
<i>Brianella corniger</i>	–	0.03 (0–1)	–	–	0.02 (0–1)	–	–	–
<i>Eudactylina parva</i>	2.44 (0–10)	4.30 (0–14)	1.38 (0–8)	4.50 (0–57)	0.70 (0–12)	3.00 (0–25)	2.94 (0–59)	–
<i>Kroeyeria sudamericana</i>	–	0.18 (0–5)	–	–	0.16 (0–2)	0.20 (0–1)	–	–
<i>Acanthochondrites inflatus</i>	–	0.03 (0–1)	–	–	–	–	–	–
Hirudinea								
Piscicolidae gen. sp.	–	–	0.38 (0–2)	–	–	–	–	–

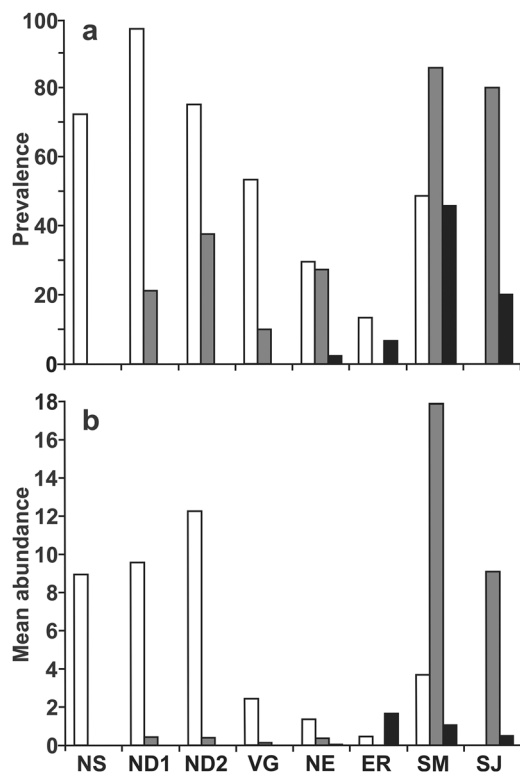


Fig. 3. Prevalence (a) and mean abundance (b) of three long-lived parasite species of *Sympterygia bonapartii* across eight samples in the South West Atlantic. Locality codes indicated in Table 1. White: *Otodistomum pristiophori*; gray: *Anisakis simplex* s.l.; black: *Pseudoterranova* sp.

that the first model has a 48.0% chance of being the best one and EvR showed that this model was more than 2.5 times more likely to be the best approximating model than the subsequent ones. Indeed, no models with $\Delta_i < 2$ were obtained (Table 6) and the predictor weight of latitude indicated that this variable had the highest relative importance

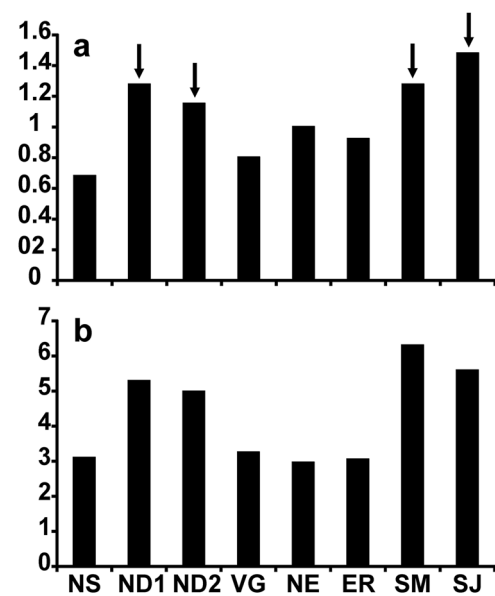


Fig. 4. Mean parasite infracommunity descriptors across eight samples of *Sympterygia bonapartii* in the South West Atlantic. a: Brillouin's index of diversity, b: Species richness. Arrowheads indicate samples caught at deep waters (below the isobath of 50 m). Locality codes indicated in Table 1.

(Table 7).

A different picture was observed when short-lived parasites were analysed. In the case of prevalence the best model included latitude and depth as predictor variables (explaining 70.1% of the total variation of data, Table 6). The w_i indicated that PS1 has a 24.6% chance of being the best model and EvR showed that this model was less than 1.6 times more likely to be the best approximating model than those models including a single variable (depth, latitude and year), all three with $\Delta_i < 2$ (Table 6). Predictor weights among models with $\Delta_i < 6$ indicated that latitude had the highest probability of being a component of the best model, but its relative importance was similar to that of

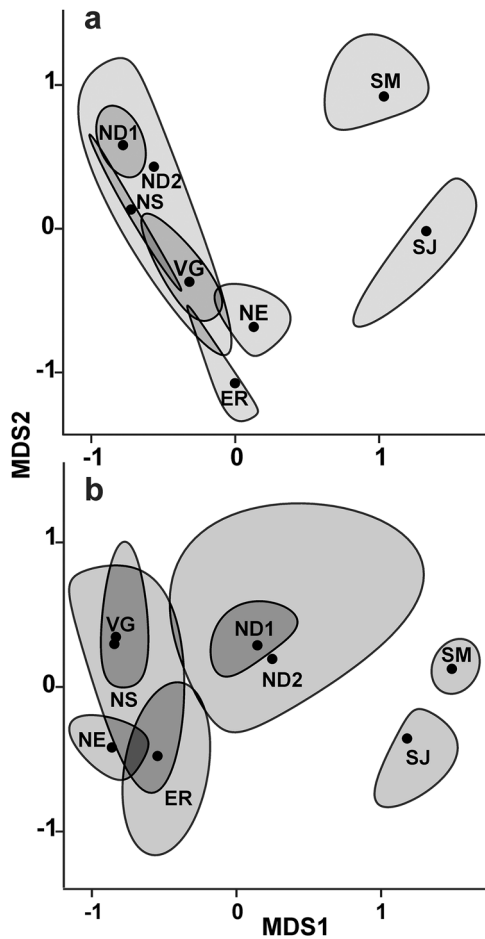


Fig. 5. Non-metric multi-dimensional scaling plot (nMDS) of bootstrap averages (50 repetitions) of parasite infracommunities in eight samples of *Sympterygia bonapartii* from the South West Atlantic based on Bray-Curtis similarity of square root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. a: long-lived parasites; b: short-lived parasites. Symbols represent the overall centroids across all repetitions. Boundary lines represent 95% confidence regions. Locality codes indicated in Table 1.

Table 4

One-factor PERMANOVA results of square-root transformed abundance of long-lived and short-lived parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts, based on the Bray-Curtis dissimilarity measure with host length as covariable. *P*-values obtained after 9999 permutations.

Data	Source	d.f.	SS	MS	Pseudo F	<i>P</i> (perm)
Long-lived parasites	Host length	1	102012	10212	13.909	< 0.001
	Locality	7	1.0893 e ⁵	15484	21.091	< 0.001
	Host length x Locality	7	12830	1832.8	2.4964	< 0.01
	Residual	175	1.2848 e ⁵	734.18		
	Total	190	2.5991 e ⁵			
Short-lived parasites	Host length	1	43477	43477	26.724	< 0.001
	Locality	7	1.5882 e ⁵	22689	13.946	< 0.001
	Host length x Locality	7	25558	3651.2	2.2443	< 0.001
	Residual	175	2.8471 e ⁵	1626.9		
	Total	190	5.1256 e ⁵			

depth and year (Table 7). When mean abundance, was analysed, the best model with $\Delta_i < 6$ included only year as predictor, explaining only 35.6% of the variation (Table 6) and having a 34.6% chance of being the best one. The three subsequent models were also composed by a single predictor, with depth and latitude showing $\Delta_i < 6$ and considerably higher values of w_i than the rest. According its predictor

Table 5

Values of t-scores of one-factor PERMANOVA post hoc pair-wise comparisons of square-root transformed abundance of parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts, based on the Bray-Curtis dissimilarity measure with host length as covariable. *P*-values obtained after 9999 permutations. Results of analyses based on long-lived and short lived parasites above and below the diagonal, respectively. Non-significant differences ($P > 0.01$) in bold. Asterisks show significant differences resulting of PERMDISP pair-wise comparisons between samples (P (perm) < 0.05). Locality codes as in Table 1.

	NS	ND1	ND2	VG	NE	ER	SM	SJ
NS	–	1.97	0.89	2.05	3.52	2.52	5.71	4.56
ND1	3.02	–	0.90	4.50*	6.90	5.65	6.22*	6.60
ND2	2.15	1.13	–	1.66	3.35	3.35	2.98	3.26
VG	2.04	3.41	2.48	–	1.16	0.78	6.73	3.82
NE	1.52	4.48	2.52	0.91	–	1.56	5.13*	3.26
ER	1.21	1.98	1.37	1.77	1.78	–	3.09*	2.46
SM	5.29*	4.19*	2.66*	7.23*	5.77	2.95	–	2.10
SJ	3.07*	3.09*	2.25*	3.55	3.69	2.36	1.97	–

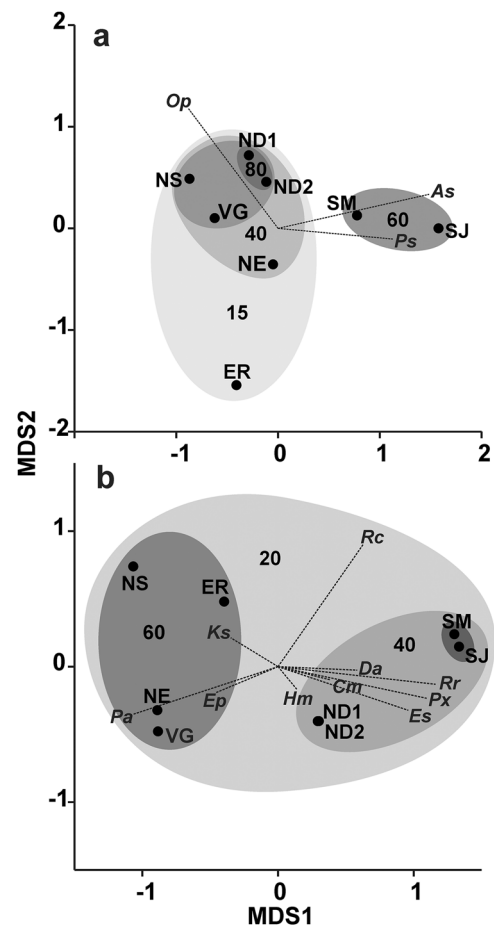


Fig. 6. Non-metric multi-dimensional scaling plot (nMDS) and cluster analyses of eight component communities (Bray-Curtis similarity on prevalence data) of *Sympterygia bonapartii* in the South West Atlantic. a: long-lived parasites; b: short-lived parasites. Results of a hierarchical agglomerative clustering 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 correlations of prevalence of individual parasite species with the nMDS axes. Locality codes as in Table 1. As: *Anisakis simplex* s.l., Cm: *Calicotyle macrocotyle*; Da: *Dolfusiella acuta*; Ep: *Eudactylina parva*; Es: *Empruthotrema* sp.; Hm: *Heteronybelinia mattisi*; Ks: *Kroeyerina sudamericana*; Op: *Otodistomum pristiophori*; Pa: *Proleptus acutus*; Ps: *Pseudoterranova* sp.; Px: *Pseudanisakis argentinensis*; Rc: *Rhinebothrium chilensis*; Rr: *Rajonchocotyle raiae*.

weight, the variable year had the highest relative importance, followed by depth and latitude both with similar relative importance (Table 7).

A single model explained the variability of both mean diversity and

Table 6

Summary table of the results of the DistLM analysis on assemblage structure of both long-lived and short-lived parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts, as well as on the averaged values of infracommunity species richness and diversity. Results are ordered by the modified Akaike information criterion and only those models with $\Delta_i < 6$ included.

Response variable	Model	AICc	R ²	Predictors	Δ_i	Wi	EvR
Prevalence long-lived parasites	PL1	59.036	0.529	3	0	0.352	–
	PL2	60.489	0.720	2, 3	1.453	0.170	2.068
	PL3	60.566	0.912	2, 1, 3	1.530	0.164	2.149
	PL4	60.918	0.704	1, 3	1.882	0.137	2.562
	PL5	62.426	0.643	3, 5	3.390	0.065	5.447
	PL6	63.309	0.197	1	4.273	0.042	8.470
	PL7	63.425	0.186	2	4.389	0.039	8.975
	PL8	63.893	0.136	5	4.857	0.031	11.342
Mean abundance long-lived parasites	AL1	57.978	0.593	3	0	0.480	–
	AL2	60.009	0.740	2, 3	2.031	0.174	2.761
	AL3	60.192	0.733	3, 5	2.214	0.159	3.025
	AL4	60.916	0.708	1, 3	2.938	0.111	4.345
	AL5	63.735	0.164	5	5.757	0.027	17.788
	AL6	63.906	0.146	2	5.928	0.025	19.375
	AL7	63.95	0.142	1	5.972	0.024	19.806
Prevalence short-lived parasites	PS1	55.967	0.701	2, 3	0	0.246	–
	PS2	56.472	0.359	3	0.505	0.191	1.287
	PS3	56.844	0.329	5	0.877	0.159	1.550
	PS4	56.891	0.325	2	0.924	0.155	1.587
	PS5	57.545	0.636	3, 5	1.578	0.112	2.201
	PS6	57.998	0.881	2, 3, 5	2.031	0.089	2.761
	PS7	59.241	0.550	2, 5	3.274	0.048	5.140
Mean abundance short-lived parasites	AS1	57.033	0.356	5	0	0.346	–
	AS2	58.363	0.239	2	1.330	0.178	1.944
	AS3	58.595	0.217	3	1.562	0.159	2.184
	AS4	59.658	0.105	1	2.625	0.093	3.715
	AS5	60.147	0.528	2, 5	3.114	0.073	4.745
	AS6	60.261	0.521	3, 5	3.228	0.069	5.023
	AS7	61.127	0.466	2, 3	4.094	0.045	7.745
	AS8	61.52	0.439	1, 5	4.487	0.037	9.426
	AS9	62.755	0.346	1, 3	5.722	0.020	17.479
	AS10	62.827	0.334	1, 2	5.794	0.019	18.120
Mean Species Richness	SR1	–4.204	0.975	2, 3, 5	–	1	–
Mean Diversity	MD1	–32.565	0.931	2, 3	–	1	–

AICc: modified Akaike information criterion; R²: proportion of explained variation for the model; Predictor variables: 1-host length, 2-depth, 3-latitude, 4-season, 5-year; Δ_i : difference between the AICc value of the best model and the AICc value for each of the other models; Wi: Akaike weight; EvR: evidence ratio.

Table 7

Relative Akaike weight of those predictor variables included in models with $\Delta_i < 6$ explaining assemblage structure of both long-lived and short-lived parasites of *Sympterygia bonapartii* in eight samples from the South West Atlantic coasts, as well as on the averaged values of infracommunity species richness and diversity.

Predictory variable	Long-lived parasites		Short-lived parasites	
	Prevalence	Mean abundance	Prevalence	Mean abundance
Mean host length	0.343	0.135	0.000	0.169
Depth	0.373	0.199	0.538	0.315
Latitude	0.888	0.924	0.638	0.292
Year	0.096	0.186	0.408	0.525

mean species richness (97.5 and 93.1%, respectively) across samples, with all other models showing $\Delta_i > 6$. The combined explanatory variables composing these models were depth, latitude and year for diversity and depth and latitude for species richness (Table 6).

None of the models with $\Delta_i < 6$ included season as explanatory variable for the response variables considered.

4. Discussion

This work extends the list of *S. bonapartii* parasites adding 9 species to previous records (Ostrowski de Núñez, 1971; Tanzola and Botté, 1998; Tanzola et al., 1998; Menoret and Ivanov, 2013, 2015; Irigoitia et al., 2016, 2017). In terms of species richness, the parasitofauna was dominated by copepods and platyhelminthes (mostly monogeneans and cestodes), which is the generalized pattern for elasmobranchs (Caira and Healy, 2004). Two species of larval anisakid nematodes were also registered as true parasites of skates. Due to their long persistence in fish tissues, larval anisakids are considered to be suitable biological tags worldwide and in the study region in particular, where they display significant latitudinal patterns (Timi, 2003, 2007). The adult trematode *O. pristiophori*, found in the coelomic cavity of rays, was a third long-lived species. These three long-lived species were used to discriminate populations of *S. bonapartii*. On the other hand, a set of short-lived species (gastrointestinal parasites and ectoparasites), present in skates at high prevalence and abundance, provided the possibility of evaluating their usefulness as biological tags after comparing the results with those to long-lived species.

The geographic patterns displayed by *A. simplex s.l.* and *Pseudoterranova* sp. (increased burdens southwards) are consistent with the findings of previous papers on bony fishes in the region (Timi et al., 2014; Cantatore and Timi, 2015). These gradual latitudinal changes, in combination with the opposite pattern revealed by *O. pristiophori*, resulted in a clear separation of samples. In fact, the results of all analyses of long-lived parasites evidenced noticeable differences between Bonaerensean and Patagonian samples. This is a common pattern of population structure across fishes in the study region, where all previous studies using parasite tags, some of them corroborating ichthyologic evidences, have arrived to similar results when comparing these regions (Cantatore and Timi, 2015; Lanfranchi et al., 2016).

Despite the high similarity between component communities from both Patagonian gulfs (samples from SM and SJ), the significant differences obtained in PERMANOVA analysis suggest the presence of discrete populations of *S. bonapartii* at these localities, with fish from SM showing higher abundance of the three parasite species. This is an expected result since San Matías Gulf is an isolated coastal basin. Its oceanographic conditions markedly differ from those on the continental shelf (Gagliardini and Rivas, 2004), because the geomorphology of the gulf mouth restricts the interchange of water with open sea (Piola and Rivas, 1997). Indeed, previous works on parasite tags have shown that discrete populations of several bony fish species inhabit in this gulf (Sardella and Timi, 2004; Braicovich and Timi, 2008; Timi et al., 2010a).

On the other hand, comparisons of infracommunity structure of long-lived parasites in the Bonaerensean region provided no conclusive evidence of similarity across samples. Despite these samples apparently compose a continuum, suggesting that a third population of *S. bonapartii* inhabits the Bonaerensean waters, some inconsistencies in their patterns of similarity were observed. In fact, results of similarity analysis at component community level also revealed a high difference between skates from ER and the rest of Bonaerensean samples. This result can be attributed to a methodological issue, since skates from ER were the smallest of the whole sample, most of them being juveniles, and nMDS does not allow making “corrections” according to fish length. Host size is one of the most important determinant of parasite community structure in fish, with increases in both parasite abundance and species richness in larger hosts being a common feature of fish-parasite systems (Poulin, 2000, 2004; Timi et al., 2010b; Timi and Lanfranchi, 2013), especially for long-lived parasites (Braicovich et al., 2017). Therefore the smaller size of the skates from ER can account by the lower values of *O. pristiophori* and the absence of *Anisakis simplex s.l.* observed in this locality. Beyond the size, the condition of “juvenile” of hosts from ER can also be responsible for the different parasite burdens registered. Nursery areas of this species are located in near-shore

estuarine waters (El Rincón and Río de la Plata estuary) and juveniles occur in coastal waters only < 50 m depth, while sub-adult and adult skates also live in the continental shelf (Mabragaña et al., 2002). The broader habitat of adult fish, including marine and estuarine waters, exposes them to a wider spectrum of infective stages, and increases the likelihood of parasite transmission compared to juveniles.

DistLM results showed that latitude, as a surrogate of water temperature, was largely responsible for the distribution of long-lived parasites across samples, for both prevalence and mean abundance. This leads to differential assemblage structure in the regions with contrasting oceanographic conditions covered by this study. In the case of prevalence, another spatial variable (depth) had also some influence on assemblages. As regards host size, it played an expectable role due to the cumulative nature of infestations by long-lived parasites (Braicovich et al., 2017). However the effect of the variable “year” was almost negligible, indicating that persistent parasites do not undergo short-term temporal variations, which supports their value as natural tags of host distribution.

In agreement with the latitudinal patterns displayed by long-lived parasites, infracommunities of short-lived parasites found in both Patagonian samples were significantly different from each other and from Bonaerensean ones. The latter, however and in contrast to long-lived species, evidenced a bathymetric rather than a latitudinal pattern. Nevertheless, the number of pairwise differences between samples increased, which cast doubts on its value as biological tags at larger geographic scale. This bathymetric pattern was enhanced by analyses at component community level, whit samples from deeper localities of the north (ND1 and ND2) which were more similar to Patagonian ones than to the rest of those found in the Bonaerensean region, considered as members of the same skate population by previous analyses.

These results are consistent with a migratory cycle displayed by *S. bonapartii*. The egg-laying period of this species is limited to spring and summer seasons. It is restricted to coastal waters in estuarine areas where adults concentrate for reproducing and feeding on estuarine benthic invertebrates, spreading over the coastal area down to 50 m in winter (Mabragaña et al., 2002). Skates and their parasites face drastic changes in environmental conditions during their migratory cycle. Indeed, moving between deep and shallow waters in the Bonaerensean region implies alternating between marine and estuarine environments, with concomitant changes in temperature and salinity. These changes can affect the transmission and survival of parasites, especially for short-lived ectoparasitic and gastrointestinal species. In fact, ectoparasites, which are in direct contact with sea water and display direct life-cycles are highly sensitive to changes in environmental conditions; e.g., parasitic copepods are recognized as highly stenohaline (Cavaleiro and Santos, 2009). As regards adult endoparasites, it is expectable not only a direct effect of physical conditions, but also an indirect one on all hosts involved in their life-cycle in a given area, because they generally display complex life-cycles and are transmitted trophically. Therefore, environment-related changes in the availability of infective stages in the population structure of intermediate hosts and in feeding habits of the host will result in differential composition of parasite assemblages.

From a zoogeographical perspective, bathymetric displacements during the migratory cycle lead *S. bonapartii* to alternate between two biogeographical provinces, the Argentine Province (coastal and shelf waters) and the Magellanic Province, which at these latitudes extends northwards along the slope, bordering the shelf waters. These provinces are characterised for presenting different assemblages of rajid species (Menni et al., 2010), which could act as alternative hosts for some of the little specific parasites of *S. bonapartii*, increasing the bathymetric differences of its parasitefauna. Although the specificity of most parasites requires further assessment, the similarity in component communities of short-lived parasites between northern deep (ND1 and ND2) and Patagonian (Magellanic) samples seems to support this hypothesis.

Although DistLM analyses showed that latitude was a relevant predictor of the distribution for short-lived parasites, its relative weight

decreased in relation to depth and year. Indeed, latitudinal patterns were clouded by bathymetric changes in parasite community structure related to host migratory cycles and by temporal variability. Depth and year, therefore, enhance differences when parasites of this guild are compared, leading to wrong conclusions on host population structure.

Despite the fact that seasonal cycles are often reported for parasites of elasmobranchs (Henderson et al., 2002; Pickering and Caira, 2014), in this study, seasons did not account for any variability in multivariate similarity. This could have been caused by an unbalanced distribution of samples across seasons since research cruises were designed for evaluating other fishery resources, but also because the influence of depth during migrations was stronger as a driver of community structure. Seasonal variations in abiotic conditions can impose strong pressure on parasite populations, modulating population fluctuations (Altizer et al., 2006) through influencing the transmission and survival of free-living stages, either directly or through the effects on other hosts involved in their life cycles (Pietrock and Marcogliese, 2003). The same causes are attributed here to the changes observed during bathymetric migrations. Nevertheless, the two samples caught at the same region (ND1 and ND2) but at different seasons (autumn and spring) were fairly similar across all analyses, corroborating the little influence of short-term temporal variations. A migratory behaviour, such as that shown by *S. bonapartii*, is rather unusual among skate species which, with few exceptions, inhabit mid-shelf or slope waters year-round being not commonly associated with estuaries (Mabragaña et al., 2015). Therefore, the effect of seasonal environmental fluctuations on parasite populations requires further research in the area, which should include other non-migrant skate species in order to assess the seasonal repeatability of these systems to establish their predictability and reliability as tools for delineation of host populations.

Beyond the cyclic nature of fluctuations in environmental conditions under a seasonal dynamic, there is also a growing evidence of the importance of multiyear oscillations, and even chaotic dynamics on parasite populations (Altizer et al., 2006), which should be more pronounced for short-lived species. In fact, the temporal variable year was a relevant determinant of data variability on transient parasites, indicating that, even if short-lived parasites were seasonally stable, their use as markers of host population structure should be restricted to a single year.

Regarding infracommunity descriptors, latitude, depth and year combined were also the best predictors of diversity, and the first two, of species richness. Both infracommunity descriptors increased with depth, a pattern mostly determined by short-lived parasites. The differential effect of spatial and temporal factors on the life history and transmission strategies of individual short-lived parasite species results in highly variable assemblages and increased differences across samples. Therefore, when analysed together, patterns displayed by suitable biological tags are hidden by the effect of more variable short-lived parasites as a consequence of the numerical dominance of the second guild when whole infracommunities are considered.

In synthesis, the parasitological evidence suggests that three populations of *S. bonapartii* can be identified in the study region by using long-lived parasite tags, one Bonaerensean and two Patagonians. On the other hand, the possibility of a discrete population living in ER requires further research including larger, adult skates. The distribution patterns of two of these species are consistent with those recorded for them in several species of bony fishes (Cantatore and Timi, 2015). This confirms their value for the host population assessment despite the low species richness of this guild. On the other hand, whereas *S. bonapartii* short-lived parasites could be acceptable to study seasonal migrations of their hosts, as proved for other host-parasite systems (MacKenzie and Abaunza, 2005), they are of little value as indicators of host population structure. As indicated by Lester and MacKenzie (2009) for transient parasites of fishes in general, their use as tags should be avoided for population assessment, either alone or combined with long-lived species. This suggestion is especially relevant for elasmobranch hosts, since

numerical dominance of temporary species in their parasite assemblages is the rule.

Commercial fishing is having an increasing impact on shark and ray populations, whose extinction risk, due to their vulnerability to fisheries pressures, is substantially higher than that of most other vertebrates (Dulvy et al., 2014). It is therefore necessary a precise assessment of abundance in space and time of these resources in order to implement management measures that ensure the conservation, recovery and sustainable use of elasmobranchs under exploitation. A required first step for such purpose is the knowledge about their population structure, and parasites, after a cautious selection of suitable species, are as reliable and robust tools for elasmobranch hosts as has been proved for teleost fish (Poulin and Kamiya, 2015; Timi and MacKenzie, 2015).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2017.07.006>.

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