



Ecotonal marine regions – ecotonal parasite communities: helminth assemblages in the convergence of masses of water in the southwestern Atlantic Ocean



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ABSTRACT

With the aim of evaluating the utility of marine parasites as indicators of ecotonal regions in the marine environment, we analysed data on assemblages of long-lived larval parasites of *Zenopsis conchifer* inhabiting the region of convergence of three masses of water in the southwestern Atlantic Oceans. These masses of water with different origins are expected to affect the structure of parasite communities by acting as sources of infective stages of helminth species typical of adjacent zoogeographical regions. Multivariate analyses at both infracommunity and component community levels, including data of four other species recognised as harbouring parasite assemblages representatives of these zoogeographical regions, were carried out to corroborate the existence of repeatable distribution patterns and to provide further evidence of the utility of parasites as zoogeographic indicators in the region. Results showed a tight correspondence with the existing zoogeographical classification in the study region, namely two zoogeographical provinces, one of which is subdivided into two districts demonstrating the ecotonal nature of parasite assemblages from the convergence region, which were characterised by a species rich component community but depauperate and heterogeneous infracommunities. The borders of biological communities have been suggested as priority areas for conservation where a fully functioning ecosystem can be protected and parasite communities can be considered as reliable indicators to define such transitional regions.

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1. Introduction

As integral components of marine ecosystems, parasitic organisms represent useful tools to explore the origins, distribution and maintenance of biodiversity (Hoberg and Klassen, 2002). Indeed, parasites are considered excellent indicators of present day and historical biogeography of their hosts at different spatial and temporal scales (Brooks and Hoberg, 2000; Waltari et al., 2007). However, relatively few studies have used parasites as indicators of zoogeographical regions in the marine realm (Rohde, 2002), with some studies failing to find a fit of parasite distributions into known zoogeographical regions (Byrnes and Rohde, 1992; González and Moreno, 2005; Marques et al., 2009), whereas others succeeded in defining zoogeographic areas congruent with those

previously established on the basis of the distribution of free living organisms (Blaylock et al., 1998, 2003; González et al., 2006).

Recently, Cantatore and Timi (2015) concluded that low host-specific parasites, defined as those parasitizing fish hosts belonging to different families, can provide information to delineate ecosystem boundaries for host communities, and therefore can help to identify the zoogeographical provinces of origin of samples in the southwestern Atlantic Ocean. Similarly, Pereira et al. (2014) proposed that these parasites can be used as indicators of ecoregions and of higher levels of biogeographic classifications in the same region. This hypothesis was later corroborated by Braicovich et al. (in press), who also suggest that the existence of repeatable distribution patterns across different host species will provide further evidence of the utility of parasites as zoogeographic indicators in the region.

Shelf waters along the Atlantic coasts of southern Brazil, Uruguay and Argentina are classified into two biogeographical

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provinces (Fig. 1), namely the Argentine Province, also called the Temperate Western South Atlantic Province, with two districts (southern Brazilian and Bonaerensean) and the Magellanic Province (Menni et al., 2010), although variable limits and subdivisions are proposed by different authors (Spalding et al., 2007; Balech and Ehrlich, 2008; Menni et al., 2010). Pereira et al. (2014) identified a set of larval helminths that characterise both districts of the Argentine Province, similarly Cantatore and Timi (2015) determined those parasite species useful as indicators of the Magellanic and Argentine provinces. All these parasites are mostly low host-specific and therefore can be useful biological indicators of the distribution of many fish species in the region (Cantatore and Timi, 2015).

The utility of parasites as geographical indicators depends on their distribution patterns which, in marine environments, are determined mainly by the characteristics of the masses of water where they live, especially those related to temperature and salinity profiles (Esch and Fernández, 1993), although for parasites with indirect life cycles, an additional requirement is that suitable hosts for all the developmental stages must be present (MacKenzie and Abaunza, 1998). These physical conditions provide sets of suitable conditions that ensure successful transmission and the completion of parasites life cycles, defining their endemic areas (MacKenzie and Abaunza, 2013). Changes in any physical factor, or in their combinations along a geographic or environmental gradient, will produce shifts in parasite loads at population and community levels, which are the basis for the use of parasites as biological indicators of host population structures (Timi and MacKenzie, 2015). However, the discriminatory power of parasite tags could be diminished in ecotonal regions where different masses of water converge, which often represent interface zones between zoogeographical areas in the marine realm and where fish could acquire parasites characteristic of different origins.

The guild of low host-specific and trophically transmitted larval endoparasites, composed by long-lived helminths (anisakid nematodes, cestodes and acanthocephalans), dominates parasite assemblages in the Bonaerensean District (Timi and Lanfranchi, 2009, 2013; Rossin and Timi, 2010; Timi et al., 2010, 2011) and should be expected to characterise the parasite communities in any fish living at these latitudes. However, in this region there is an area

with complex and variable oceanographic conditions, located off the coast, on the continental slope around the 38°S in the Argentine–Uruguayan Common Fishing Zone, where hydrographical features are driven mainly by the confluence of two opposite currents, the poleward flowing Brazil Current, carrying subtropical waters and the equatorward flowing Malvinas Current composed of subantarctic waters (Acha et al., 2004; Piola et al., 2010), which extends northwards of the Magellanic Province along the slope, bordering shelf waters. The resulting pattern of the surface circulation is the existence of a strong thermohaline front associated with the formation of meanders and eddies, a complex pattern that also extends in the deep layers along the continental slope (Provost et al., 1995; Maamaatuaiahutapu et al., 1998). The convergence of these masses of water with different origins could produce changes in the parasite communities at these latitudes, acting as sources of infective stages of helminth species typical of other zoogeographical regions.

This hypothesis is tested here by analysing the parasite fauna of the silvery John dory *Zenopsis conchifer* Gill, 1862 caught in the ecotonal region of convergence between Brazil and Malvinas Currents. *Zenopsis conchifer* is a deep-sea demersal species that occurs in the Atlantic and Indian Oceans (Zidowitz et al., 2002). In the southwestern Atlantic Ocean the austral limit of this species is the northern Argentine Sea (Zidowitz et al., 2002), where it is a typical inhabitant of upper-slope bottoms and seamounts (Haimovici et al., 1994; Martins and Schwingel, 2012). Data on parasites of *Z. conchifer* are comparatively analysed in relation to other fish species, previously studied simultaneously in the zoogeographic provinces/districts that converge in this region. The finding of recurrent patterns of parasite distribution across fish species will confirm both their value as zoogeographical indicators in the southwestern Atlantic Ocean and the identity of those species to be selected as biological tags in future studies.

2. Materials and methods

2.1. Fish and parasites sampling

A total of 44 specimens of *Z. conchifer* were examined for parasites (Table 1). Fish were caught by trawl during a research cruise at the Argentine–Uruguayan Common Fishing Zone (35°32′–35°35′S; 53°06′–53°25′W) at depths between 94 and 117 m, in October 2011. Fish were either kept fresh or deep frozen in plastic bags at –18 °C until examination. After defrosting, each fish was measured for total length (cm). Parasites were recovered from the body surface, gills, branchial and body cavities, and viscera (stomach, intestine, liver, gonads and mesenteries) after examination under a stereoscopic microscope. Prevalence and mean abundance were calculated for each parasite species following Bush et al. (1997).

To reveal recurrent distribution patterns of parasites across host species, additional samples of four fish species from different habits, sizes and trophic levels were included in multivariate analyses. Data on these samples, totalling 466 examined fish, most of them previously published by the authors, are summarised in Table 1. Only those fishes parasitised by at least one species of long-lived and low host-specific parasite (Table 2) were included in the analyses. Long-lived parasites, namely those found at larval stages in body cavity or tissues, were chosen because samples were caught in different seasons and years and these species, which persist for long periods or even for the entire life of hosts, are more reliable for proper comparisons, reducing possible effects of short-term temporal variations on parasite loads and allowing the locality effects to be more apparent. Low host-specific parasites were selected because they are capable of infecting any of the analysed fish species, and therefore can show recurrent patterns of

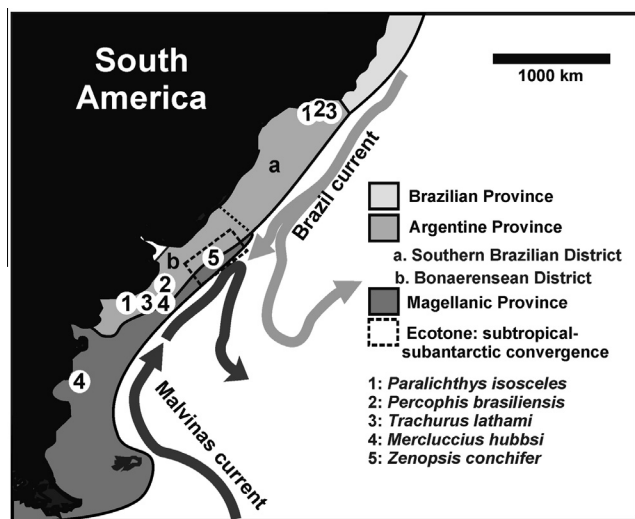


Fig. 1. Map showing the sampling localities for each host species (numbers) in the southwestern Atlantic Ocean. Shaded areas show the biogeographic provinces and letters (a, b) show the districts of the Argentine Province according Menni et al. (2010). Brazil (subtropical) and Malvinas (subantarctic) currents are indicated by arrows.

Table 1

Composition of samples of five fish species and their biogeographical origin in the southwestern Atlantic Ocean.

Host species	N	TL ± S.D. (cm)	Biogeographical province	Biogeographical district	Habitat	Source
<i>Zenopsis conchifer</i>	44	27.4 ± 4.99	Ecotonal zone	–	Deep-sea demersal	Present study
<i>Paralichthys isosceles</i>	40	31.3 ± 1.40	Argentine	Southern Brazilian	Benthic	Alarcos et al. (2016)
<i>Paralichthys isosceles</i>	51	27.9 ± 2.11	Argentine	Bonaerensean	Benthic	Alarcos et al. (2016)
<i>Percophis brasiliensis</i>	40	39.9 ± 2.14	Argentine	Southern Brazilian	Demersal	Braicovich et al. (in press)
<i>Percophis brasiliensis</i>	48	37.9 ± 4.34	Argentine	Bonaerensean	Demersal	Unpublished data
<i>Trachurus lathami</i>	50	19.3 ± 0.60	Argentine	Southern Brazilian	Pelagic	Braicovich et al. (2012)
<i>Trachurus lathami</i>	145	20.0 ± 0.71	Argentine	Bonaerensean	Pelagic	Braicovich et al. (2012)
<i>Merluccius hubbsi</i>	42	43.5 ± 3.50	Argentine	Bonaerensean	Demersal	Unpublished data
<i>Merluccius hubbsi</i>	50	41.8 ± 3.45	Magellanic	–	Demersal	Unpublished data

TL, total length.

Table 2

Prevalence and mean abundance of low host-specific and long-lived larval helminths in four fish species from different zoogeographical regions in the southwestern Atlantic Ocean.

Parasites	<i>Paralichthys isosceles</i>				<i>Percophis brasiliensis</i>				<i>Trachurus lathami</i>				<i>Merluccius hubbsi</i>			
	SB		Bo		SB		Bo		SB		Bo		SB		Bo	
	P	MA	P	MA	P	MA	P	MA	P	MA	P	MA	P	MA	P	MA
<i>Grillotia carvajalregorom</i>	59.6	30.77	100	332.39	90.0	7.35	100	255.56	96.0	4.02	100	172.20	97.6	100.69	38.1	0.84
<i>Grillotia patagonica</i> ^a	–	–	–	–	–	–	–	–	–	–	–	–	4.8	0.05	16.8	0.60
<i>Callitetrarhynchus gracilis</i> ^a	–	–	–	–	2.5	0.03	–	–	26.0	0.32	–	–	–	–	–	–
Tentaculariidae gen. sp.	32.7	1.30	58.8	6.08	17.5	0.25	27.1	0.38	4.0	0.06	–	–	–	–	–	–
<i>Hysterothylacium aduncum</i>	–	–	11.7	0.12	–	–	–	–	–	–	20.7	0.28	42.9	0.67	98.2	11.00
<i>Hysterothylacium</i> sp.	73.1	28.12	37.2	0.63	87.5	5.32	66.7	2.25	88.0	21.44	11.0	0.15	50.0	2.02	–	–
<i>Anisakis simplex</i> s.l.	11.5	0.22	–	–	–	–	4.2	0.04	4.0	0.08	4.1	0.05	52.4	1.36	98.2	46.96
<i>Contraecum pelagicum</i>	–	–	51.0	1.37	–	–	–	–	8.0	0.16	36.5	1.02	–	–	–	–
<i>Contraecum</i> sp. 1	–	–	–	–	–	–	–	–	–	–	–	–	97.6	85.71	85.0	41.50
<i>Contraecum</i> sp. 2	–	–	–	–	–	–	–	–	–	–	–	–	9.5	0.14	62.8	7.66
<i>Terranova galeocerdonis</i>	–	–	–	–	5.0	0.05	–	–	4.0	0.04	6.2	0.16	–	–	–	–
<i>Pseudoterranova cattani</i> ^a	–	–	2.0	0.02	–	–	–	–	–	–	–	–	–	–	–	–
<i>Raphidascaris</i> sp. ^a	44.2	2.68	–	–	17.5	0.18	–	–	84.0	3.54	–	–	–	–	–	–
<i>Corynosoma australe</i>	–	–	92.2	14.7	2.5	0.03	89.6	9.15	–	–	91.0	8.85	90.5	27.74	26.5	0.70
<i>Corynosoma cetaceum</i>	–	–	–	–	2.50	0.03	56.25	2.10	–	–	9.7	1.14	9.5	0.10	–	–
<i>Bolbosoma turbinella</i>	25.0	0.6	–	–	7.5	0.08	–	–	66.0	1.98	–	–	16.7	0.17	–	–

Bo, Bonaerensean district of the Argentine Province; Ma, Magellanic Province; SB, South Brazilian district of the Argentine Province; P, prevalence; MA, mean abundance.

^a Species not found in *Zenopsis conchifer*.

distribution. According to their geographic location, samples were assigned to two biogeographic provinces (Argentine or Magellanic) and to two districts within Argentine Province (southern Brazilian and Bonaerensean) as well as to the transitional zone of convergence between Brazil and Malvinas Currents (Table 1; Fig. 1).

2.2. Similarity analysis

Similarity in parasite species composition was computed at the component community level (Bush et al., 1997) using data on prevalence and mean abundance. Due to the large differences in values of mean abundance across parasite species (Table 2), data were square-root transformed in order to down-weight the importance of very prevalent/abundant species so that the less dominant species played some role in determining similarity amongst samples (Clarke and Gorley, 2015). The Bray-Curtis similarity index (Magurran, 1988) was calculated between all possible pairs of component communities (host species and zones). Non-metric multidimensional scaling analyses (nMDS) (Clarke and Gorley, 2015) were performed to visualise the geographic patterns in the composition of parasite assemblages across component communities. In all cases, the fit of the MDS ordinations was quantified by a value of stress. An indication of the underlying species differences in community structure was obtained by the strength of their correlation with nMDS axes, visualised using vector overlays based on Pearson correlations.

Hierarchical agglomerative clustering of samples was applied to similarities using group-average linking (Clarke and Gorley, 2015) and a similarity profile test after 9999 permutations (SIMPROF, Clarke et al., 2014) was undertaken to determine whether the differences seen in the cluster analysis were significant, representing natural group structure in the samples. The dendrograms of clusters and those groups significantly different in the SIMPROF analyses were overlaid on the nMDS plot to integrate the results of both analyses.

Similarity in parasite species composition was also computed at the infracommunity level (Bush et al., 1997). Again, the Bray-Curtis similarity index was calculated between all possible pairs of infracommunities (individual hosts) on square-root transformed values of abundance and nMDS analyses were performed and quantified by a value of stress. Differences in infracommunities amongst samples were examined in more detail using canonical analysis of principal co-ordinates (CAP) (Anderson and Willis, 2003; Anderson et al., 2008) based on Bray-Curtis dissimilarities. Potential overparameterization was prevented by choosing the number of axes (*m*) that maximised leave-one-out allocation success to groups (Anderson and Robinson, 2003). To test for significant differences in infracommunities amongst the samples, a permutation 'trace' test (sum of squared canonical eigen values) was applied, and *P* was obtained after 9999 permutations. For CAP analyses, specimens of *Z. conchifer* were used as a 'blind' sample in the 'adding new samples' subroutine of the CAP analyses, which places the

new samples onto the canonical axes of the obtained CAP model, with each being classified into one of the existing groups.

Variability in species composition amongst individual fish for a given fish sample, which can be considered as a measurement of β -diversity (Anderson et al., 2006), was calculated as the average Bray-Curtis dissimilarity from an individual unit to the group centroid, with the centroid being defined in the principal coordinate space of the dissimilarity measure used. These multivariate dispersions and their pairwise differences were calculated by applying the routine PERMDISP (Anderson et al., 2008).

All similarity and distance measures, as well as nMDS, clustering, PERMDISP and CAP analyses were implemented in PRIMER V7 and PERMANOVA+ for PRIMER packages (Anderson et al., 2008; Clarke et al., 2014). *P* values <0.05 were considered significant and *P* < 0.01 are indicated.

3. Results

3.1. Parasites of *Z. conchifer*

The parasite fauna of *Z. conchifer* comprised 20 parasite species (Table 3). The monogenean *Pseudempleurosoma* sp. was detected in the oesophagus of the last hosts examined, being only six fish examined for this species.

A total of 1956 metazoan parasites were counted, with a high proportion of them being represented by *Hysterothylacium spirale* (1349 specimens, representing 69% of all parasites found); this species also dominated 84% of infracommunities. As a consequence, the guild of adult endoparasites accounted for 73% of the total number of parasites, whereas low host-specific larval endoparasites represented a smaller proportion (23%) and ectoparasites accounted for only 4% of individuals.

When only long-lived larval helminths were considered and analysed comparatively with the other host species, the higher values of species richness were observed at the component

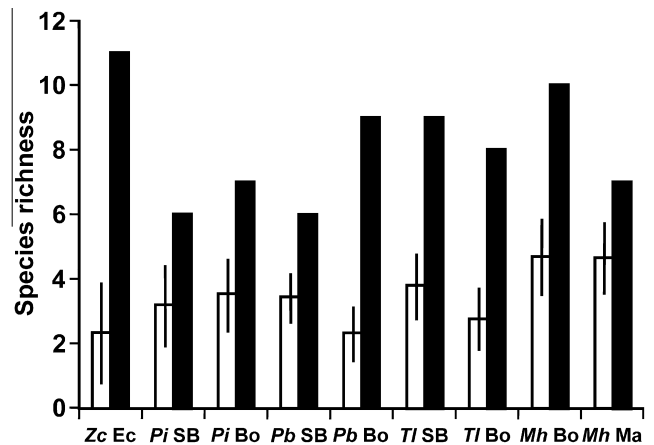


Fig. 2. Infracommunity mean species richness and S.D. (white bars) and component community species richness (black bars) of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. Host species: Zc, *Zenopsis conchifer*; Pi, *Paralichthys isosceles*; Pb, *Percophis brasiliensis*; Tl, *Trachurus lathami*; Mh, *Merluccius hubbsi*. Regions: Ec, Ecotone; SB, southern Brazilian District; Bo, Bonaerensean District; Ma; Magellanic Province.

community level for *Z. conchifer*, whereas infracommunities showed the lower values of mean species richness (Fig. 2).

3.2. Similarity analyses of component communities

Bidimensional nMDS analyses on prevalence data revealed an apparent pattern of separation between samples following a biogeographical scheme (Fig. 3), which was substantially different from random as shown by their low stress level (0.06). Indeed, cluster analyses showed that hakes from the Magellanic Province and *Z. conchifer* branched first in the cluster, whereas those from

Table 3
Taxonomic composition, developmental stage, site, prevalence (P) and mean abundance (MA) \pm S.D. of parasites of *Zenopsis conchifer*.

	Stage	Habitat	P	MA \pm S.D.
MONOGENEA				
<i>Pseudempleurosoma</i> sp. ^a	Adult	Oesophagus	33.3	0.50 \pm 0.84
DIGENEA				
<i>Derogenes varicus</i> (Müller, 1784)	Adult	Stomach	6.8	0.11 \pm 0.44
<i>Elytrophalloides oatesi</i> (Leiper and Atkinson, 1914)	Adult	Stomach	2.3	0.02 \pm 0.15
CESTODA				
<i>Eubothrioides</i> sp.	Adult	Intestine	68.2	1.75 \pm 3.19
<i>Scolex polymorphus</i> Rudolphi, 1819	Plerocercoid	Intestine	6.8	0.75 \pm 4.10
<i>Grillotia carvajalregorum</i> Menoret and Ivanov, 2009	Plerocercoid	Mesenteries/stomach serose	36.4	2.52 \pm 7.44
Tentaculariidae gen. sp.	Plerocercoid	Mesenteries	4.5	0.05 \pm 0.21
Unidentified larva	Plerocercoid	Mesenteries	13.6	1.5 \pm 6.16
NEMATODA				
<i>Hysterothylacium spirale</i> Rossin, Datri, Incorvaia and Timi, 2011	Adult	Stomach/intestine	100	30.66 \pm 20.61
<i>Hysterothylacium aduncum</i> (Rudolphi, 1802)	Larva III	Mesenteries	15.9	0.23 \pm 0.60
<i>Hysterothylacium</i> sp.	Larva III	Mesenteries	6.8	0.09 \pm 0.36
<i>Anisakis simplex</i> s.l.	Larva III	Mesenteries/stomach serosa	77.3	2.25 \pm 2.62
<i>Contracaecum pelagicum</i> Johnston and Mawson, 1942	Larva III	Mesenteries	22.0	0.50 \pm 1.30
<i>Contracaecum</i> sp. 2	Larva III	Mesenteries	2.3	0.18 \pm 1.21
<i>Terranova galeocerdonis</i> (Thwaite, 1927)	Larva III	Mesenteries	9.1	0.09 \pm 0.29
<i>Ascarophis</i> sp.	Larva	Stomach	2.3	0.09 \pm 0.60
ACANTHOCEPHALA				
<i>Bolbosoma turbinella</i> (Diesing, 1851)	Juvenile	Mesenteries	38.6	0.52 \pm 0.79
<i>Corynosoma australe</i> Johnston, 1937	Juvenile	Mesenteries	20.4	1.48 \pm 4.28
<i>Corynosoma cetaceum</i> Johnston and Best, 1942	Juvenile	Mesenteries	2.3	0.02 \pm 0.15
COPEPODA				
<i>Chondracanthus hoi</i> Braicovich, Lanfranchi, Incorvaia and Timi, 2013	Adult	Gills/branchial cavity	70.5	1.59 \pm 1.76

^a Data calculated from six hosts examined.

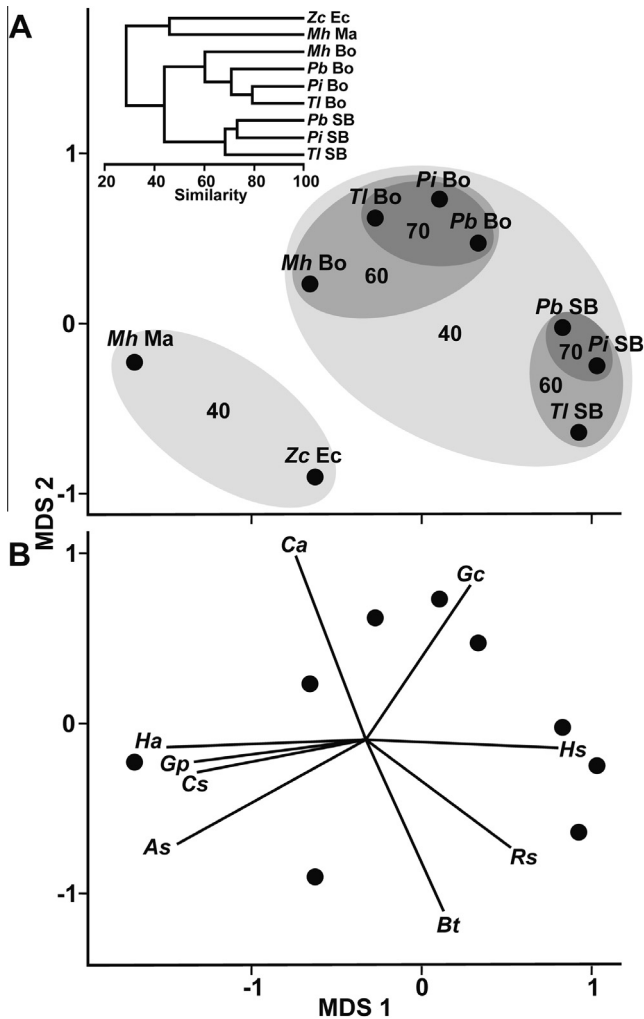


Fig. 3. Non-metric two-dimensional ordination plot and cluster analyses based on Bray-Curtis similarity on prevalence of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. (A) Results of a hierarchical agglomerative clustering in the upper right corner and overlaid on the non-metric multidimensional scaling analyses plot with similarity levels represented by shading, values given as numbers inside each shaded area. (B) Vector overlays are Pearson correlations of parasite species with the canonical analysis of principal co-ordinates axes (restricted to those having $|r| > 0.75$). Host species: Zc, *Zenopsis conchifer*; Pi, *Paralichthys isosceles*; Pb, *Percophis brasiliensis*; Tl, *Trachurus lathami*; Mh, *Merluccius hubbsi*. Regions: Bo, Bonaerensean District, Ec, Ecotone, Ma, Magellanic Province; SB, southern Brazilian District. Parasite species: As, *Anisakis simplex* s.l.; Bt, *Bolbosoma turbinella*; Ca, *Corynosoma australe*, Cs, *Contracaecum* sp. 2.; Gc, *Grillotia carvajalregorum*; Gp, *Grillotia patagonica*, Ha, *Hysterothylacium aduncum*; Hs, *Hysterothylacium* sp.; Rs, *Raphidascaris* sp.

the Argentine Province branched into two groups, corresponding to both its districts (Bonaerensean and southern Brazilian). The SIMPROF test identified two significant groups (SIMPROF, $P < 0.05$), corresponding to both Provinces. When vectors corresponding to Pearson correlations of individual species (only correlations with $|r| > 0.75$ are shown) were superimposed with the nMDS axes (Fig. 3A), *Corynosoma australe* and *Grillotia carvajalregorum* were strongly related to Bonaerensean samples from the Argentine Province, on the other hand *Hysterothylacium* sp., *Raphidascaris* sp. and *Bolbosoma turbinella* were mainly associated with the separation of samples from the southern Brazilian District along the first axis, with the latter also related to *Z. conchifer*. The rest of species with ($|r| > 0.75$) were related to the Magellanic province (Fig. 3B).

Analyses on mean abundance data revealed similar patterns to those of prevalence (Fig. 4), with low stress level (0.01). Cluster

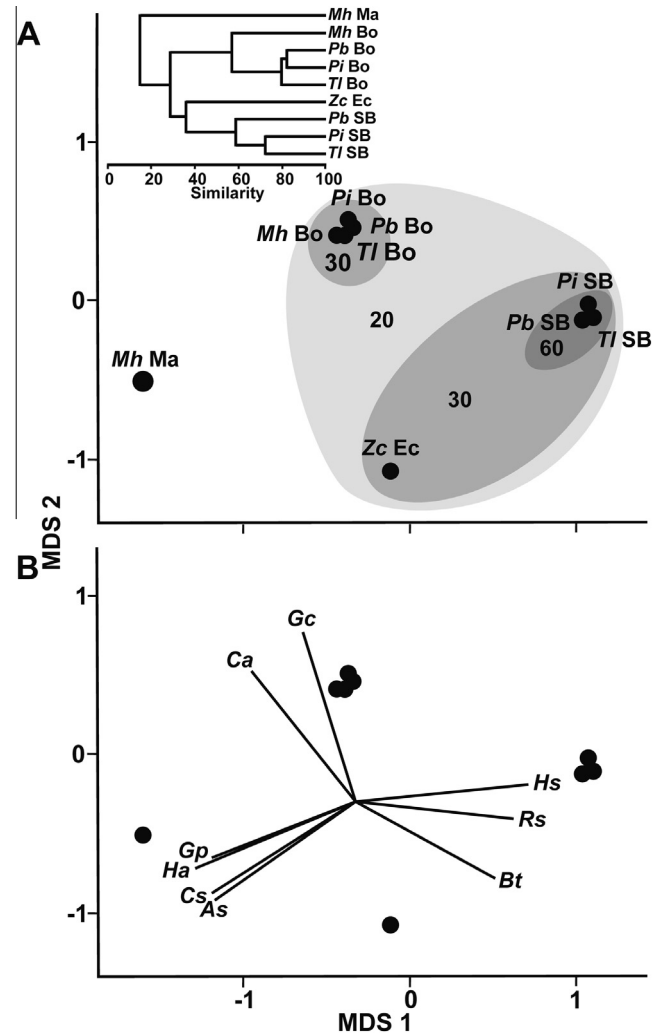


Fig. 4. Non-metric two-dimensional ordination plot and cluster analyses based on Bray-Curtis similarity on square-root transformed mean abundance of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. (A) Results of a hierarchical agglomerative clustering in the upper right corner and overlaid on the multidimensional scaling analyses plot with similarity levels represented by shaded areas, with values given as numbers inside each shaded area. (B) Vector overlays are Pearson correlations of parasite species with the canonical analysis of principal co-ordinates axes (restricted to those having $|r| > 0.75$). Host species: Zc, *Zenopsis conchifer*; Pi, *Paralichthys isosceles*; Pb, *Percophis brasiliensis*; Tl, *Trachurus lathami*; Mh, *Merluccius hubbsi*. Regions: Bo, Bonaerensean District, Ec, Ecotone, Ma, Magellanic Province; SB, southern Brazilian District. Parasite species: As, *Anisakis simplex* s.l.; Bt, *Bolbosoma turbinella*; Ca, *Corynosoma australe*, Cs, *Contracaecum* sp. 2.; Gc, *Grillotia carvajalregorum*; Gp, *Grillotia patagonica*, Ha, *Hysterothylacium aduncum*; Hs, *Hysterothylacium* sp.; Rs, *Raphidascaris* sp.

analyses showed the same three groups representing biogeographical classification of the region, although a SIMPROF test showed only significant differences between both Provinces (SIMPROF, $P < 0.05$). However, in this case *Z. conchifer* grouped with fish from the southern Brazilian District (Fig. 4A). The same sets of indicator species were observed after overlaying Pearson correlations (only correlations with $|r| > 0.75$ are shown) of individual species (Fig. 4B).

3.3. Similarity analyses of infracommunities

For analyses at infracommunity level, four individual hosts (three specimens of *Z. conchifer* and one of *Paralichthys isosceles* from Brazil) were excluded because they were not parasitised by

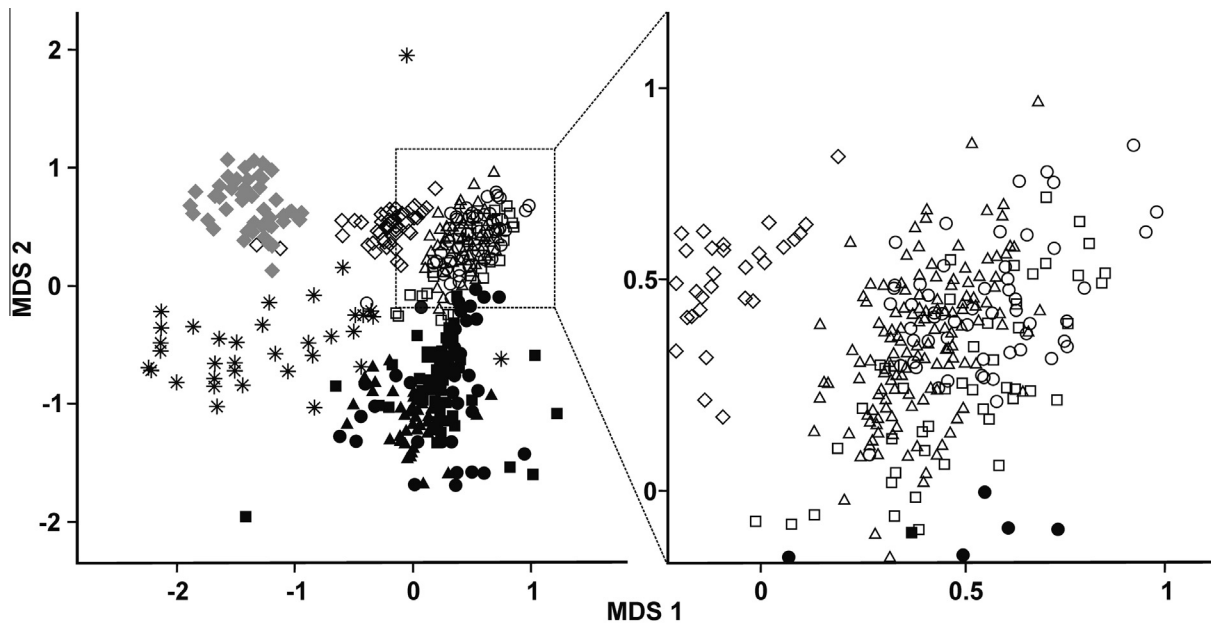


Fig. 5. Non-metric two-dimensional ordination plot based on Bray-Curtis dissimilarities on square-root transformed abundance of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. Asterisks, *Zenopsis conchifer* from ecotone zone; circles, *Paralichthys isosceles*; squares, *Percophis brasiliensis*; triangles, *Trachurus lathami*; rhombs, *Merluccius hubbsi*; black, southern Brazilian District; white, Bonaerensean District; grey, Magellanic Province.

long-lived larval helminths. Bidimensional nMDS analyses on square root-transformed abundance data revealed the same biogeographical pattern as analyses at the component community level (Fig. 5), although with a relatively high stress level (0.12). Specimens of *P. isosceles*, *Percophis brasiliensis* and *Trachurus lathami* from the Bonaerensean District were tightly clumped in the bidimensional space, irrespective of the species, whereas the same three species were more loosely grouped in the southern Brazilian District. *Merluccius hubbsi* from the Bonaerensean District occupied an intermediate space between Bonaerensean species and their conspecifics from the Magellanic Province, whereas individual *Z. conchifer* were scattered in an intermediate position amongst all the other samples. A better picture of sample distribution is obtained by a three-dimensional nMDS (stress level = 0.08) (Supplementary Movie S1).

The CAP showed significant differences amongst the samples ($tr = 3.29$, $P < 0.01$). The selected orthonormal principal coordinates (PCO) axes ($m = 8$) described 99.2% of the variation in the data cloud, with 78.4% correct allocations of the pre-established groups, and a misclassification error of 21.6%. The two first canonical axes resulting from the CAP separated the samples in a similar way to the nMDS (Fig. 6) and a strong association between the multivariate data 'cloud' and the hypothesis of group differences was indicated by the reasonably large size of their canonical correlations ($\delta_1 = 0.98$ and $\delta_2 = 0.96$). Cross validation of the results (Table 4) showed that the higher percentages of correctly allocated fish occurred in both samples of *M. hubbsi*, whereas samples from both districts of the Argentine Province showed lower proportions of correct allocations, given mainly by misclassification of hosts, assigned to other samples caught in the same district. Indeed, when the correct allocations of fish to zoogeographical district were considered, the percentages increased notably. After adding the sample of *Z. conchifer*, individual John dories were mainly allocated to the Magellanic Province (46.3% of them), whereas 34.1 and 19.5% were assigned to southern Brazil and Bonaerensean Districts, respectively, however the final percentage was below the 21.1% allocation success for eight groups expected by chance alone. A

better picture of discrimination of samples is obtained by a three-dimensional CAP (Supplementary Movie S2).

Multivariate dispersions (Fig. 7) showed that samples from the Bonaerensean District were more homogeneous in species composition and abundance that their counterparts from other regions, although significant differences amongst individual fish were observed for *P. isosceles* and *T. lathami* (both $P(\text{perm}) < 0.01$), but not for *P. brasiliensis* and *M. hubbsi* (both $P(\text{perm}) < 0.05$). Samples of *Z. conchifer*, on the other hand, were significantly more heterogeneous than any other samples (all $P(\text{perm}) < 0.01$).

4. Discussion

With the exception of *H. spirale* and *Chondracanthus hoi*, previously described from *Z. conchifer* in the study region (Rossin et al., 2011; Braicovich et al., 2013), all other species represent new records for this host. Nevertheless, most parasite species found in silvery John dory have been recorded in other hosts inhabiting the southwestern Atlantic coasts, the exception obviously being the specific ones (including *Pseudempleurosoma* sp. and *Eubothrioides* sp.).

The component parasite community of *Z. conchifer* in the study area is composed of 20 species, a species richness equivalent to other fish species analysed at these latitudes. This assemblage is, however, exceptional in the region by being dominated numerically by adult parasites, because at the same latitude, more coastal fishes in the Bonaerensean District of the Argentine Province harbour, as a rule, parasite assemblages largely dominated by the guild of larval endoparasites (Timi and Lanfranchi, 2009, 2013; Rossin and Timi, 2010; Timi et al., 2010, 2011; Braicovich and Timi, 2015). In fact, this compositional difference reflects the proportionally lower abundance of larval parasites in relation to fish species inhabiting shallower waters, with adult parasites resulting as dominant components of these assemblages.

Results of multivariate analyses at the component community level showed a tight correspondence with the existing zooge-

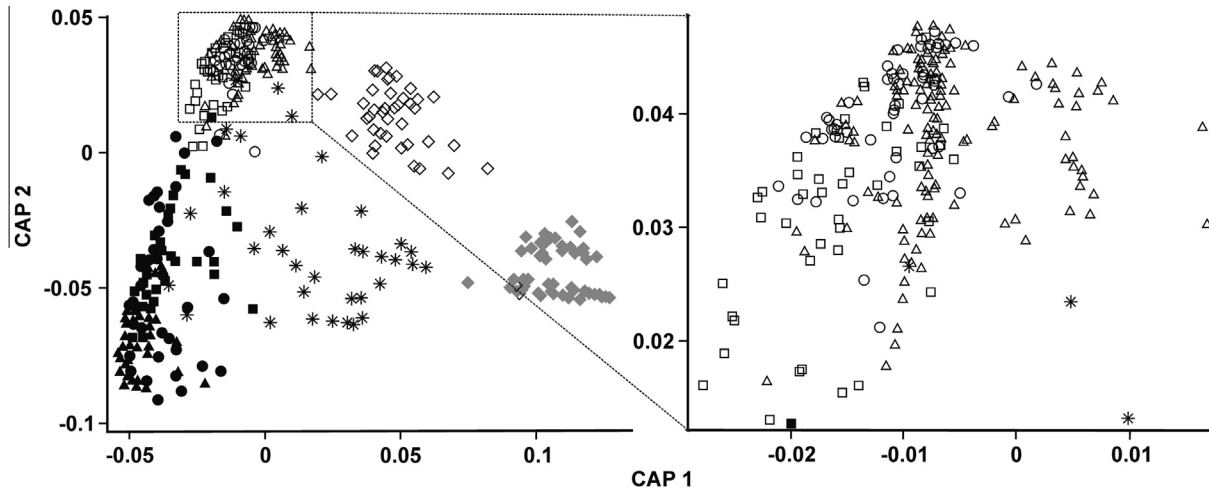


Fig. 6. Canonical analysis of principal co-ordinates bi-plot based on Bray-Curtis dissimilarities on square-root abundance data of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. Asterisks, *Zenopsis conchifer* from ecotone zone; circles, *Paralichthys isoceles*; squares, *Percophis brasiliensis*; triangles, *Trachurus lathami*; rhombs, *Merluccius hubbsi*; black, southern Brazilian District; white, Bonaerensean District; grey, Magellanic Province.

Table 4

Results of the cross validation of analysis of principal co-ordinates analyses (leave-one-out allocation of individual fish of four species to one of eight samples). Rows correspond to group memberships, including the percentage of correctly classified fish to their sample or region.

Original group	Pi SB	Pi Bo	Pb SB	Pb Bo	Tl SB	Tl Bo	Mh Bo	Mh Ma	Total	% (sample)	% (region)
Pi SB	22	0	10	2	5	0	0	0	39	56.4	94.9
Pi Bo	0	33	0	6	0	11	0	0	50	66.0	100
Pb SB	3	0	32	1	4	0	0	0	40	80.0	97.5
Pb Bo	0	13	1	22	0	12	0	0	48	45.8	97.9
Tl SB	4	0	4	0	42	0	0	0	50	84.0	100
Tl Bo	0	9	0	13	0	123	0	0	145	84.8	100
Mh Bo	0	0	0	0	0	1	41	0	42	97.6	97.6
Mh Ma	0	0	0	0	0	0	1	49	50	98.0	98.0

Mh, *Merluccius hubbsi*; Pb, *Percophis brasiliensis*; Pi, *Paralichthys isoceles*; Tl, *Trachurus lathami*; Bo, Bonaerensean district of the Argentine Province; Ma, Magellanic Province; SB, South Brazilian district of the Argentine Province.

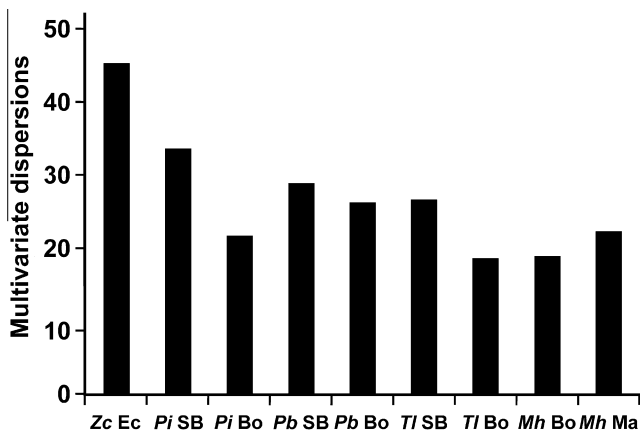


Fig. 7. Multivariate dispersions (average Bray-Curtis dissimilarity from an individual unit to the group centroid) of long-lived and low host-specific parasites in five fish species distributed in the southwestern Atlantic Ocean following a pre-established biogeographic scheme. Host species: Zc, *Zenopsis conchifer*; Pi, *Paralichthys isoceles*; Pb, *Percophis brasiliensis*; Tl, *Trachurus lathami*; Mh, *Merluccius hubbsi*. Regions: Ec, Ecotone; SB, southern Brazilian District; Bo, Bonaerensean District; Ma, Magellanic Province.

graphical classification in the study, namely two zoogeographical provinces, one of them subdivided in two districts. Indeed, similarity in both prevalence and mean abundance of parasites across different samples showed that hakes from Patagonian waters

(Magellanic Province) were the most different, being clearly separate from those fishes from both districts of the Argentine Province including conspecifics from the Bonaerensean District. These results reflect the effect of the physical characteristics of each ecosystem and its trophic webs on parasite assemblages (Marcogliese, 2001, 2002; Luque and Poulin, 2004), which determined that fish with different habits, trophic levels and sizes displayed recurrent patterns, grouping together according their geographical origin, but separated from conspecifics from other regions. Thus, each region harbours singular parasite faunas, clearly defined by their own characteristic species that can be considered typical of each environment (Cantatore and Timi, 2015; Braicovich et al., in press). In this scheme *Z. conchifer* was closely associated with either Magellanic or southern Brazilian samples when prevalence or mean abundance, respectively, were analysed, but not to Bonaerensean fishes. This is a consequence of the relatively lower burdens of typical Bonaerensean parasites such as *G. carvajalregorom* and *C. australe*, as well as to the influence of parasites with high burdens typical of southern Brazilian (i.e. *B. turbinella*) and Magellanic regions (i.e. *Hysterothylacium aduncum*, *Contraecaecum* sp. 2). The sample of *M. hubbsi* from the Bonaerensean District was also parasitised by helminth species of different origins, but the considerably larger amounts of larvae typical of the Bonaerensean District resulted in a higher similarity of these hake with the other Bonaerensean species. This is related to the higher bathymetric distribution of hakes, which at these latitudes inhabit deep as well as shallower waters below the isobath of

50 m (Cousseau and Perrotta, 2004), acquiring parasites in more coastal waters. The composition of parasite component communities and their higher species richness in samples caught in the ecotonal region indicate that the convergence of masses of water that define the oceanography of this region (Piola and Rivas, 1997) act as sources of infective stages of helminth species typical of other zoogeographical regions.

It can be also postulated that the structure of parasite assemblages of *Z. conchifer* in this region could be a consequence of migratory movements from other regions. Nevertheless, silvery John dory is considered a poor swimmer (Quéro et al., 1997) and, except for a bathymetric age segregation that could be related to ontogenetic movements to deeper waters for reproductive purposes (Martins and Schwingel, 2012), no migratory movements are known for this species in the study region. However, as the study area is located in the southern limit of distribution of this species, the only possible migration, if any, would be latitudinal displacement from the southern Brazilian District.

Analyses at an infracommunity level yielded similar patterns to those at the component community level, demonstrating the ecotonal nature of parasite assemblages from the convergence region. Indeed, individual silvery John dories caught in the interface zone were distributed in an intermediate space between South Brazilian, Bonaerensean and Magellanic samples in both nMDS and CAP graphs. This intermediate position in the multivariate space agreed with cross validation of results of CAP, which showed that specimens of *Z. conchifer* were assigned to different regions, due to the identity of parasites they harbour and to the heterogeneity of the assemblages they compose. Indeed, multivariate dispersions indicated that parasite assemblages of *Z. conchifer* were significantly more heterogeneous than in any other sample.

Multivariate dispersions can be interpreted as a measure of β -diversity (Anderson et al., 2006) by considering the average dissimilarity of an individual unit from the group centroid as representative of the variability in species composition amongst sampling units for a given area. This is equivalent to the concept of β -diversity (Whittaker, 1960) that represents the proportion by which a given area is richer than the average of samples within it. The higher β -diversity of parasite assemblages of *Z. conchifer*, regarding the other fish species herein considered, can be, at least partially, a consequence of the low species richness of its infracommunities, which increases dissimilarities between individual fish and, consequently, their distances to the group centroid. This variability is, in the case of the set of long-lived parasites included in the analyses, enhanced by the higher species richness observed at the component community level, which increases the probability of producing variable assemblages that can be identified, depending on their specific composition, as characteristic of different masses of water and therefore from different biogeographical units.

The higher species richness in ecotones, described as the “edge effect” defined by Odum (1959) as the tendency for increased population species richness and density in the junction zone between communities, occurs here simply because the ecotone contains representatives of species characteristic of adjacent communities, which are supplied by the convergent masses of water. Nevertheless, the abundances of species found in *Z. conchifer* are lower when compared with those in other fish from the respective regions of origin, possibly related to host characteristics such as diet breadth and composition or trophic level, as well as to its habitat in deep waters, considering that parasite abundance declines with depth in marine fishes (Marcogliese, 2002).

Larvae of *Anisakis* are often identified as suitable biological tags of the geographical distribution of their fish hosts worldwide and in the southwestern Atlantic Ocean in particular (Timi, 2007; Cantatore and Timi, 2015). *Anisakis simplex* sensu lato is a species

complex whose members cannot be differentiated morphologically from each other or from other species such as *Anisakis typica*, *Anisakis ziphidarum* and *Anisakis nascettii* at the larval stage, thus requiring the application of molecular systematics (Mattiucci and Nascetti, 2008; Mattucci et al., 2014); consequently this lack of taxonomic resolution based on morphology alone can affect interpretations of hosts distribution based on parasite tags. In the southwestern Atlantic Ocean, five species of *Anisakis* have been identified genetically, *Anisakis pegreffii* in Patagonian waters (Mattiucci and Nascetti, 2008), and *Anisakis physeteris*; *A. typica*, *Anisakis paggiae* and *A. nascettii* in Brazilian waters (Di Azevedo et al., 2015, 2016). *Anisakis typica* has been so far reported from warmer temperate and tropical waters (Mattiucci et al., 2002; Mattiucci and Nascetti, 2008) and it is possible that this species occurs in sympatry in fishes inhabiting the convergence of subtropical and subantarctic waters. Despite no morphological evidence of different species being observed in the specimens of *Anisakis* found in *Z. conchifer*, a molecular characterisation of these larvae could provide further evidence of their value as zoogeographical indicators in the region. This could be also the case for other anisakids such as *Contracaecum* spp. for which three morphological types were observed in the samples analysed.

The value of parasites as zoogeographical indicators in the southwestern Atlantic Ocean has been addressed in previous papers, either as discriminators between Magellanic and Argentine Provinces (Cantatore and Timi, 2015) or between the districts of the latter (Braicovich et al., in press) in which those indicator species that characterise each biogeographical unit were identified. These results are herein corroborated through the finding of recurrent patterns across different fish species with variable habits and embracing both scales of the zoogeographical scheme in the region (the provinces and its subdivisions). Furthermore, we believe this is the first study attempting to characterise parasite assemblages in an interface region where masses of water, and the fauna they transport, converge. Indeed, in this region the confluence of Brazil and Malvinas Currents produces a thermohaline sub-surface front between subtropical shelf waters and subantarctic shelf waters, located near the 50 m isobaths beneath a low salinity surface layer generated by the discharge of the Río de la Plata and Patos Lagoon (Acha et al., 2004). The supply of infective stages by these masses of water with different origins drives the formation of “ecotonal” parasite assemblages in this transitional region, knowledge of which could help to detect biogeographical boundaries. As an example, samples of *Dules auriga*, caught during the same research cruise at similar dates and latitudes, but at shallower depths (53–63 m) displayed parasite assemblages typical of shelf waters of the Bonaerensean District (Braicovich and Timi, 2015).

The identification of ecotonal parasite assemblages could be relevant for the delineation of those interface regions defined by marine fronts, which are characterised by high primary and secondary productivity (Acha et al., 2004), therefore being generally subjected to strong fishery pressures (Alemany et al., 2014) and requiring the implementation of management programmes. Furthermore, the borders of biological communities are suggested as priority areas for conservation where a fully functioning ecosystem can be protected (Primack, 2006) and parasite communities can be considered as reliable indicators to define such transitional regions.

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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.ijpara.2016.07.004>.

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