

Similarity in parasite communities of the teleost fish *Pinguipes brasilianus* in the southwestern Atlantic: Infracommunities as a tool to detect geographical patterns

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ABSTRACT

Patterns of distance decay in similarity among communities of the fish *Pinguipes brasilianus* (Teleostei: Pinguipedidae) from five areas in the southwestern Atlantic were investigated to determine whether the rate of decay varied depending on the community level or the parasite guild analyzed (ectoparasites, adult endoparasites and larval endoparasites). Similarities in species composition were computed at both the component community and infracommunity levels. Similarity indices were calculated between all possible pairs of assemblages from different zones. Infracommunity similarity values between and within host populations were averaged. Significance of linear regressions for similarity values against distance was assessed using randomization tests. Different patterns were observed for each guild, and similarity among infracommunities within host populations varied accordingly. Decay in similarity over distance was recorded for most communities. The slopes differed significantly between infracommunities and component communities in all cases, and stronger decay was always observed for infracommunities. Different geographical patterns in parasite communities were a consequence of variability in parasite availability in the different regions, modulated by oceanographic conditions, as well as variation among species in terms of host specificity and life-cycles strategies. Infracommunities showed a stronger effect of distance than component communities, probably due to the influence of short term and local variability of oceanographic conditions.

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1. Introduction

Understanding geographical variation in the composition, abundance and diversity of parasite communities is one of the most important challenges for parasite ecology (Luque and Poulin, 2007; Poulin, 2007a). Parasite species richness has been commonly shown as highly variable and poorly repeatable in space at local or regional geographical scales (Poulin 2007b; Bordes and Morand, 2008). However, during recent decades, some large-scale geographical patterns in parasite diversity have been found, the most conspicuous of those being a latitudinal gradient in species richness (Rohde, 1992, 1999, 2005; Rohde and Heap, 1998), which shows that in marine fish, parasite diversity varies as a function of latitude.

More recently, another macroecological pattern has been uncovered by parasite ecologists, the distance decay of similarity in species composition among communities (Poulin and Morand,

1999; Poulin, 2003). It consists of a decrease in the proportion of species shared by two communities with increasing distance between them, and is the outcome of ecological or evolutionary phenomena shaping spatial patterns in biodiversity and biogeography (Nekola and White, 1999; Soininen et al., 2007).

A negative relationship between community similarity and geographic distance is often attributed to environmental gradients (Nekola and White, 1999; Soininen et al., 2007). However, non-contiguous regions with similar environmental conditions harbor distinct assemblages of vertebrates and plants, suggesting that other factors can play a role (Bjorholm et al., 2008). Some authors have emphasized dispersal limitation due to geographic barriers (Nekola and White, 1999), but spatially limited dispersal can generate distance decay in community similarity even when no barriers are present (Bjorholm et al., 2008). A combination of both environmental gradients and dispersal limitation is expected to produce a negative relationship between community similarity and geographic distance (Qian et al., 2005), and community ecologists have long debated whether spatial patterns of biodiversity are limited by these factors.

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The rate at which biological similarity decays with increasing distance can shed light on some of the processes acting on it and parasite communities, because all their species can be enumerated, represent good models for investigations of such rates (Poulin, 2003). Therefore, the increasing number of studies reporting a distance decay of similarity for parasite assemblages is not surprising. These studies have focused on helminth parasites of mammals (Poulin, 2003; Brouat and Duplantier, 2007), freshwater fishes (Poulin, 2003; Fellis and Esch, 2005; Seifertová et al., 2008), marine fishes (Oliva and Gonzalez, 2005; Pérez-del-Olmo et al., 2009) and marine molluscs (Thieltges et al., 2009), as well as of arthropod ectoparasites of mammals (Krasnov et al., 2005; Vinarski et al., 2007).

Although similarity in the composition of several parasite communities investigated to date appears to decay exponentially or linearly with increasing distance, many others showed no such pattern. A variety of processes related either to the parasites, their host or its habitat have been identified as causes of similarity decrease for those parasite communities displaying this pattern, such as the vagility and dispersal rates of the host, phylogenetic distance between host populations, the host geographic range and the existence of a favorable centre of distribution, as well as stochastic events, environmental gradients, habitat fragmentation or the composition and structure of the parasite supracommunity (Poulin, 2003; Fellis and Esch, 2005; Krasnov et al., 2005; Oliva and Gonzalez, 2005; Brouat and Duplantier, 2007; Vinarski et al., 2007; Seifertová et al., 2008; Pérez-del-Olmo et al., 2009).

The present state of knowledge, however, makes it difficult to discern any general rule governing the distance decay of similarity in species composition among parasite assemblages. This is particularly due to the use of different measurements of similarity (namely Jaccard's, Sørensen's qualitative and quantitative, and Morisita's indices), the choice of which is still under discussion (see Baselga, 2007; Soininen and Hillebrand, 2007) and the use of different geographical scales, which preclude a comparison of rates at which biological similarity decreases. However, almost all previous studies share a common feature: they all tested the distance decay of similarity at the component community level. To our knowledge, only Pérez-del-Olmo et al. (2009) have recently tested the similarity-distance decay hypothesis on a marine host–parasite system inferring the relationship at the component community level, but also from abundance data at the infracommunity level of the booby, *Boops boops*, in Spain.

Component communities (the assemblage of populations of all parasite species exploiting a host population at one point in time; Bush et al., 1997) are long-lived assemblages that can last as long as the host population persists in time (Poulin, 2007c). They are formed over evolutionary time scales by different processes, such as speciation, extinction, colonization or host switching (Poulin, 2007c). Their species richness is influenced by rare species, and therefore by sampling effort (Guégan and Kennedy, 1996), and species that are rare in one area but common in others can increase considerably in similarity, especially qualitative similarity. On the other hand, infracommunities (all parasites of different species in the same host individual; Bush et al., 1997) are assembled over ecological time scales by infection, intra- and inter-specific interactions and demographic processes (Poulin, 2007c). Infracommunities also allow robust statistical testing and the effect of rare species is negligible in comparisons between large samples. Furthermore, infracommunities can be completely quantified, and their similarity values are not estimated, but real. Therefore, infracommunities could be useful indicators of local or regional environmental conditions. Despite that, and with the exception of the paper by Pérez-del-Olmo et al. (2009), no other studies of similarity decay with increasing distance have been carried out at this community level.

Coastal marine fish, which live in a continuous habitat without real barriers, show the highest values of similarity among their parasite communities among vertebrate host species (Poulin, 1997). However, Oliva and Gonzalez (2005), the first study on similarity decay in parasite assemblages of marine fish, have found a significant decay of similarity in the composition of parasite communities of three of the four host species analyzed. On the other hand, Pérez-del-Olmo et al. (2009) found no consistent evidence to support the decay of compositional similarity over distance for component communities, but detected that geographical distance between localities contributes significantly to the decay of similarity estimated from parasite abundance at the infracommunity level. These analyses were based on binary (presence–absence) data for component communities and abundance for infracommunities, and on similarity measurements different from those previously applied in other studies, namely distance matrices using the neighbor joining method for component communities and Mahalanobis distances derived from a linear discriminant analysis for infracommunities. Therefore, the present study is to our knowledge the third one investigating such patterns in marine fishes, the second one analyzing the similarity-distance decay at infracommunity level and the first one based on both binary and abundance data, using similarity measurements previously tested in other host–parasite systems (Jaccard and Sørensen similarity indices).

The present study is based on our own data on parasite assemblages, which ensures taxonomic consistency, and also on hosts gathered over a short time scale (around 1 year) avoiding the influence of longer-term processes. In addition, locality effects exceed seasonal ones, indicating that short-term processes are also negligible in the study system (Timi et al., 2009). Finally it covers the entire distributional range of the host species, a geographical scale not previously investigated in this kind of study in a marine environment.

The first objective of this study was to determine whether the similarity in the species composition of parasite communities of a marine fish tends to decay exponentially with increasing distance among host populations in the southwestern Atlantic. The second objective was to assess whether the distance decay patterns that have been shown for several parasite component communities also apply to infracommunities and to determine whether the rate of decay differed depending on both the community level and the parasite guild analyzed (ectoparasites, adult endoparasites and larval endoparasites). We expected a stronger effect of distance on similarity decay at the infracommunity level than for component communities, because short-term and local variability in oceanographic conditions should produce a higher rate of distance decay when individual hosts are considered as habitats.

2. Materials and methods

2.1. Fish and parasite sampling

The data set comprises the parasite communities of the Brazilian sandperch, *Pinguipes brasilianus* Cuvier, 1829 from five areas in the southwestern Atlantic (Fig. 1), including the northern and southern boundaries of its range (Rio de Janeiro, Brazil and Nuevo Gulf, Argentina) (Rosa and Rosa, 1997). Data from four zones in Argentinean waters were obtained from previous studies which aimed to use parasites as indicators for discriminating among fish populations (Timi et al., 2008, 2009). Therefore, there are significant differences among them. The data sets are summarized in Table 1. Fifty fish were randomly selected from each of the four zones in the Argentinean Sea, and an additional sample of 50 sandperches from Cabo Frio, Rio de Janeiro, was included in the

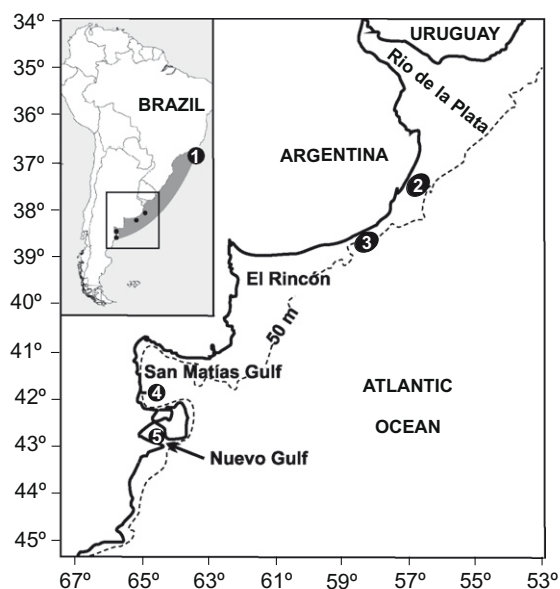


Fig. 1. Map showing the study area and the sampling sites. South American map showing the distribution of *Pinguipes brasiliensis* in dark grey. 1, Rio de Janeiro; 2, Villa Gesell; 3, Miramar; 4, Puerto Lobos; 5, Craker Bay.

comparisons. According to their geographic location, samples can be assigned to different faunistic provinces in the Atlantic environment of South America: those from Rio de Janeiro (RJ) belong to the Brazilian Province which occupies the area between the Orinoco delta and State of Santa Catarina (Floeter and Gasparini, 2000), whereas those from Villa Gesell (VG) and Miramar (MI) to the Argentine Province (Bonaerense region), and those from north Patagonian gulfs, Puerto Lobos (PL) and Craker Bay (CB) to the ecotone between the Argentine and Magellanic Provinces (Floeter and Gasparini, 2000; Bogazzi et al., 2005).

Fish were either kept fresh or deep frozen in plastic bags at -18°C until examination. After thawing, the total length was measured (T_L , cm). Parasites were recovered from the body surface, gills, branchial and body cavities and viscera (stomach, intestine, liver, gonads, and mesenteries) by stereoscopic microscopy.

2.2. Community descriptors

The following community descriptors were calculated at the infracommunity level: number of parasites in each infracommunity, species richness and Brillouin's index of diversity, the latter only for those fish harboring at least two parasite species (Magurran, 1988). Because data did not meet the requirements for parametric tests, the effects of locality on each community descriptor were analyzed with Kruskal–Wallis and a posteriori Tukey tests (Zar, 1999).

2.3. Similarity analysis

Similarity in parasite species composition and geographical distance were computed at component community and infracom-

munity levels. Both the Jaccard and Sørensen similarity indices (qualitative and quantitative, respectively) (Magurran, 1988) were calculated between all possible pairs of host populations (component communities) and pairs of hosts (infracommunities) from different zones. Similarity values of infracommunities between each pair of host populations were averaged. Sørensen's indices for component communities were calculated on average total abundance.

As infracommunities can be purely stochastic assemblages, coming together entirely at random (Poulin, 2007c), their similarity among host populations could also vary randomly. Therefore the "intrinsic" similarity (between all possible pairs of infracommunities within each host population) was calculated, averaged and compared with those between host populations. The underlying idea was that if intrinsic variability is higher than between host populations, the species composition of such assemblage has a certain identity and structure.

Distance between pairs of host populations was calculated as the shortest linear distance between sampling localities obtained from a map, following the coastline below the 50 m isobath. Linear regressions were calculated for log-transformed similarity values against untransformed distance values (Poulin, 2003). The slopes of regression lines were compared by means of Student's *t* tests (Zar, 1999). Each parasite assemblage was used in more than one pairwise comparison, and consequently was not truly independent from distance in a statistical sense. Therefore the significance of each regression model was tested using a randomization approach (Manly, 1997), with all regression probabilities based on 10,000 permutations. This was achieved using the RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, WY, USA).

3. Results

3.1. Comparisons of community descriptors

The parasite fauna of *P. brasiliensis* comprised 39 parasite species along its range. Parasite burdens, in terms of prevalence and mean abundance, varied among the five component communities from the considered zones (Table 2). Seventeen species were exclusive to RJ, six to VG and two to CB, with the rest shared by two or more zones. Only three species, *Microcotyle pseudoperis*, *Scolex polymorphus* and *Paracapillaria argentinensis*, were present in all five zones.

At the infracommunity level, for all parasite species combined, the species richness was significantly higher in samples from RJ than in all other localities, whereas the total number of parasites was similar among the three northern zones and higher than in the north Patagonian gulfs (Figs. 2A and B; Table 3). Diversity, on the other hand, behaved the same as species richness; fishes from PL always displayed the lowest values of all infracommunity descriptors (Fig. 2C; Table 3). When component communities were compared among zones, species richness and total number of parasites showed a similar pattern to infracommunities (Figs. 2D and E; Table 3), whereas diversity at both southern localities was higher than in the two central zones (Fig. 2F; Table 3).

This general pattern changed when separating the parasite species into the three guilds (Table 3). Both infracommunity ectoparasite species richness and total number of parasites were also

Table 1
Composition of samples of *Pinguipes brasiliensis* in five zones of the southwestern Atlantic.

Host population	Locality code	Latitude, longitude	Date of capture	<i>n</i>	Total length (cm) \pm SD	Reference
Cabo Frio, Rio de Janeiro	RJ	22°53'S, 42°00'W	February, 2006	50	35.62 \pm 4.29	Present study
Villa Gesell	VG	37°15'S, 57°23'W	February, 2007	50	34.21 \pm 3.50	Timi et al. (2009)
Miramar	MI	38°03'S, 57°30'W	July–August, 2006	50	33.88 \pm 2.74	Timi et al. (2009)
Puerto Lobos	PL	42°00'S, 65°10'W	December, 2006	50	33.05 \pm 3.09	Timi et al. (2008)
Craker Bay	CB	42°09'S, 64°05'W	December, 2006	50	37.07 \pm 3.10	Timi et al. (2008)

Table 2
Taxonomic composition, guild, prevalence and mean abundance of parasites of *Pinguipes brasiliensis* in five zones of the southwestern Atlantic.

Parasite species	Guild	Prevalence					Mean abundance ± SD				
		RJ	VG	MI	PL	CB	RJ	VG	MI	PL	CB
MONOGENEA											
<i>Microcotyle pseudoperis Amato and Cezar, 1994</i>	EC	26	6	26	12	16	0.7 ± 1.4	0.1 ± 0.2	0.4 ± 0.7	0.2 ± 0.5	0.2 ± 0.5
<i>Pseudempleurosoma gibsoni Santos, Mourão & Cárdenas, 2001</i>	EC	22	0	0	0	0	0.3 ± 0.7	0	0	0	
<i>Encotyllabe</i> sp.	EC	18	0	0	0	0	0.3 ± 0.7	0	0	0	
DIGenea											
<i>Neolebouria georgenascimentoi Bray, 2002</i>	AE	0	4	0	52	72	0	0.1 ± 0.4	0	5.4 ± 10.3	7.6 ± 10.1
<i>Aponurus laguncula Loos, 1907</i>	AE	0	2	0	0	0	0	0.02 ± 0.1	0	0	0
<i>Derogenes varicus Müller, 1784</i>	AE	0	2	0	0	0	0	0.02 ± 0.1	0	0	0
<i>Parahemius merus</i> (Linton, 1910)	AE	6	0	0	0	0	0.7 ± 3.0	0	0	0	
<i>Lecithochirium microstomum</i> Chandler, 1935	AE	60	0	0	0	0	1.7 ± 2.1	0	0	0	
<i>Leurodera decora</i> Linton, 1910	AE	30	0	0	0	0	0.7 ± 1.5	0	0	0	
<i>Bucephalus</i> sp.	AE	42	0	0	0	0	2.6 ± 4.3	0	0	0	
<i>Stephanostomum</i> sp.	AE	4	0	0	0	0	0.04 ± 0.2	0	0	0	
<i>Proctoeces</i> sp.	AE	40	0	0	0	0	0.6 ± 0.9	0	0	0	
Opelcoelidae gen. sp.	AE	0	0	0	6	34	0	0	0	0.2 ± 0.8	5.1 ± 13.2
Didimozoidae gen. sp.	LE	70	0	0	0	0	5.5 ± 7.6	0	0	0	
Digenea fam. gen. sp. 1	LE	4	0	0	0	0	0.1 ± 0.4	0	0	0	
Digenea fam. gen. sp. 2	LE	2	0	0	0	0	0.02 ± 0.1	0	0	0	
CESTODA											
<i>Callitetrarhynchus gracilis</i> (Rudolphi, 1819)	LE	4	0	0	0	0	0.1 ± 0.4	0	0	0	
<i>Grillotia</i> sp., plerocercus	LE	54	100	100	10	0	0.8 ± 1.1	31.8 ± 45.1	33.6 ± 36.2	0.2 ± 0.5	0
<i>Scolex polymorphus</i> Müller, 1784	LE	20	46	58	2	4	0.4 ± 0.9	11.5 ± 42.9	6.6 ± 8.8	0.02 ± 0.1	0.04 ± 0.2
<i>Anonchocephalus</i> sp.	AE	0	2	0	0	0	0	0.02 ± 0.1	0	0	0
NEMATODA											
<i>Anisakis simplex</i> (Rudolphi, 1809)	LE	0	2	2	2	4	0	0.02 ± 0.1	0.02 ± 0.1	0.02 ± 0.1	0.04 ± 0.2
<i>Hysterothylacium</i> sp.	LE	18	4	2	0	0	0.5 ± 1.5	0.04 ± 0.2	0.02 ± 0.1	0	0
<i>Hysterothylacium aduncum</i> (Rudolphi, 1802)	AE	0	2	0	0	0	0	0.02 ± 0.1	0	0	0
<i>Raphidascaris</i> sp.	LE	66	0	0	0	0	2.3 ± 3.2	0	0	0	0
<i>Paracapillaria argentinensis</i> Timi, Rossin, Lanfranchi & Etchegoin, 2007	AE	22	28	4	28	30	1.7 ± 5.1	0.8 ± 1.7	0.4 ± 2.79	0.9 ± 1.9	0.5 ± 0.9
<i>Terranova</i> sp.	LE	0	0	0	0	10	0	0	0	0	0.1 ± 0.4
<i>Pseudoterranova</i> sp.	LE	0	0	0	0	10	0	0	0	0	0.1 ± 0.4
<i>Cucullanus carioca</i> Vicente & Fernandez, 1973	AE	14	10	8	0	0	0.4 ± 1.3	0.1 ± 0.3	0.1 ± 0.3	0	0
<i>Ascarophis marina</i> (Szidat, 1961)	LE	0	4	0	0	0	0	0.1 ± 0.5	0	0	0
ACANTHOCEPHALA											
<i>Corynosoma australe</i> Johnston, 1937	LE	0	96	94	64	50	0	35.5 ± 38.5	12.6 ± 16.8	2.0 ± 5.9	0.8 ± 1.0
<i>Corynosoma cetaceum</i> Johnston & Best, 1942	LE	0	6	2	0	0	0	0.1 ± 0.5	0.02 ± 0.1	0	0
<i>Heterosentis brasiliensis</i> Vieira, Felizardo & Luque, 2009	AE	24	0	0	0	0	0.2 ± 0.4	0	0	0	0
<i>Heterosentis</i> sp.	AE	0	4	0	0	0	0	0.1 ± 0.3	0	0	0
<i>Gorgorhynchus</i> sp.	AE	10	0	0	0	0	0.1 ± 0.3	0	0	0	0
HIRUDINEA											
Piscicolidae gen. sp.	EC	10	0	0	0	0	0.1 ± 0.3	0	0	0	0
COPEPODA											
<i>Neobrachiella spinicephala</i> (Ringuet, 1945)	EC	0	46	32	26	42	0	0.8 ± 1.1	0.6 ± 1.1	0.3 ± 0.7	1.1 ± 2.0
<i>Trifur tortuosus</i> Wilson, 1917	EC	0	4	2	58	84	0	0.04 ± 0.2	0.02 ± 0.1	0.8 ± 0.9	1.7 ± 1.4
ISOPODA											
Cymothoidae gen. sp.	EC	8	0	0	0	0	0.1 ± 0.4	0	0	0	0
Gnathiidae gen. sp.	EC	100	6	38	0	2	21.5 ± 22.6	0.1 ± 0.6	1.2 ± 2.0	0	0.02 ± 0.1

RJ, Rio de Janeiro; VG, Villa Gesell; MI, Miramar; PL, Puerto Lobos; CB, Craker Bay; EC, ectoparasite; AE, adult endoparasite; LE, larval endoparasite.

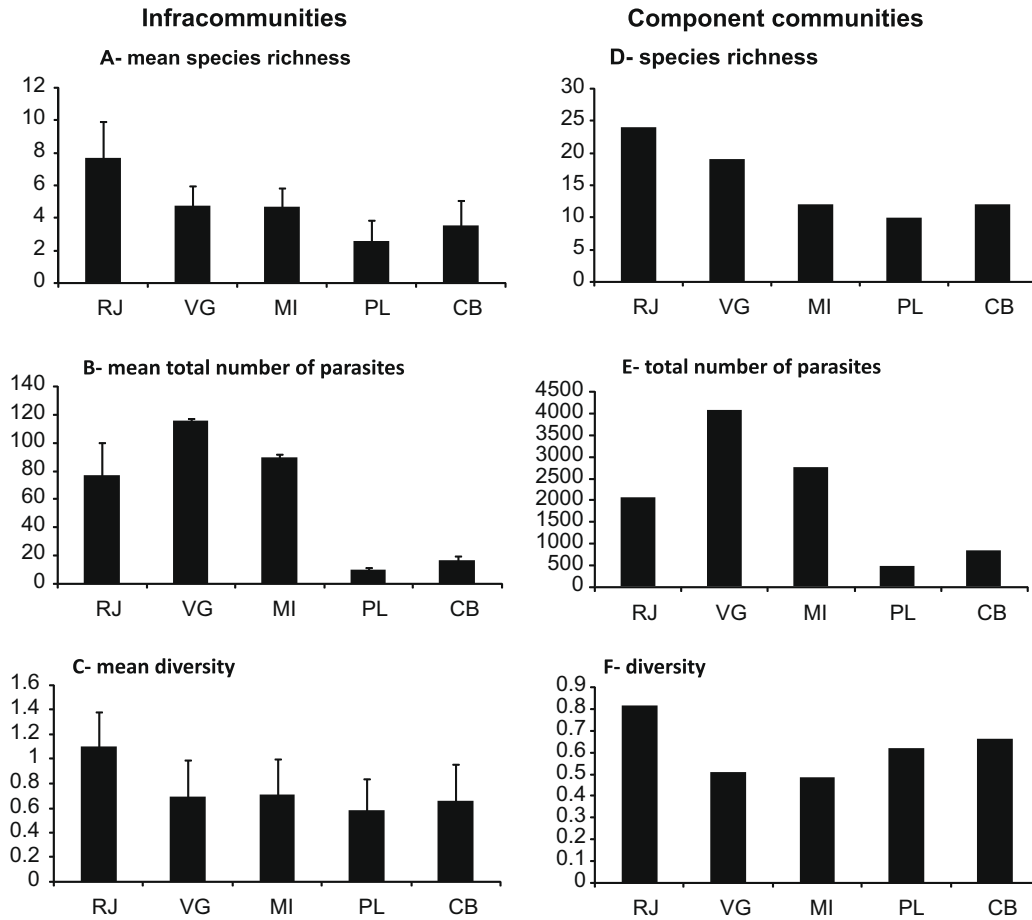


Fig. 2. Mean infracommunity and component community descriptors of parasite assemblages of *Pinguipes brasiliensis* in five zones of the southwestern Atlantic. RJ, Rio de Janeiro; VG, Villa Gesell; MI, Miramar; PL, Puerto Lobos; CB, Craker Bay.

Table 3
Comparisons of infracommunity descriptors of parasites of *Pinguipes brasiliensis* among five zones of the southwestern Atlantic.

	H	P	RJ-VG	RJ-MI	RJ-PL	RJ-CB	VG-MI	VG-PL	VG-CB	MI-PL	MI-CB	PL-CB
<i>Species richness</i>												
Total	94.7	<0.001	RJ > VG	RJ > MI	RJ > PL	RJ > CB	ns	VG > PL	Ns	MI > PL	Ns	PL < CB
Ectoparasites	55	<0.001	RJ > VG	RJ > MI	RJ > PL	Ns	ns	Ns	VG < CB	ns	Ns	ns
Adult endoparasites	124.8	<0.001	RJ > VG	RJ > MI	RJ > PL	RJ > CB	ns	Ns	VG < CB	MI < PL	MI < PL	ns
Larval endoparasites	139.1	<0.001	ns	ns	RJ > PL	RJ > CB	ns	VG > PL	VG > CB	MI > PL	MI > CB	ns
<i>Total number of parasites</i>												
Total	111.3	<0.001	ns	ns	RJ > PL	RJ > CB	ns	VG > PL	VG > CB	MI > PL	MI > CB	ns
Ectoparasites	117.9	<0.001	RJ > VG	RJ > MI	RJ > PL	RJ > CB	ns	Ns	VG < CB	ns	Ns	PL < CB
Adult endoparasites	119.2	<0.001	RJ > VG	RJ > MI	RJ > PL	ns	ns	VG < PL	VG < CB	MI < PL	MI < CB	PL < CB
Larval endoparasites	187.1	<0.001	RJ < VG	RJ < MI	RJ > PL	RJ > CB	ns	VG > PL	VG > CB	MI > PL	MI > CB	ns
<i>Diversity</i>												
Total	65.4	<0.001	RJ > VG	RJ > MI	RJ > PL	RJ > CB	ns	ns	Ns	ns	ns	ns
Ectoparasites	9.26	0.06	–	–	–	–	–	–	–	–	–	–
Adult endoparasites	38.6	<0.001	RJ > VG	–	RJ > PL	RJ > CB	–	ns	Ns	–	–	ns
Larval endoparasites	6.56	0.16	–	–	–	–	–	–	–	–	–	–

H, Kruskal–Wallis statistics; P, probability; RJ, Rio de Janeiro; VG, Villa Gesell; MI, Miramar; PL, Puerto Lobos; CB, Craker Bay; ns, not significant.

higher in RJ (Fig. 3A and B) and diversity showed no differences among localities (Fig. 3C). Species richness and total number of parasites in component communities showed a similar pattern to infracommunities (Figs. 3D and E), but diversity was notably lower in RJ (Fig. 3F).

Mean infracommunity species richness and diversity of adult endoparasites were higher in RJ, richness being extremely low in MI (Fig. 3A and C); on the other hand, CB showed the highest value

for the total number of parasites (Fig. 3B). A similar pattern was observed for all indices at component community level (Fig. 3D–F), but in this case species richness was also considerably higher in VG when compared to that of infracommunities. Finally, infracommunity indices of larval endoparasites showed different trends: species richness was similar among the three northern zones and significantly higher than in north Patagonian gulfs, PL and CB (Fig. 3A); the total number of parasite individuals was nota-

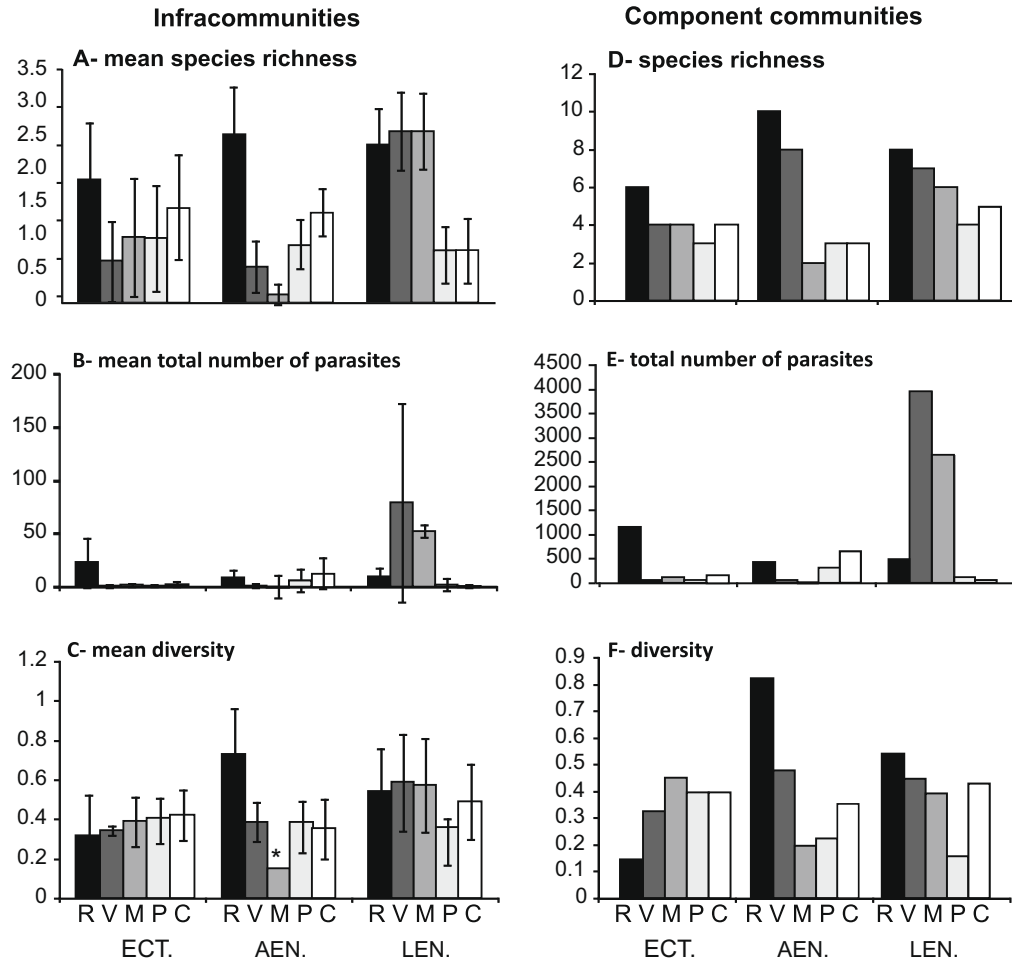


Fig. 3. Mean infracommunity and component community descriptors of parasite assemblages of *Pinguipes brasiliensis* in five zones of the southwestern Atlantic, discriminated by parasite guild. R, Rio de Janeiro; V, Villa Gesell; M, Miramar; P, Puerto Lobos; C, Craker Bay; ECT., ectoparasites; AEN., adult endoparasites; LEN., larval endoparasites; , value based on a single infracommunity.

bly higher in the central zones (Fig. 3B) and diversity showed no variation among zones (Fig. 3C). At the level of component community, differences among zones were less evident for species richness than among infracommunities (Fig. 3D) but similar to infracommunities for the total number of parasites (Fig. 3E). Diversity was similar among most zones except for its low value in PL (Fig. 3F). The relative importance of each guild, in terms of relative abundance, is shown in Fig. 4, with ectoparasites prevailing in RJ, larval endoparasites in VG and Mi, and adult endoparasites in PL and CB.

3.2. Similarity analyses

The qualitative “intrinsic” similarity, considering all parasites, was higher in the central zone (MI and VG); a similar pattern was observed for quantitative similarity, but in this case fish from RJ showed similar values to those of VG (Table 4). On the other hand, ectoparasite infracommunities were qualitatively and quantitatively more homogeneous at the northern and southern ends of the study area (CB and RJ). Intrinsic similarity for assemblages composed of adult endoparasites was higher among fish from CB than in all other zones, with extremely low values in both Bonae- rensis samples; the opposite trend was observed for larval endoparasites.

Similarity between pairs of zones also showed differences between analyses of the whole sample and those of individual guilds

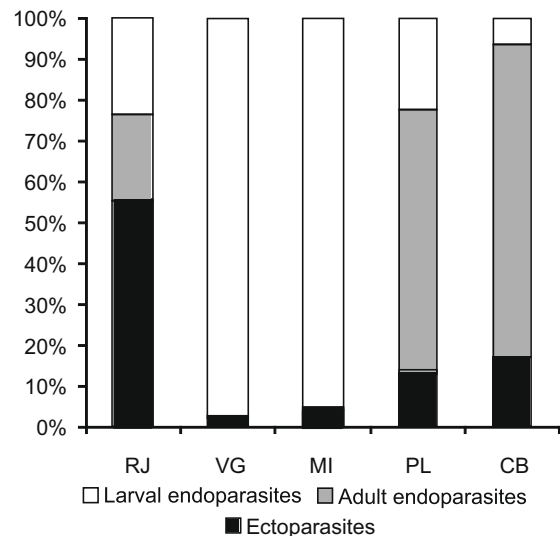


Fig. 4. Relative abundance of parasite guilds of *Pinguipes brasiliensis* in five zones of the southwestern Atlantic. RJ, Rio de Janeiro; VG, Villa Gesell; MI, Miramar; PL, Puerto Lobos; CB, Craker Bay.

(Table 5). For the whole sample, almost all mean values of similarity were smaller than intrinsic similarity in the respective

Table 4

Mean (plus SD) for qualitative (Jaccard) and quantitative (Sørensen) similarity indices of parasite infracommunities of *Pinguipes brasiliensis* within five zones of the southwestern Atlantic.

		Craker Bay	Puerto Lobos	Miramar	Villa Gesell	Rio de Janeiro
Total	Jaccard	0.36 ± 0.22	0.30 ± 0.23	0.55 ± 0.16	0.51 ± 0.18	0.33 ± 0.14
	Sørensen	0.29 ± 0.22	0.24 ± 0.22	0.46 ± 0.20	0.37 ± 0.21	0.38 ± 0.18
Ectoparasites	Jaccard	0.48 ± 0.36	0.26 ± 0.37	0.15 ± 0.28	0.18 ± 0.37	0.54 ± 0.26
	Sørensen	0.40 ± 0.30	0.24 ± 0.34	0.13 ± 0.24	0.15 ± 0.30	0.50 ± 0.26
Adult endoparasites	Jaccard	0.38 ± 0.36	0.24 ± 0.37	0.004 ± 0.06	0.05 ± 0.18	0.22 ± 0.23
	Sørensen	0.26 ± 0.28	0.13 ± 0.24	0.003 ± 0.05	0.04 ± 0.16	0.22 ± 0.24
Larval endoparasites	Jaccard	0.20 ± 0.37	0.34 ± 0.43	0.77 ± 0.20	0.73 ± 0.20	0.37 ± 0.27
	Sørensen	0.17 ± 0.32	0.25 ± 0.35	0.48 ± 0.21	0.39 ± 0.22	0.28 ± 0.24

Table 5

Mean (plus SD) for qualitative (Jaccard) and quantitative (Sørensen) similarity indices of parasite infracommunities of *Pinguipes brasiliensis* among zones of the southwestern Atlantic. Qualitative and quantitative similarity over and below the main diagonal, respectively.

	Craker Bay	Puerto Lobos	Miramar	Villa Gesell	Rio de Janeiro
<i>Total</i>					
Craker Bay	–	0.31 ± 0.22	0.11 ± 0.11	0.13 ± 0.12	0.01 ± 0.04
Puerto Lobos	0.23 ± 0.21	–	0.17 ± 0.15	0.19 ± 0.15	0.02 ± 0.04
Miramar	0.03 ± 0.04	0.06 ± 0.08	–	0.50 ± 0.18	0.12 ± 0.09
Villa Gesell	0.04 ± 0.05	0.07 ± 0.12	0.37 ± 0.19	–	0.08 ± 0.08
Rio de Janeiro	0.01 ± 0.02	0.01 ± 0.03	0.05 ± 0.06	0.03 ± 0.04	–
<i>Ectoparasites</i>					
Craker Bay	–	0.36 ± 0.38	0.08 ± 0.17	0.12 ± 0.24	0.02 ± 0.06
Puerto Lobos	0.31 ± 0.33	–	0.06 ± 0.16	0.09 ± 0.23	0.01 ± 0.06
Miramar	0.07 ± 0.16	0.05 ± 0.16	–	0.11 ± 0.26	0.21 ± 0.30
Villa Gesell	0.10 ± 0.21	0.08 ± 0.21	0.09 ± 0.22	–	0.04 ± 0.16
Rio de Janeiro	0.01 ± 0.03	0.004 ± 0.02	0.13 ± 0.21	0.02 ± 0.10	–
<i>Adult endoparasites</i>					
Craker Bay	–	0.29 ± 0.37	0.01 ± 0.05	0.05 ± 0.15	0.02 ± 0.07
Puerto Lobos	0.17 ± 0.25	–	0.01 ± 0.07	0.06 ± 0.19	0.02 ± 0.09
Miramar	0.002 ± 0.03	0.004 ± 0.05	–	0.01 ± 0.09	0.01 ± 0.06
Villa Gesell	0.03 ± 0.11	0.04 ± 0.15	0.01 ± 0.07	–	0.03 ± 0.11
Rio de Janeiro	0.01 ± 0.05	0.02 ± 0.08	0.004 ± 0.04	0.02 ± 0.09	–
<i>Larval endoparasites</i>					
Craker Bay	–	0.26 ± 0.41	0.18 ± 0.20	0.18 ± 0.20	0.002 ± 0.02
Puerto Lobos	0.21 ± 0.34	–	0.28 ± 0.27	0.29 ± 0.26	0.02 ± 0.07
Miramar	0.04 ± 0.07	0.07 ± 0.10	–	0.75 ± 0.20	0.16 ± 0.15
Villa Gesell	0.05 ± 0.09	0.08 ± 0.14	0.38 ± 0.20	–	0.15 ± 0.15
Rio de Janeiro	0.001 ± 0.02	0.01 ± 0.06	0.04 ± 0.06	0.04 ± 0.06	–

Similarity between zones ≥ similarity within one of the compared zones in bold.

localities, the only exception being the qualitative similarity between the nearby sites CB and PL. The same trend was observed for Jaccard and Sørensen indices applied to ectoparasite assemblages for this pair of localities and the two northern ones, RJ and VG. Adult endoparasites, on the other hand, not only showed the lowest values of similarity, but half of the comparisons showed higher values of similarity than those within one of the compared samples. Finally, for larval endoparasites, comparisons between CB and PL behaved as for other guilds, and the mean Jaccard index between VG and MI was also higher than within VG.

A decay in similarity of parasite assemblages over distance was recorded for most communities analysed using both similarity indices, the exception being the adult endoparasites, which showed a decrease in qualitative similarity with distance only for component communities (Table 6, Fig. 5). Therefore, this guild was excluded from further analysis. The slopes differed significantly between infracommunities and component communities in all cases ($P < 0.01$).

The Jaccard similarity index for the total community, despite showing the highest determination coefficient for both infracommunities and component communities (Table 6), decreased with distance with a lower slope than individual guilds at the component community level, whereas for infracommunities the highest

rate of decay was observed for larval endoparasites. In all cases, stronger similarity decay was observed for infracommunities in relation to component communities. A similar picture was observed for Sørensen's index, with the exception that the highest determination coefficient was observed for ectoparasites at the component community level, which also showed a more pronounced slope than infracommunities. Jaccard's index also showed a weaker slope than Sørensen's index for component communities, whereas the opposite situation was observed for infracommunities, with the exception of ectoparasites.

4. Discussion

To our knowledge the present findings represent the first description of parasite communities of *P. brasiliensis* in Brazilian waters, where this host showed the highest values of both species richness and number of endemic species. Two of the three species common to all zones, *M. pseudoperis* and *P. argentinensis*, are specific to pinguipedids in the studied zone (Amato and Cezar, 1994; Timi et al., 2007) and contributed greatly to the similarity among all studied fish populations. *Scolex polymorphus*, in turn, is a complex of larval cestode species (Chambers et al., 2000; Braicovich

Table 6
Regression statistics for the decay of similarity with distance in parasite communities of *Pinguipes brasiliensis* from five zones in the southwestern Atlantic. Intercepts are in units of ln (similarity), and slope values are in units of ln (similarity) per 1000 km distance.

Similarity index	Community level	Parasite guild	Intercept	Slope	r ²	P	
Jaccard	Component community	Total	-0.352	-0.182	0.96	<0.01	
		Ectoparasites	0.093	-0.289	0.87	<0.01	
		Adult endoparasites	1.636	-0.233	0.66	<0.01	
	Infracommunity	Larval endoparasites	Total	1.876	-0.245	0.80	<0.01
			Ectoparasites	-0.385	-0.430	0.84	0.03
		Adult endoparasites	Total	-0.721	-0.318	0.51	0.02
			Larval endoparasites	-1.526	-0.106	0.05	0.57
		Larval endoparasites	Total	0.117	-0.599	0.69	<0.01
			Ectoparasites				
Sørensen	Component community	Total	-0.589	-0.331	0.53	0.02	
		Ectoparasites	-0.047	-0.582	0.86	<0.01	
		Adult endoparasites	-0.543	-0.206	0.34	0.08	
	Infracommunity	Larval endoparasites	Total	-0.670	-0.419	0.54	0.01
			Ectoparasites	-0.746	-0.418	0.73	<0.01
		Adult endoparasites	Total	-0.692	-0.459	0.66	<0.01
			Larval endoparasites	-1.748	-0.085	0.03	0.66
		Larval endoparasites	Total	-0.614	-0.543	0.73	0.02
			Ectoparasites				

and Timi, 2008); these parasites can have different geographical distributions and cannot be used as a reliable indicator of similarity among host populations. The rest of the species, with the probable exception of *Cucullanus carioca*, *Neolebouria georgenascimentoi*, *Neobrachiella spinicephala* and *Heterosenis brasiliensis*, which also seem to be specific at the family or genus level (Vicente and Fernandes, 1973; Bray, 2002; Etchegoin et al., 2006; Vieira et al., 2009;), are not host-specific parasites, and are commonly reported parasitizing unrelated fish species. Typical examples of this group include several larval species (such as *Corynosoma australe*, *Grillotia* sp., *Hysterothylacium* sp.) in the central region of the study area, whose presence in fish hosts depends mainly on their availability in the compound community (Timi, 2007; Timi and Lanfranchi, 2009; Lanfranchi et al., in press).

Variations in diet composition or preferences could also be important in explaining the differences found in both faunal composition and burdens among zones. Accordingly, differential availability of both prey and infective stages of parasites have been highlighted as causes of spatial changes in parasite burden at a regional scale for *P. brasiliensis* and other fish species in the same region (Timi, 2003, 2007; Braicovich and Timi, 2008; Timi et al., 2008, 2009; Timi and Lanfranchi, 2009). Indeed, the geographical distribution of ectoparasite species with direct life cycles is mainly determined by environmental conditions. These conditions also have an influence on the distribution of endoparasites, either directly or via their effects on other host species (MacKenzie and Abaunza, 1998) and local environmental factors can regulate the survival and transmission success of infective stages causing spatial variations in parasite burdens (Pietroock and Marcogliese, 2003).

As a consequence of the differences in the parasite burdens among the different regions, parasite communities varied with respect to all descriptors. A more complex picture was observed when these comparisons were made separately for each parasite guild, which showed evident patterns of differential dominance in the three regions analyzed (Brazil, northern Argentina and Patagonian gulfs). A third level of variability was observed when parasite assemblages were analyzed at either infracommunity or component community levels, especially for species richness and diversity.

Therefore, the variation among parasite species (and guilds) in terms of host specificity (at larval or adult stage), their life-cycles strategies and availability evidently produce different geographical patterns in parasite communities. Consequently, it is not surprising that different responses to geographical distance were observed for

different guilds of parasites in a single host species. Such differences have been reported between ecto- and endoparasites in marine fishes from Chile (Oliva and Gonzalez, 2005), as well as for allogetic and autogenic species in freshwater fishes (Fellis and Esch, 2005). However, with the exception of Pérez-del-Olmo et al. (2009), no previously published studies have attempted to compare the effect of geographical distance between the two lowest levels of parasite community hierarchy, although comparisons between component and compound communities have been achieved for mite assemblages in rodent hosts (Vinarski et al., 2007).

An exponential decay of similarity, which implies a constant proportional reduction in similarity per unit distance (Poulin, 2003), was observed for most communities analyzed. Distance decay of similarity among parasite assemblages of *P. brasiliensis* could be due to the existence of geographic gradients in environmental conditions. Indeed, South American Atlantic coasts are orientated along a north–south axis. Two water currents characterize water circulation in the southwestern Atlantic Ocean, the Brazil Current (warm and saline waters) and the Malvinas Current (cold, low salinity subantarctic waters) both running parallel to the coast (Martos, 1989. Synopsis on the reproductive biology and early life history of *Engraulis anchoita*, and related environmental conditions in Argentine waters. The physical environment. Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. Montevideo, Uruguay, 21–23 August 1989. Workshop Report 584 N°. 65, Annex V, pp. 1–2. Montivideo: Intergovernmental Oceanographic Commission/UNESCO.). In this area, several oceanographic variables show latitudinal gradients, including water temperature, which decrease southwards (Bakun and Parrish, 1991; Hoffmann et al., 1997). Temperature, as a correlate of energy input, is a good predictor of latitudinal gradients in species richness and diversity (Rohde, 1992, 1999). The thermal gradient characteristic of the southwestern Atlantic is therefore expected to have a sufficient influence on the structure of parasite populations and communities, in terms of both composition and abundance, to produce a gradual change in parasite community structure in fish species inhabiting this region.

The localities of capture are distributed along this latitudinal/environmental gradient, therefore it is expected that geographic distance is correlated with this “environmental” distance, with geographic distance thus emerging as a predictor of similarity for parasite communities of *P. brasiliensis*, probably due to differential species responses to environmental variation (Vinarski et al., 2007). However, similarity can also decrease with geographic dis-

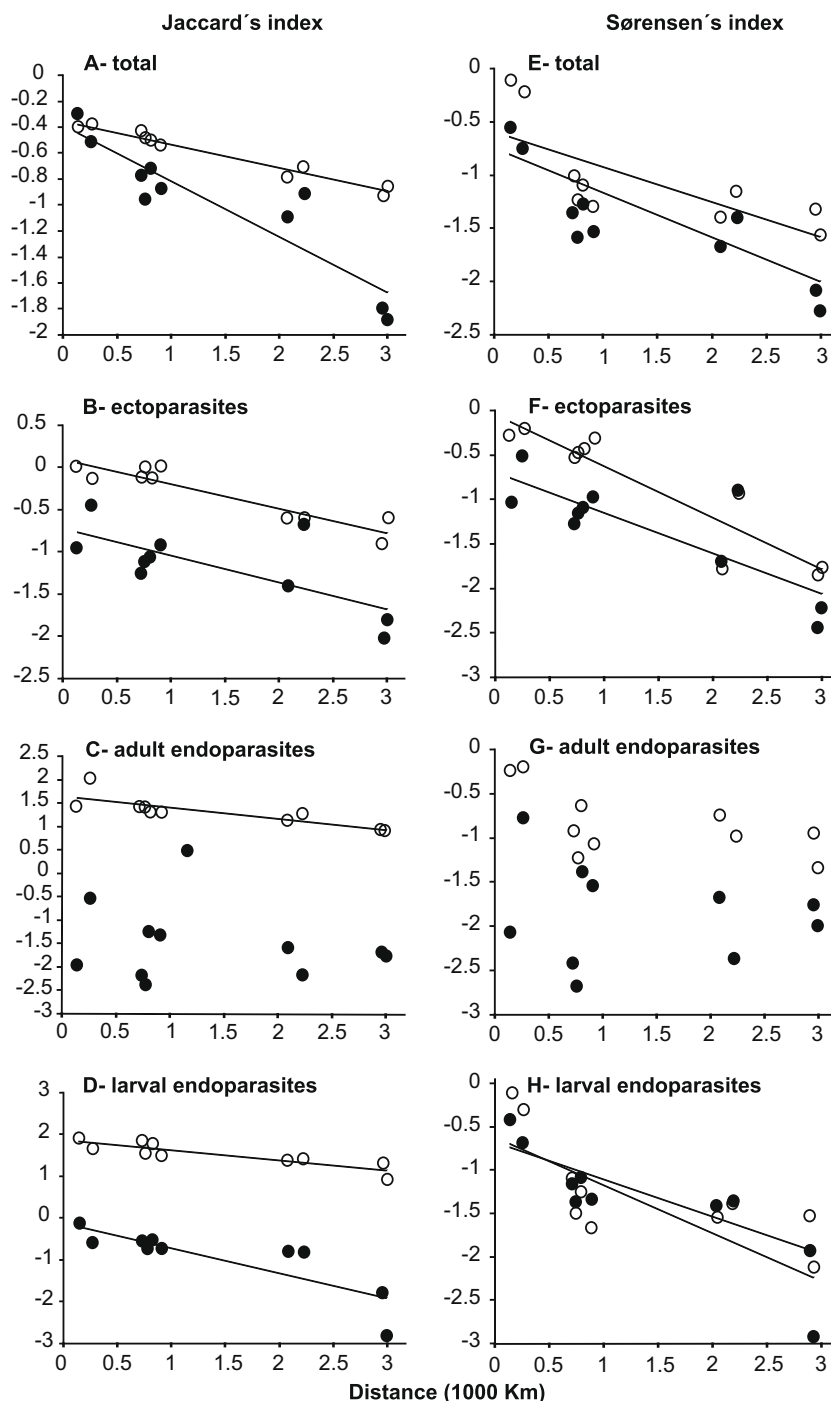


Fig. 5. Relationship between qualitative (Jaccard) and quantitative (Sørensen) log-transformed similarity and geographic distance in parasite species composition for both parasite fauna and different parasite guilds in *Pinguipes brasilianus* from five zones of the southwest Atlantic. Black circles: mean infracommunity similarity; white circles: component community similarity. Lines indicate that there is a significant relationship between the two variables.

tance as a result of a higher probability that geographic barriers occur over greater distances, and of the limited dispersal abilities of organisms, even in homogenous environments (Nekola and White, 1999; Brouat and Duplantier, 2007; Soininen et al., 2007).

Despite no geographic barriers existing in marine systems, the Rio de la Plata, in the study area, can represent a barrier for the dispersion of many marine parasites through an important discharge of freshwater in the Atlantic (mean river discharge estimated is $24,000 \text{ m}^3 \text{ s}^{-1}$, Acha et al., 2008). Furthermore, the composition and distribution of marine communities are governed by the

dynamics of oceanographic conditions on a regional scale. The abundance and distribution patterns of marine parasites are determined mainly by temperature and salinity profiles (Esch and Fernández, 1993) through the influence of physical conditions on both food webs and the availability of infective stages for trophically transmitted parasites (Klimpel and Rükert, 2005).

The oceanographic conditions in the study are not homogeneous, and have been identified as a primary cause of the differences in parasite burdens of *P. brasilianus*, through their influence on parasite transmission, as well as on the distribution of all hosts

involved in their life cycles (Timi et al., 2009). Indeed, the zones analyzed in the present study are located in different coastal basins, which display contrasting oceanographic and biological characteristics. Southeastern Brazilian coastal waters represent a region characterized by the convergence between two current systems, the warm, coast-hugging, southward-flowing Brazil Current and the cold, northward-flowing Malvinas/Falkland Current (Braga, 2001). In particular, the Cabo Frio (RJ) area is strongly characterized by a year-round upwelling which is the major contributor to the coldest surface water being found near this area (Castelao and Barth, 2006), whereas the zone of Villa Gesell, although greatly influenced by the Brazil current (tropical warm and saline waters), is also affected by the discharge of the Río de la Plata (Martos, 1989; Bakun and Parrish, 1991; Guerrero and Piola, 1997), mainly during spring and summer (Guerrero et al., 1997). On the other hand, southern samples were caught in enclosed and semi-enclosed areas, such as the semi-protected coastal areas of El Rincón (Miramar), San Matías Gulf (Puerto Lobos) and Nuevo Gulf (Craker Bay), which can generate their own oceanographic features. In the Argentinean Sea, all these locally modified waters create frontal zones with important biological properties (Acha et al., 2004). They provide reproductive grounds and zones of concentration for juveniles of several fish species by promoting retention of larvae (Guerrero and Piola, 1997; Piola and Rivas, 1997). In fact, two marine fronts are present in the central region of the study area, one associated with the Río de la Plata Estuary and other in the El Rincón Estuary (Acha et al., 2004). The processes associated with the formation of these fronts also influence the distribution of mesozooplankton between both zones, which have been classified as different faunistic areas (Marrari et al., 2004). In contrast, the San Matías Gulf is an isolated coastal basin, with oceanographic conditions differing markedly from those on the continental shelf (Gagliardini and Rivas, 2004). Furthermore, the geomorphology of the gulf mouth restricts the interchange of water with the open sea (Piola and Rivas, 1997), and its physical characteristics are thought to be responsible for larval retention and therefore stock discreteness in other fish species inhabiting the gulf (Di Giacomo et al., 1993).

All evidence indicates that these zones, with contrasting oceanographic characteristics, harbour different fish populations, mainly of resident species, as has been indicated by some ichthyological studies and others using parasites as biological tags (see Braicovich and Timi, 2008). Therefore, the observed similarity decay with distance, due to the existence of a latitudinal/environmental gradient, is probably enhanced by local oceanographic processes acting as barriers for parasite dispersal.

However, similarity among assemblages of adult endoparasites, although showing a negative relationship with distance, was only significant at the component community level for the qualitative Jaccard's index. On the other hand, similarity based on abundance data, such as the Sørensen index applied here, is probably affected more by local conditions than by geographic distance (Fellis and Esch, 2005).

Pérez-del-Olmo et al. (2009) attributed the lack of relationship between similarity and distance for the component communities they investigated to the dispersal of parasite colonizers across host populations (horizontal neighborhood colonization), but the detected spatial structure in quantitative comparisons was related to a vertical neighborhood colonization associated with larval dispersion at a local level. In other words, the authors argue that the structural, and not the compositional, divergence increases with geographical distance, owing to different turnover distances in parasite communities at different scales. Whereas it is likely that the influence of local environmental characteristics is higher for infracommunities than for component communities of *P. brasiliensis*, as shown by the comparisons of the slopes of most regressions, the

findings by Pérez-del-Olmo et al. (2009) based on all parasite species of the bogue could not be generalized to the present host-parasite system. Firstly, because in the present work each guild behaved differentially in relation to distance, and second because the compositional (qualitative) similarity always showed lower slopes than structural (quantitative) similarity at the component community level, indicating the influence of different methodologies to detect relationships. A quantitative analysis at the level of component communities of bogue could shed some light on this subject.

Other studies have found that geographic distance does not explain variation in similarity values of parasite component communities for several host species (Poulin, 2003; Krasnov et al. 2005; Oliva and Gonzalez, 2005; Brouat and Duplantier, 2007), as was the case for adult endoparasites in the present paper. For some marine fishes, this has been attributed to the proportion of the host geographic range analyzed or to homogeneity over the geographical area studied and qualitative similarity between adjacent areas (Oliva and Gonzalez, 2005). In the present paper, the whole distributional range of *P. brasiliensis* was sampled, and the significant decay observed for other guilds indicates that adjacent areas are not homogeneous. Instead, the similarity was as low between neighboring zones as between distant zones for adult endoparasites, therefore environmental (oceanographic) heterogeneity, and not homogeneity, could be responsible for the absence of a distance decay pattern for adult endoparasites.

Due to the biological and oceanographic differences between faunistic provinces, but also between regional coastal basins, the study area can be likened to a fragmented habitat, where both host and parasite dispersal levels could be very low. In the present study, adult endoparasites seem to be more affected than other guilds; in fact the proportion of endemic species (76.5%) was higher than those of ectoparasites (50%) and larval endoparasites (57.1%). This assumption, however, requires further study because some of the parasite species restricted to Brazilian waters, such as *Parahemiurus merus* or *Lecithochirium microstomum*, are commonly reported in other host species from Argentinean waters (Timi et al., 1999), and their life-cycle pathways, rather than dispersal abilities, could be affected differentially by local conditions.

The present study confirmed the occurrence of distance decay patterns for infracommunities which, as expected, undergo a stronger and significantly different effect of distance than component communities, probably due to a higher effect of short-term and local variability in oceanographic conditions when individual hosts are considered as habitats. This level of parasite community hierarchy can, therefore, be investigated to assess the effect of distance on assemblage similarity when higher levels, namely component or compound communities, show no such patterns. It is also evident that different parasite guilds respond differentially to the effects of geographic distance, and should be analyzed separately.

The rates of similarity decay with distance found here for a marine fish (slopes ranging from 0.18 to 0.60) were similar to that reported for the freshwater fish *Esox lucius*, and higher than that for *Perca flavescens*, by Poulin (2003) in freshwater environments. This result contrasts with the finding of Oliva and Gonzalez (2005), who found that the slopes of the relationship between distance and similarity in the marine fishes studied were lower (three orders of magnitude) than those recorded by Poulin (2003). Oliva and Gonzalez (2005) concluded that distance decay in similarity is greater among fragmented freshwater habitats than in open and continuous marine systems because exchange and dispersal of species is probably constrained in the former. However, their result is a consequence of the effect of the geographical scale utilized (nautical miles) on the parameters of the regression function, whereas the scale units used by Poulin (2003) and in the present study were the same (1000 km). Therefore, with the available information,

host (and parasite) dispersal probabilities over geographical distance seem to be no more constrained in freshwater than in marine environments. The present results also agree with those by Pérez-del-Olmo et al. (2009), in downplaying the importance of host vagility as a primary determinant of similarity decay among parasite assemblages in marine fish.

Finally, and in agreement with previous studies on the use of parasites as biological tags for stock discrimination of *P. brasiliensis* (Timi et al., 2008, 2009), the differences at both population and community levels, as well as the low similarity values between Brazilian and Argentinean samples, indicate that sandperches from the area of Rio de Janeiro clearly constitute an independent population, as has been demonstrated for *Cynoscion guatucupa* (Timi et al., 2005), the only previous study aimed at discriminating fish populations between Argentinean and Brazilian waters.

Further studies, including other host species from the same sampling localities, could test the generality of the similarity patterns observed for each guild in order to determine whether the oceanographic conditions in the southwestern Atlantic drive fish parasite assemblages toward general geographical patterns.

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References

- Acha, E.M., Mianzán, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America physical and ecological process. *J. Mar. Syst.* 44, 83–105.
- Acha, E.M., Mianzán, H., Guerrero, R.A., Carreto, J., Giberto, D., Montoya, N., Carnigan, M., 2008. An overview of physical and ecological processes in the Rio de la Plata Estuary. *Cont. Shelf Res.* 28, 1579–1588.
- Amato, J.F.R., Cezar, A.D., 1994. A new species of *Microcotyle* van Beneden & Hesse, 1863, parasitic of “namorado”, *Pseudoperca numida* Ribeiro, 1903 and *O. semifasciata* (Cuvier, 1829), from the coast of the State of Rio de Janeiro. *Brazil. Rev. Bras. Parasitol. Vet.* 3, 41–44.
- Bakun, A., Parrish, R.H., 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *J. Mar. Sci.* 48, 343–361.
- Baselga, A., 2007. Disentangling distance decay of similarity from richness gradients: response to Soinen et al. 2007. *Ecography* 30, 838–841.
- Bjorholm, S., Svenning, J.-C., Skov, F., Balslev, H., 2008. To what extent does Tobler's 1st law of geography apply to macroecology? A case study using American palms (*Arecaceae*). *BMC Ecol.* 8, 11.
- Bogazzi, E., Baldoni, A., Rivas, A., Martos, P., Reta, R., Orensanz, J.M., Lasta, M., DellArciprete, P., 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the Southwestern Atlantic. *Fish. Oceanogr.* 14, 359–376.
- Bordes, F., Morand, S., 2008. Helminth species diversity of mammals: parasite species richness is a host species attribute. *Parasitology* 135, 1701–1705.
- Braga, A.C., 2001. O ambiente e a biodiversidade. In: Bizerril, C.R.S.F., Costa, P.A.S. (Eds.), *Peixes Marinhos do Estado do Rio de Janeiro*. Fundação de Estudos do Mar, Rio de Janeiro, pp. 13–32.
- Braicovich, P.E., Timi, J.T., 2008. Parasites as biological tags for stock discrimination of the Brazilian flathead in the South West Atlantic. *J. Fish Biol.* 73, 557–571.
- Bray, R.A., 2002. Three species of plagioporine opecoelids (Digenea), including a new genus and two new species, from marine fishes from off the coast of Chile. *Syst. Parasitol.* 51, 227–236.
- Brouat, C., Duplantier, J.-M., 2007. Host habitat patchiness and the distance decay of similarity among gastro-intestinal nematode communities in two species of *Mastomys* (southeastern Senegal). *Oecologia* 152, 715–720.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. Revisited. *J. Parasitol.* 83, 575–583.
- Castelao, R.M., Barth, J.A., 2006. Upwelling around Cabo Frio, Brazil: the importance of wind stress curl. *Geophys. Res. Lett.* 33, L03602.
- Chambers, C.B., Cribb, T.H., Malcolm, J.K., 2000. Tetrathyllidean metacestodes of teleosts of the Great Barrier Reef, and the use of *in vitro* cultivation to identify them. *Folia Parasitol.* 47, 285–292.
- Di Giacomo, E.E., Calvo, J., Perier, M.R., Morriconi, E., 1993. Spawning aggregations of *Merluccius hubbsi*, in Patagonian waters: evidence for a single stock? *Fish Res.* 16, 9–16.
- Esch, G.W., Fernández, J.C., 1993. *A Functional Biology of Parasitism*. Chapman & Hall, London.
- Etchegoin, J.A., Timi, J.T., Lanfranchi, A.L., 2006. Redescription of *Neobrachiella spinicephala* (Ringuet, 1945) parasitic on *Pinguipes brasiliensis* Cuvier, 1829 from Argentina, with the first description of the male. *Acta Parasitol.* 51, 290–293.
- Fellis, K.J., Esch, G.W., 2005. Variation in life cycle affects the distance decay of similarity among bluegill sunfish parasite communities. *J. Parasitol.* 91, 1484–1486.
- Floeter, S.R., Gasparini, J.L., 2000. The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *J. Fish Biol.* 56, 1099–1114.
- Gagliardini, D.A., Rivas, A.L., 2004. Environmental characteristic of San Matías gulf obtained from LANDSAT-TM and ETM+ data. *Gayana (Concepción)* 68, 186–193.
- Guégan, J.-F., Kennedy, C.R., 1996. Parasite richness/sampling effort/host range: the fancy three-piece jigsaw puzzle. *Parasitol. Today* 12, 367–369.
- Guerrero, R.A., Piola, A.R., 1997. Masas de agua en la plataforma continental. In: Boschi, E.E. (Ed.), *El Mar Argentino y sus Recursos Pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, vol. 1. INIDEP, Mar del Plata, Argentina, pp. 107–118.
- Guerrero, R.A., Acha, E.M., Framinan, M.B., Lasta, C.A., 1997. Physical oceanography of the Río de la Plata Estuary, Argentina. *Cont. Shelf Res.* 17, 727–742.
- Hoffmann, J., Núñez, M., Piccolo, M., 1997. Características climáticas del océano Atlántico sudoccidental. In: Boschi, E.E. (Ed.), *El Mar Argentino y sus Recursos Pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, vol. 1. INIDEP, Mar del Plata, Argentina, pp. 163–193.
- Klimpel, S., Rükert, S., 2005. Life cycle strategy of *Hysterothylacium aduncum* to become the most abundant anisakid fish nematode in the North Sea. *Parasitol. Res.* 97, 141–149.
- Krasnov, B.R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S., Poulin, R., 2005. Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographic distance or faunal similarity? *J. Biogeogr.* 32, 633–644.
- Lanfranchi, A.L., Rossini, M.A., Timi, J.T., in press. Parasite infracommunities of a specialised marine fish species in a compound community dominated by generalist parasites. *J. Helminthol.*
- Luque, J.L., Poulin, R., 2007. Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology* 134, 865–878.
- MacKenzie, K., Abaunza, P., 1998. Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fish Res.* 38, 45–56.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, New Jersey.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, second ed. Chapman & Hall, London.
- Marrari, M., Viñas, M.D., Martos, P., Hernández, D., 2004. Spatial patterns of mesozooplankton distribution in the Southwestern Atlantic Ocean (34–41 S) during austral spring: relationship with the hydrographic conditions. *J. Mar. Sci.* 61, 667–679.
- Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26, 867–878.
- Oliva, M.E., Gonzalez, M.T., 2005. The decay of similarity over geographical distance in parasite communities of marine fishes. *J. Biogeogr.* 32, 1327–1332.
- Pérez-del-Olmo, A., Fernández, M., Raga, J.A., Kostadinova, A., Morand, S., 2009. Not everything is everywhere: the distance decay of similarity in a marine host-parasite system. *J. Biogeogr.* 36, 200–209.
- Pietrock, M., Marcogliese, D.J., 2003. Free-living endohelminth stages: at the mercy of environmental conditions. *Trends Parasitol.* 19, 293–299.
- Piola, A.R., Rivas, A.L., 1997. Masas de agua en la plataforma continental. In: Boschi, E.E. (Ed.), *El Mar Argentino y sus Recursos Pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, vol. 1. INIDEP, Mar del Plata, Argentina, pp. 119–132.
- Poulin, R., 1997. Species richness of parasite assemblages: evolution and patterns. *Annu. Rev. Ecol. Syst.* 28, 341–358.
- Poulin, R., 2003. The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *J. Biogeogr.* 30, 1609–1615.
- Poulin, R., 2007a. The structure of parasite communities in fish hosts: ecology meets geography and climate. *Parassitologia* 49, 169–172.
- Poulin, R., 2007b. Are there general laws in parasite ecology? *Parasitology* 134, 763–776.
- Poulin, R., 2007c. *Evolutionary Ecology of Parasites*, second ed. Princeton University Press, Princeton.
- Poulin, R., Morand, S., 1999. Geographical distances and the similarity among parasite communities of conspecific host populations. *Parasitology* 119, 369–374.
- Qian, H., Ricklefs, R.E., White, P.S., 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecol. Lett.* 8, 15–22.
- Rohde, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527.
- Rohde, K., 1999. Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* 22, 593–613.
- Rohde, K., 2005. *Marine Parasitology*. Csiro Publishing, CAB International.

- Rohde, K., Heap, M., 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *Int. J. Parasitol.* 28, 461–474.
- Rosa, I.L., Rosa, R.S., 1997. Systematic revision of the South American species of Pinguipedidae (Teleostei, Trachinoidei). *Rev. Bras. Zool.* 14, 845–865.
- Seifertová, M., Vyskočilová, M., Morand, S., Šimková, A., 2008. Metazoan parasites of freshwater cyprinid fish (*Leuciscus cephalus*): testing biogeographical hypotheses of species diversity. *Parasitology* 138 (5), 1417–1435.
- Soininen, J., Hillebrand, H., 2007. Disentangling distance decay of similarity from richness gradients – response to Baselga (2007). *Ecography* 30, 842–844.
- Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. *Ecography* 30, 3–12.
- Thieltges, D.W., Ferguson, M.A.D., Jones, C.S., Krakau, M., de Montaudouin, X., Noble, L.R., Reise, K., Poulin, R., 2009. Distance decay of similarity among parasite communities of three marine invertebrate hosts. *Oecologia* 160, 163–173.
- Timi, J.T., 2003. Parasites of Argentine anchovy in the Southwest Atlantic: latitudinal patterns and their use for discrimination of host populations. *J. Fish Biol.* 63, 90–107.
- Timi, J.T., 2007. Parasites as biological tags for stock discrimination in marine fish from South American Atlantic waters. *J. Helminthol.* 81, 107–111.
- Timi, J.T., Lanfranchi, A.L., 2009. The metazoan parasite communities of the Argentinean sandperch *Pseudoperca semifasciata* (Pisces: Perciformes) and their use to elucidate the stock structure of the host. *Parasitology* 136, 1209–1219.
- Timi, J.T., Martorelli, S.R., Sardella, N.H., 1999. Digenetic trematodes parasitic on *Engraulis anchoita* (Pisces: Engraulidae) from Argentina and Uruguay. *Folia Parasitol.* 46, 132–138.
- Timi, J.T., Luque, J.L., Sardella, N.H., 2005. Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination. *J. Fish Biol.* 67, 1603–1618.
- Timi, J.T., Rossin, M.A., Lanfranchi, A.L., Etchegoin, J.A., 2007. A new species of *Paracapillaria* (Nematoda: Capillariidae) parasitizing the Brazilian sandperch, *Pinguipes brasiliensis*, (Pisces: Pinguipedidae) from Argentina. *J. Parasitol.* 93, 922–924.
- Timi, J.T., Lanfranchi, A.L., Etchegoin, J.A., Cremonte, F., 2008. Parasites of the Brazilian sandperch, *Pinguipes brasiliensis* Cuvier: a tool for stock discrimination in the Argentine Sea. *J. Fish Biol.* 72, 1332–1342.
- Timi, J.T., Lanfranchi, A.L., Etchegoin, J.A., 2009. Seasonal stability and spatial variability of parasites in Brazilian sandperch *Pinguipes brasiliensis* from the Northern Argentine Sea: evidence for stock discrimination. *J. Fish Biol.* 74, 1206–1225.
- Vicente, J.J., Fernandes, B.M.M., 1973. Sobre um nematódeo do gênero *Cucullanus* Muller, 1777 parasito de “Namorado” (Nematoda, Camallanoidea). *Atas Soc. Biol. Rio de Janeiro* 17, 31–33.
- Vieira, F.M., Felizardo, N.N., Luque, J.L., 2009. A new species of *Heterosentis* Van Cleave, 1931 (Acanthocephala, Arhythmacanthidae) parasitic in *Pseudoperca numida* Miranda Ribeiro, 1903 (Perciformes, Pinguipedidae) from southeastern Brazilian coastal zone. *J. Parasitol.* 95, 747–750.
- Vinarski, M.B., Korralo, N.P., Krasnov, B.R., Shenbrot, G.I., Poulin, R., 2007. Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host-species composition or environment. *J. Biogeogr.* 34, 1691–1700.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth ed. Prentice-Hall Inc., Englewood Cliffs, New Jersey.