GEOGRAPHICAL PATTERNS OF PARASITE INFRACOMMUNITIES IN THE ROUGH SCAD, *TRACHURUS LATHAMI* NICHOLS, IN THE SOUTHWESTERN ATLANTIC OCEAN

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ABSTRACT: We assessed temporal variability in parasite infections of rough scad (*Trachurus lathami*) in 3 samples from Miramar (MI) in 2008, separated by periods of 1 mo, and 2 samples from Villa Gesell (VG), 1 each in 2008 and 2009 (Buenos Aires Province, Argentina), respectively. A sample was also obtained from Cabo Frio (CF) (Brazil) in 2009 to compare differences in parasite communities between fish from this locality and each Argentinean locality. All rough scad were parasitized by at least 1 of 27 parasite species. Similarity-based multivariate analysis revealed significant differences between localities, but temporal homogeneity in each Argentinean locality. Overall, prevalence and abundance of parasite species were most similar between samples from MI and VG, while the greatest differences occurred between samples from MI and CF. A canonical analysis of principal coordinates showed significant differences among samples. *Grillotia carvajalregorum* was the most important species in determining the position of Argentinean samples, especially those from MI, while *Ectenurus virgulus*, *Raphidascaris* sp., and *Hysterothylacium* sp. were the most important species related to fish from CF. The parasite assemblage of *T. lathami* showed a notable temporal persistence within the same locality and a high variability at the spatial scale, suggesting the existence of 3 independent stocks of *T. lathami* in South Atlantic waters.

The rough scad, *Trachurus lathami*, the only member of the genus inhabiting the western Atlantic (Saccardo, 1987), is widely distributed from the Gulf of Maine, United States (43°00′N) to the San Matías Gulf (41°30′S) in Argentina. It is an abundant and extremely important forage species for commercially valuable fish species along the Atlantic coast (Ciechomski and Cassia, 1980) and has the potential to become an alternative to the declining fisheries of other small pelagic fish such as sardines, *Sardinella brasiliensis* (Saccardo and Katsuragawa, 1995).

In southern Brazil and Uruguay, *T. lathami* undergo seasonal migrations (Saccardo and Katsuragawa, 1995). Concentrations of this species, which occur off the state of Rio Grande do Sul in southern Brazil in summer and autumn, move northward in summer whereas those appearing off Uruguay and southern Brazil during winter and spring come from southern areas off Argentina. Thus, it has been suggested that 2 populations inhabit the southern Brazilian waters (Cousseau and Perrotta, 2004). The same behavior is observed along the northern Argentinean coast, with adults appearing in coastal waters during spring to reproduce (Cousseau and Perrotta, 2004), although the source of this assemblage is still unknown.

Understanding the complex processes involved in the variability of abundance of pelagic fish stocks, especially within short and medium time scales, would increase the ability to predict the abundance and commercial exploitation of these resources which, in turn, should enhance the capacity to properly manage the fisheries and ensure their sustainable exploitation (Fréon et al., 2005). Since the 1970s, an increasing emphasis has been placed upon parasites as indicators of ecological relationships in terms of ecological and phylogenetic relationships (Campbell et al., 1980), and parasites have also been widely used to discriminate fish populations or stocks as well as to trace fish migration (Williams et al., 1992; MacKenzie and Abaunza, 1998; MacKenzie, 2002). Although the terms 'stock' and 'population' are presently used interchangeably (Begg and Waldman, 1999), we use the concept in the context of 'ecological stocks', i.e., subpopulations of fish distinguished by behavioral differences but between which there may be a considerable amount of gene flow (MacKenzie, 2002).

The existence of spatial variability in the composition and abundance of fish parasite assemblages constitutes the basis for this methodology, which focuses on the differences among parasite populations and communities between zones (MacKenzie and Abaunza, 1998; Begg and Waldman, 1999; MacKenzie, 2002; Power et al., 2005). In fact, parasites have been used extensively as biological markers to identify and delineate populations of other *Trachurus* species in different regions of the world, e.g., *Trachurus trachurus* from north and northwest of Spain (Abaunza et al., 1995) and the northeast Atlantic and Mediterranean Sea (MacKenzie et al., 2008), *Trachurus* spp. from the eastern Atlantic (Gaevskaya and Kovaleva, 1980), and *Trachurus murphyi* (=*Trachurus symmetricus murphyi*) from the southeastern Pacific Ocean (Avdeev, 1992; George-Nascimento and Arancibia, 1992; Aldana et al., 1995; George-Nascimento, 2000).

Most studies using parasites as indicators have only examined a single sample at each locality, largely ignoring the potential temporal variability of parasite communities (Chavez et al., 2007). This approach, however, requires a high degree of temporal repetition in the composition and structure of parasite communities to allow comparative studies over long-term temporal scales.

Studies on seasonal repeatability of population and community attributes of fish parasites in the northern Argentinean Sea have demonstrated that parasite assemblages are stable seasonally (Timi et al., 2009; Braicovich and Timi, 2010), and also on shorter temporal scales (Rossin and Timi, 2010), because of the dominance of long-lived and relatively non-specific larval helminths in the parasite communities of all fish species studied in the region (Timi, 2007). Consequently, these parasites provide predictability for the infracommunities to which they belong, independent of the host species, including *T. lathami*.

Therefore, before large-scale spatial comparisons of parasite assemblages of *T. lathami* can be made between localities, estimates of temporal variations are needed to avoid their possible confounding effects. The aim of the present study was, therefore, 3-fold: (1) to assess the occurrence of between-month variations in the composition of the parasite infracommunities of *T. lathami* in a single locality from Argentinean Sea; (2) to evaluate the effect of between-year variability on parasites

FIGURE 1. Map showing the study area and the sampling sites.

burdens of *T. lathami*; and (3) to identify the existence of different stocks in 3 zones of the south Atlantic waters.

MATERIALS AND METHODS

Fish samples and parasite inventories

In total, 273 specimens of *T. lathami* were examined for parasites. Fish were caught by commercial trawlers in 3 zones along the coast of the southwestern Atlantic (Fig. 1). To assess the effect of temporal (between-month) variability on parasite loads, 3 samples were obtained from the Miramar area (MI; Buenos Aires Province, Argentina), separated by periods of 1 mo during spring when adult fish arrive in coastal waters. To evaluate the effect of inter-annual variation, we examined samples from the Villa Gesell area (VG; Buenos Aires Province, Argentina) caught in September 2008 and August 2009. A sample from Cabo Frío (CF; State of Rio de Janeiro, Brazil) collected in October 2009 was used to assess geographic differences (Table I).

Fish were either kept fresh or deep frozen in individual plastic bags at −18 C until necropsy. After thawing, the total length (TL in cm) of each fish was measured and parasites from the gills, branchial and body cavities, and viscera (stomach, intestine, liver, gonads, and mesenteries) were collected with the aid of a stereoscopic microscope.

The prevalence and mean abundance (± SD) were calculated for most parasite species in each sample following Bush et al. (1997). Two parasites were excluded from further analyses: (1) larval *Ascarophis marina* found in the alimentary tract and considered an accidental parasite, and (2) *Scolex polymorphus*, a species complex of larval cestodes (Chambers et al., 2000) with different geographical distributions and, therefore, unreliable indicators of similarity among host populations (Braicovich and Timi, 2008). These two parasites cannot be used as reliable indicators of similarity among host populations (Braicovich and Timi, 2008). Only the prevalence was recorded for the microparasites (*Goussia cruciata* and *Ceratomyxa* sp.). These parasites and cysts of unknown etiology (see MacLean et al., 1987) were excluded from further comparative analyses. Fish lengths in different samples were compared using a 1-way ANOVA or a *t*-test (Zar, 1999), depending on the number of samples compared. Multivariate analysis on parasite infracommunity data was implemented in PERMANOVA+ for PRIMER package (Anderson et al., 2008). As a similarity measure in all analyses, the Bray-Curtis index, which considers the differences in abundance of each shared parasite species (Magurran, 1988), was used with untransformed data. Comparative analyses were restricted to those species with a prevalence of >10% in at least 1 of the compared samples.

Analyses of temporal variability

The differences in infracommunity composition were tested by means of a 1-way permutational multivariate analysis of variance (PERMANOVA) of samples from MI. Following Anderson et al. (2008), a permutation of residuals with a reduced model was used as the method of permutation. A sequential sum of squares (Type I SS) was applied because host size was introduced as a covariable (ANCOVA model) due to the known effect of fish size–age on parasite burdens. The structure of parasite infracommunities between monthly samples (1 × 3 factorial design, with month as the random factor) was compared by testing for main effects after 9,999 permutations.

The differences in infracommunity composition between years were tested using samples from VG in a similar way as those for monthly samples using a 1 × 2 factorial design with years as the random factor.

Analyses of geographic variability

Differences between localities were analyzed by pooling fish from each Argentinean locality as a single sample (Table I). Chi square analyses and a posteriori multiple comparisons for proportions were used to test for significant differences in prevalence between zones. Abundances of individual species were compared by univariate PERMANOVA tests,

TABLE I. Composition of samples of *Trachurus lathami* in three zones of the southwestern Atlantic.

Locality	Locality code	Latitude, longitude	Date of capture	n	Total length (cm) ± SD
Miramar	MI	38°34′S, 58°3′W	September 2008	49	19.8 ± 0.7
Miramar	MI	38°34′S, 58°3′W	October 2008	46	20.1 ± 0.7
Miramar	MI	38°34′S, 58°3′W	November 2008	50	20.1 ± 0.8
Villa Gesell	VG	36°44′S, 55°44′W	September 2008	42	19.4 ± 0.8
Villa Gesell	VG	36°44′S, 55°44′W	August 2009	36	19.6 ± 0.9
Cabo Frio	CF	22°53′S, 42°00′W	October 2009	50	19.3 ± 0.6
Miramar (pooled sample)	MIP	38°34′S, 58°3′W	September–November 2008	145	20.0 ± 0.7
Villa Gesell (pooled sample)	VGP	36°44′S, 55°44′W	August 2008, October 2009	78	19.5 ± 0.9

applied as in previous analyses but with a 1×3 factorial design with zones as fixed factors.

Zones were considered as fixed factors based on the following regional characteristics: they belong to 2 different faunistic provinces in the South American Atlantic, i.e., CF to the Brazilian Province and VG and MI to the Argentine Province (Floeter and Gasparini, 2000; Bogazzi et al., 2005). These zones are located in different coastal basins which display contrasting oceanographic and biological characteristics. These differences are evident even between the 2 areas of Argentina, despite their proximity. The zone of VG is influenced by the Brazilian current (tropical warm and saline waters) and is also greatly affected by the discharge of the Río de la Plata (Bakun and Parrish, 1991; Guerrero et al., 1997). Samples from MI were caught in the northern boundary of a semi-enclosed area of El Rincón which generates its own oceanographic features. In the Argentinean Sea, locally modified waters in both MI and VG create frontal zones with important biological properties (Acha et al., 2004). These waters provide reproductive grounds and zones of concentration for juveniles of several fish species by promoting retention of larvae (Piola and Rivas, 1997). The fronts also influence the distribution of mesozooplankton between both zones, which have been classified as different faunistic areas (Marrari et al., 2004). All evidence indicates that these zones, with different oceanographic characteristics, harbor different fish populations, mainly of resident species (Jaureguízar et al., 2006). Therefore, local oceanographic processes in Argentine waters can also act as barriers for parasite dispersal, leading to significant differences in composition of fish parasite assemblages between VG and MI, as has been recorded for other fish species (Timi et al., 2009; Timi and Lanfranchi, 2009), indicating that in each zone fish are exposed to qualitative and qualitatively different assemblages of infective stages of parasites.

Because PERMANOVA is sensitive to differences in multivariate dispersion between groups, e.g., homogeneity of variances that can inflate Type 1 error even when centroids have identical locations, the same models were tested for differences in dispersion using the PERMDISP routine (Anderson et al., 2008). Dispersions were measured as distances to the centroids, and each term in the analysis was tested using 9,999 permutations, with significant terms investigated using a posteriori pairwise comparisons with the PERMANOVA t-statistic (Anderson et al., 2008). PEMANOVA and PERMDISP multivariate analyses were repeated to compare the structure of parasite infracommunities between geographic zones. Where differences were detected by PERMANOVA, pair-wise comparisons were used to determine which samples differed. In the particular case of geographic comparisons, multivariate PERMANOVA analyses were repeated on untransformed data for long-lived parasites only because this group of parasites is recommended for studies on fish stock discrimination (see Lester and MacKenzie, 2009). The same analyses were done on square-root transformed abundances in order to down-weight the importance of very abundant species, allowing for the awareness that less-dominant species can play some role in determining similarity among samples (Clarke and Gorley, 2006).

Differences of infracommunities among samples were examined in more detail using canonical analysis of principal coordinates (CAP), not only to confirm the possible differences found by PERMANOVA but also to characterize them in order to identify those species responsible for such differences (Anderson and Willis, 2003; Anderson et al., 2008). Principal coordinates (PCO) were calculated from the resemblance matrix, and potential over-parameterization was prevented by choosing the number of PCO axes (m) that maximized 'leave-1-out' allocation success to groups (Anderson and Robinson, 2003). To test for significant differences in infracommunities among the samples, a permutation "trace" test (sum of squared canonical eigenvalues) was applied, and P was obtained after 9,999 permutations. An indication of the underlying species differences in community structure was obtained by the strength of their correlation of the canonical discriminant axes coordinates with diagnostic compounds visualized using vector overlays based on Spearman correlations. Only species correlations of $|r| > 0.4$ were considered significant.

RESULTS

General pattern

All rough scad were parasitized by at least 1 of the 27 species of parasites listed in Tables II and III. The larval cestode *Grillotia*

carvajalregorum was particularly abundant in Argentinean samples, dominating in 100% of infracommunites, while third-stage larva of *Hysterothylacium* sp. and the adult digenean *Ectenurus virgulus* dominated the infracommunities (46% each) in the Brazilian sample.

Four species were found only in fish from CF, and 9 were exclusive to MI and VG; the rest were found in all locations. Eleven species are reported as new host records for *T. lathami* and are indicated by (*) in the tables.

Analyses of temporal variability

No significant differences were observed for host TL between samples from MI ($F_{2, 144} = 2.05$, $P > 0.05$). PERMANOVA results showed that a significant amount of the variability of data was accounted for by host size (*Pseudo* $F_1 = 8.62$, P *[perm]* < 0.001). The lack of interaction of host length with month (*Pseudo* $F_2 = 0.77$, P *[perm]* > 0.015), however, shows that the nature of the relationship between fish size and the parasite's community structure does not differ between different levels of the factor. Furthermore, considering the variations among samples due to host size, no significant variability was detected among the assemblages in each month (*Pseudo* $F_2 = 1.90$, P *[perm]* > 0.05).

No significant differences were observed for host TL between samples from VG ($t_{76} = 1.087$, $P > 0.05$). As in previous comparisons, PERMANOVA results showed that a significant amount of the variability of data was accounted for by host size (*Pseudo* $F_1 = 12.12$, P *[perm]* < 0.001), with the relationship between this variable and the structure of assemblages not differing between years (*Pseudo* $F_1 = 1.44$, P *[perm]* > 0.05). Also, no significant variability was detected between the assemblages in either year (*Pseudo* $F_1 = 0.64$, P *[perm]* > 0.05).

Analyses of geographic variability

Because no differences in parasite infracommunity structure were observed for the 3 samples from MI and the 2 samples from VG, fish were pooled in each locality (MIP and VGP). However, mean host TL in the CF, MIP, and VGP samples differed significantly among the zones ($F_{2, 272} = 21.575$, $P < 0.01$). This variability was due to significant differences between MIP and the other 2 samples (both $P < 0.01$), whereas fish from VGP and CF did not differ in TL ($P > 0.05$).

Comparisons of parasite prevalence (Table IV) showed that most parasite species varied significantly between zones. Only *Lernanthropus trachuri* and a pseudophyllidean plerocercoid did not differ among samples. The fewest differences in prevalence were observed between MIP and VPG (2 species) and the most were between CF and MIP (10 species). *Ectenurus virgulus* and *Monascus filiformis* differed between Argentinean samples. Prevalence of *M. filiformis*, *G. carvajalregorum*, *Contracaecum* sp., *Hysterothylacium aduncum* larvae, and *Corynosoma australe* was significantly lower in CF than in the other 2 zones; the opposite trend was observed for the rest of the species.

Comparisons of abundance of individual species between zones (Table V) showed differences in all species except for a pseudophyllidean plerocercoid and *L. trachuri* ($P > 0.05$). A significant effect of fish TL ($P < 0.01$) on parasite abundance was observed for most species; the exceptions include *Gastrocotyle trachuri*, *Pseudaxine trachuri*, *Callitetrarhynchus gracilis*, a pseudophyllidea plerocercoid, and *L. trachuri*. Pair-wise comparisons

TABLE II. Taxonomic composition, stage, microhabitat, prevalence (P), and mean abundance ± standard deviation (MA ± S.D) of parasites of five samples of *Trachurus lathami* in 2 areas from the Argentinean coast.*

| Parasite species | Site† | Miramar | | | | | | Villa Gesell | | | |
| | | September 2008 | | October 2008 | | November 2008 | | September 2008 | | August 2009 | |
		P	MA ± SD	P	MA ± SD	P	MA ± SD	P	MA ± SD	P	MA ± SD
Cysts of unknown etiology	GI	32.7	0.9 ± 1.9	21.7	0.4 ± 1.3	10.0	0.1 ± 0.4	11.9	0.3 ± 0.7	16.7	0.6 ± 1.4
APICOMPLEXA											
Goussia cruciata Thélohan, 1892*‡	LI	25.5	—	40.0	—	37.8	—	12.2	—	16.7	—
MYXOSPOREA											
Ceratomyxa sp.*§	GB	0	—	0	—	7.7	—	9.1	—	11.8	—
MONOGENEA											
Gastrocotyle trachuri Dillon and Hargis, 1965, adult	GI	2.0	0.02 ± 0.1	19.6	0.5 ± 1.7	14	0.5 ± 1.9	0	0	8.3	0.2 ± 0.3
Pseudaxine trachuri Parona and Perugia, 1889,* adult	GI	0	0	4.4	0.04 ± 0.2	4	0.1 ± 0.3	0	0	2.8	0.1 ± 0.2
DIGENEA											
Aponurus laguncula Looss, 1905, adult	ST	2.0	0.02 ± 0.1	0	0	0	0	0	0	0	0
Ectenurus virgulus Linton, 1910,* adult	ST	77.6	5.4 ± 5.6	58.7	1.9 ± 2.8	28.0	1.2 ± 3.0	45.2	1.8 ± 2.8	0	0
Monascus filiformis Rudolphi, 1819, adult	ST; IN	18.4	0.6 ± 1.6	54.3	3.7 ± 8.1	52.0	1.5 ± 2.0	14.3	0.3 ± 0.9	11.1	0.4 ± 0.8
CESTODA											
Callitetrarhynchus gracilis (Rudolphi, 1819),* plerocercus	ME	0	0	0	0	0	0	2.4	0.02 ± 0.2	0	0
Grillotia carvajalregorum Menoret and Ivanov, 2009, plerocercus	ME	100	162.8 ± 124.1	100	193.0 ± 222.0	100	162.5 ± 136	100	92.9 ± 69.3	100	109.2 ± 91.8
Pseudophyllidea plerocercoid*	ME	6.1	0.04 ± 0.5	6.5	0.09 ± 0.4	12.0	0.2 ± 0.8	28.6	0.4 ± 0.6	2.8	0.1 ± 0.2
Scolex polymorphus Müller, 1784, plerocercoid	IN	2.0	0.04 ± 0.3	2.2	0.02 ± 0.2	6.0	0.2 ± 0.9	4.8	0.1 ± 0.6	5.6	0.1 ± 0.2
NEMATODA											
Unidentified spiruroid larva*	ME	0	0	0	0	0	0	2.4	0.02 ± 0.2	0	0
Ascarophis marina (Szidat, 1961), larva	ST	0	0	34.8	1.1 ± 2.0	0	0	0	0	0	0
Anisakis simplex s.l. (Rudolphi, 1809), third-stage larva	ME	2.0	0.1 ± 0.4	4.4	0.04 ± 0.2	6.0	0.1 ± 0.2	2.4	0.02 ± 0.2	2.8	0.1 ± 0.2
Contracaecum sp., third-stage larva	ME	28.6	0.6 ± 1.4	30.4	0.7 ± 1.9	50.0	1.8 ± 4.4	33.3	0.5 ± 0.9	25.0	0.6 ± 0.8
Hysterothylacium sp., third-stage larva	ME	16.3	0.2 ± 0.6	2.2	0.02 ± 0.1	14.0	0.2 ± 0.6	28.6	0.5 ± 1.0	27.8	0.9 ± 1.5
Hysterothylacium aduncun (Rudolphi, 1802), third-stage larva	ME	20.4	0.3 ± 0.6	17.4	0.2 ± 0.5	24.0	0.4 ± 0.9	11.9	0.1 ± 0.3	5.6	0.1 ± 0.4
Hysterothylacium aduncun (Rudolphi, 1802), adult	ST	2.0	0.02 ± 0.1	13.0	0.1 ± 0.3	2.0	0.02 ± 0.1	0	0	2.8	0.1 ± 0.2
Terranova galeocerdonis (Thwaite, 1927), third-stage larva	ME	4.1	0.1 ± 0.5	6.5	0.3 ± 1.3	8.0	0.1 ± 0.4	0	0	0	0
ACANTHOCEPHALA											
Bolbosoma turbinella (Diesing, 1851),* juvenile	ME	0	0	0	0	0	0	0	0	2.8	0.1 ± 0.2
Corynosoma australe Johnston, 1937, juvenile	ME	87.8	5.4 ± 7.3	89.1	11.9 ± 19.7	96.0	9.4 ± 10.1	88.1	8.3 ± 11.2	88.9	9.3 ± 9.5
Corynosoma cetaceum Johnston and Best, 1942, juvenile	ME	10.2	0.1 ± 0.4	13.0	0.2 ± 0.7	6.0	0.08 ± 0.3	14.3	0.6 ± 1.8	2.8	0.1 ± 0.3
CRUSTACEA											
Lernanthropus trachuri Brian, 1903, adult	GI	10.2	0.2 ± 0.7	13.0	0.3 ± 1.2	14.0	0.3 ± 0.8	11.9	0.3 ± 0.9	2.8	0.1 ± 0.3

* New host record.
† GI, gills; IN, intestine; LI, liver; GB, gall bladder; ME, mesenteries; ST, stomach.
‡ Prevalence calculated over 47 hosts in September, 46 in October, and 46 in November 2008, and 41 in September 2008 and 36 in August 2009.
§ Prevalence calculated over 6 hosts in September, 7 in October, and 13 in November 2008, and 11 in September 2008 and 17 in August 2009.

showed that the highest number of significant differences in abundance occurred in those comparisons involving hosts from Brazil, while between MIP and VGP only *E. virgulus*, *M. filiformis*, *G. carvajalregorum*, and *Bolbosoma turbinella* showed significant differences. PERMIDISP results indicated that most species differing between zones also exhibited differences in their multivariate dispersion, with the exception of *G. carvajalregorum*. Except for *Contracaecum* sp. and *C. australe*, most pair-wise tests showed significant differences between MIP–VGP and, for *E. virgulus*, between VGP–CF.

PERMANOVA results on untransformed and square-root transformed data of the 3 sample groups for all parasites, and for long-lived parasites, showed a strong effect of host size on infracommunity structure (Table VI), with a significant interaction between host length and locality, revealing that the nature of the relationship between the covariate and the multivariate responses differ between the different levels of this factor. Significant variability was detected among zones after considering the variations among samples due to host size. Pair-wise tests between localities showed that there were significant differences between all pairs of localities (all $P < 0.01$) (Table VI).

Based on their deviations from centroids, dispersion of parasite infracommunities varied significantly among samples (all species, raw abundances $F_{2,272} = 7.8363$; long-lived species, raw abundances $F_{2,272} = 13.095$; and long-lived species square-root transformed data $F_{2,272} = 15.304$; all P [perm] < 0.01). A posteriori tests revealed that significant differences only involved comparisons of fish from CF (all $P < 0.01$).

The CAP analysis also showed significant differences among samples ($tr = 1.15$; $P = 0.0001$) (Fig. 2). The orthonormal PCO axes selected ($m = 9$) described 98% of the variation in the data cloud, with a high percentage of correct allocations (75.5%). The first 2 canonical axes resulting from CAP analysis clearly separated samples. The strong association between the multivariate data cloud and the hypothesis of group differences was indicated by the large size of their canonical correlations ($\delta_1 = 0.99$ and $\delta_2 = 0.42$). Indeed, samples from CF were distinguishable from those of MIP and VGP (Fig. 2). No clear separation was observed among the southern samples, although those from VGP were slightly separated from those of MIP (Fig. 2). When vectors corresponding to Spearman correlations of individual species were superimposed with the CAP axes (restricted to those species having correlation coefficients >0.40), *G. carvajalregorum* and *C. australe* were the most important species in determining the position of Argentinean samples; the former linked especially to those from MIP while *E. virgulus*, *Raphidascaris* sp., and *Hysterothylacium* sp. were followed in importance by *G. trachuri*, *P. trachuri*, and *B. turbinella*, the most important species related to fish from CF (Fig. 2). Cross-validation results showed that the lowest percentage of correctly allocated fish occurred in VGP, with 41% of hosts grouped with the MIP sample. Conversely, a lower proportion of fish from MIP (24%) were allocated to VGP. Samples from CF, all grouped together, showed a complete allocation success (Table VII).

DISCUSSION

This is the first survey of the entire parasite fauna of *T. lathami* in the southwestern Atlantic; previous records of parasites from this host come mainly from taxonomic studies of individual parasite species such as *M. filiformis* and *L. trachuri* in Argentina (Girola et al., 1992; Timi and Etchegoin, 1996) and of *Aponurus laguncula*, *Scolex pleuronectis* (=*S. polymorphus*), *Contracaecum* sp., and *Terranova* sp. in Brazil (Fernandes et al., 1985; Luque and Poulin, 2004). *Gastrocotyle trachuri* was previously reported in *T. lathami* from Venezuela (Nasir and Fuentes, 1983); these authors also reported 2 other monogenean species, *Allogastrocotyle bivaginalis* and *Pseudaxinoides cariacoensis*, not found in the present study. The 11 remaining species are all new records for the rough scad, although 2 of them have been previously reported in congeneric species, namely the coccidian *G. cruciata* and the monogenean *P. trachuri* (Llewellyn, 1956; Kovaleva, 1968; Gestal and Azevedo, 2005; MacKenzie et al., 2008).

There was negligible temporal variation in the structure of parasite infracommunities of *T. lathami* in both of the Argentine localities. These results are consistent with previous analyses of temporal stability of the parasite community structure in fishes of this region (Timi et al., 2005, 2009; Braicovich and Timi, 2010), which is determined by non-trophically transmitted larval parasites (Timi, 2007; Timi and Lanfranchi, 2009; Rossin and Timi, 2010). In fact, as in other hosts investigated, the dominant species in Argentinean samples was the larval *G. carvajalregorum* followed in importance by *C. australe*. Both of these species are long-lived larval parasites, whose persistence for long periods in fishes was responsible for the observed temporal stability of the infracommunities in these fish. Their importance is especially evident considering that short lived-parasites, i.e., ectoparasites and gastrointestinal adults, who can vary either seasonally or geographically as fish migrate, were included in the analyses. Nevertheless, this temporal stability in the structure of parasite assemblages in *T. lathami* should be tested over longer periods, where variability could occur, as in the case of *Trachurus symmetricus murphyi* from the southeastern Pacific Ocean; i.e., the composition patterns of the metazoan parasite communities differed between samples separated by 4 to 6 yr (George-Nascimento, 2000).

Temporal variability of parasite assemblages can be a confounding factor for the identifications of fish stocks; therefore, the use of parasites as biological tags requires a high degree of temporal repeatability in the composition and structure of parasite communities to allow comparative studies over long periods (Timi et al., 2009). Parasite communities in the Argentinean Sea fulfill this requirement, permitting spatial comparisons independent of the month or year of capture.

Spatial comparisons showed a clear differentiation of parasite infracommunities in Brazilian *T. lathami* relative to the Argentine infracommunities. The differences at both parasite population and community levels, and between both regions, demonstrate the potential of parasites for discriminating stocks of rough scad, each of which have their own indicator species. The dominant species in Brazil were the larval *Hysterothylacium* sp. and the adult digenean *E. virgulus*, whereas *G. carvajalregorum* and *C. australe* are of little importance in this region. This finding reinforces the hypothesis of the existence of different stocks in South American Atlantic waters based on differential migratory patterns of this species along Brazilian coasts (Saccardo and Katsuragawa, 1995). One stock inhabits waters off the southwestern Brazilian coast while a different stock that occurs along the extreme southern Brazilian and Uruguayan coasts migrates to Argentinean waters during warmer seasons (Saccardo and

TABLE III. Taxonomic composition, stage, microhabitat, prevalence (P), and mean abundance ± standard deviation (MA ± SD) of parasites in three samples of *Trachurus lathami* from the South Atlantic coast.*

Parasite species	Site†	Miramar pooled		Villa Gesell pooled		Cabo Frio	
		P	MA ± SD	P	MA ± SD	P	MA ± SD
Cysts of unknown etiology	GI	21.4	0.5 ± 1.4	14.1	0.3 ± 1.1	18	0.3 ± 0.8
APICOMPLEXA							
Goussia cruciata Thélohan, 1892‡	LI	33.8	—	14.3	—	76.7	—
MYXOSPOREA							
Ceratomyxa sp.§	GB	7.7	—	10.7	—	0	—
MONOGENEA							
Gastrocotyle trachuri Dillon and Hargis, 1965, adult	GI	11.7	0.3 ± 1.5	3.8	0.04 ± 0.2	48.0	1.5 ± 3.1
Pseudaxine trachuri Parona and Perugia, 1889, adult	GI	7.6	0.2 ± 1.0	1.3	0.01 ± 0.1	48.0	1.7 ± 3.4
Unidentified monogenean	OE	0	0	0	0	4.0	0.04 ± 0.2
DIGENEA							
Aponurus laguncula Looss, 1905, adult	ST	0.7	0.1 ± 0.1	0	0	26.0	0.3 ± 0.6
Ectenurus virgulus Linton, 1910, adult	ST	54.5	2.8 ± 4.4	24.4	1.0 ± 2.2	96.0	4.0 ± 2.9
Monascus filiformis Rudolphi, 1819, adult	ST, IN	41.4	1.9 ± 5.0	12.8	0.3 ± 0.9	0	0
Sthephanostomum sp.* (metacercaria)	OE	0	0	0	0	8.0	0.1 ± 0.6
CESTODA							
Calliterarhynchus gracilis (Rudolphi, 1819), plerocercoid	ME	0	0	1.3	0.01 ± 0.1	26.0	0.3 ± 0.6
Grillotia carvajalregorum Menoret and Ivanov, 2009, plerocercus	ME	100	172.2 ± 164.5	100	100.0 ± 80.0	96.0	4.0 ± 2.9
Nybelinia sp.,* plerocercoid	ME	0	0	0	0	4.0	0.1 ± 0.3
Pseudophyllidea plerocercoid	ME	8.3	0.1 ± 0.6	16.7	0.2 ± 0.5	4.0	0.04 ± 0.2
Scolex polymorphus Müller, 1784, plerocercoid	IN	3.4	0.1 ± 0.5	5.1	0.1 ± 0.4	0	0
NEMATODA							
Unidentified spiruroid larva	ME	0	0	1.3	0.01 ± 0.1	6.0	0.1 ± 0.2
Ascarophis marina (Szidat, 1961), adult	ST	11.0	0.4 ± 1.2	0	0	0	0
Anisakis simplex s.l. (Rudolphi, 1809), third-stage larva	ME	4.1	0.1 ± 0.3	2.6	0.03 ± 0.2	4.0	0.1 ± 0.4
Contracaecum sp., third-stage larva	ME	36.5	1.0 ± 2.9	29.5	0.5 ± 0.9	8.0	0.2 ± 0.7
Hysterothylacium sp., third-stage larva	ME	11.0	0.2 ± 0.5	28.2	0.5 ± 1.2	88.0	21.4 ± 25.0
Hysterothylacium aduncun (Rudolphi, 1802), third-stage larva	ME	20.7	0.3 ± 0.7	9.0	0.1 ± 0.3	0	0
Hysterothylacium aduncun (Rudolphi, 1802), adult	ST	5.5	0.1 ± 0.2	1.3	0.01 ± 0.1	0	0
Raphidascaris sp.,* third-stage larva	ME	0	0	0	0	84.0	3.5 ± 4.1
Terranova galeocerdonis (Thwaite, 1927), third-stage larva	ME	6.2	0.2 ± 0.8	0	0	4.0	0.04 ± 0.2
ACANTHOCEPHALA							
Bolbosoma turbinella (Diesing, 1851), juvenile	ME	0	0	1.3	0.01 ± 0.1	66.0	2.0 ± 3.5
Corynosoma australe Johnston, 1937, juvenile	ME	91.0	8.9 ± 13.4	88.5	8.4 ± 10.0	0	0
Corynosoma cetaceum Johnston and Best, 1942, juvenile	ME	9.7	0.1 ± 0.5	9.0	0.3 ± 1.3	0	0
CRUSTACEA							
Lernanthropus trachuri Brian, 1903, adult	GI	12.4	0.3 ± 0.9	7.7	0.2 ± 0.7	10	0.2 ± 0.5

* New host record.
† GI, gills; IN, intestine; LI, liver; GB, gall bladder; ME, mesenteries; ST, stomach; OE, oesophagus.
‡ Prevalence calculated over 130 hosts in Maramar and 77 in Villa Gesell, Argentina, and 43 hosts in Cabo Frio, Brazil.
§ Prevalence calculated over 26 hosts in Miramar and 28 in Villa Gesell, Argentina, and 7 hosts in Cabo Frio, Brazil.

TABLE IV. Comparisons of prevalence of component parasite species of *Trachurus lathami* among 3 zones of the Brazilian and Argentine Seas.

Species	χ^2	P	Prevalence* MIP–VGP	Prevalence* MIP–CF	Prevalence* VGP–CF
Goussia cruciata	47.3	<0.01	NS	<	<
Gastrocotyle trachuri	48.4	<0.01	NS	<	<
Pseudaxine trachuri	66.6	<0.01	NS	<	<
Ectenurus virgulus	70.2	<0.01	>†	<	<
Monascus filiformis	42.8	<0.01	>	>	>†
Callitetrarhynchus gracilis	55.0	<0.01	NS	<	<
Grillotia carvajalregorum	259.8	<0.01	NS	>	>
Pseudophyllidea plerocercoid	6.4	<0.05	NS	NS	NS
Contracaecum sp.	14.6	<0.01	NS	>	>†
Hysterothylacium sp.	105.0	<0.01	NS	<	<
Hysterothylacium aduncun larva	15.5	<0.01	NS	>	NS
Raphidascaris sp.	221.4	<0.01	AB	<	<
Bolbosoma turbinella	161.0	<0.01	NS	<	<
Corynosoma australe	171.1	<0.01	NS	>	>
Lernanthropus trachuri	1.2	<0.01	NS	NS	NS

* MIP, Miramar, pooled sample; VGP, Villa Gesell, pooled sample; CF, Cabo Frio; NS, not significant ($P > 0.05$); AB, absent in both samples.
† $P < 0.05$.

Katsuragawa, 1995). The Brazilian specimens examined herein came from Cabo Frio, a locality situated in the northern limit of distribution proposed for the southwestern Brazilian population (Saccardo and Katsuragawa, 1995); therefore, future studies including samples from intermediate regions are needed to determine the number of stocks of *T. lathami* along the Brazilian coasts.

Previous studies comparing parasite communities of fishes between Brazilian and Argentinean coasts have shown similar patterns (Timi et al., 2005, 2010). These are expected results because distant host populations are likely to share less species than are adjacent ones, owing to their high degree of isolation

(Pérez del Olmo et al., 2009). A distance decay of similarity in species composition among parasite communities has been documented between Brazilian and Argentinean waters, where latitudinal patterns in species distribution reflect those in oceanographic conditions (Timi et al., 2010) due to differential responses of individual species to environmental variation (Timi, 2007).

The same reasons explain the similarity between samples from the neighboring localities of MIP and VGP, which showed comparable values of both prevalence and abundance for most of the parasite species. In fact, only *M. filiformis* and *E. virgulus*, 2 adult and short-lived gastrointestinal digeneans, varied in terms of

TABLE V. PERMANOVA, PERMDISP P, and *Pseudo-F* values for general and pair-wise comparisons of the abundance of component parasite species of *Trachurus lathami* among three zones from Argentinean and Brazilian seas*†.

Parasite species	PERMANOVA *Pseudo-F*$_{(2, 272)}$	PERMANOVA P	Pair-wise MIP–VGP P	Pair-wise MIP–CF P	Pair-wise VGP–CF P	PERMDISP *Pseudo-F*$_{(2, 272)}$	PERMDISP $P_{(Disp)}$	Pair-wise Permdisp MIP–VGP P	Pair-wise Permdisp MIP–CF P	Pair-wise Permdisp VGP–CF P
Gastrocotyle trachuri*	24.496	<0.01	NS	<0.01	<0.01	65.445	<0.01	<0.05	<0.01	<0.01
Pseudaxine trachuri*	39.034	<0.01	NS	<0.01	<0.01	128.85	<0.01	<0.05	<0.01	<0.01
Ectenurus virgulus	13.126	<0.01	<0.05	<0.01	<0.01	21.364	<0.01	<0.01	<0.01	NS
Monascus filiformis	15.094	<0.01	<0.01	<0.01	<0.01	118.58	<0.01	<0.01	<0.01	<0.01
Callitetrarhynchus gracilis*	31.706	<0.01	NS	<0.01	<0.01	224.17	<0.01	<0.01	<0.01	<0.01
Grillotia carvajalregorum	165.41	<0.01	<0.01	<0.01	<0.01	0.81307	NS	—	—	—
Pseudophyllidea plerocercoid*	2.8456	>0.05	—	—	—	—	—	—	—	—
Contracaecum sp.	2.9668	<0.05	NS	<0.05	<0.05	31.327	<0.01	NS	<0.01	<0.01
Hysterothylacium sp.	163.05	<0.01	NS	<0.01	<0.01	116.07	<0.01	<0.01	<0.01	<0.01
Hysterothylacium aduncun larva	3.0181	<0.05	NS	NS	NS	41.848	<0.01	<0.05	<0.01	<0.01
Raphidascaris sp.	217.62	<0.01	AB	<0.01	<0.01	551.31	<0.01	AB	<0.01	<0.01
Bolbosoma turbinella	120.19	<0.01	<0.05	<0.01	<0.01	412.41	<0.01	<0.01	<0.01	<0.01
Corynosoma australe	51.933	<0.01	NS	<0.01	<0.01	164.39	<0.01	NS	<0.01	<0.01
Lernanthropus trachuri*	0.16291	>0.05	—	—	—	—	—	—	—	—

* TL did not affect the abundances.
† MIP, Miramar, pooled sample; VGP, Villa Gesell, pooled sample; CF, Cabo Frio; NS, not significant ($P > 0.05$); AB, absent in both samples.

TABLE VI. One-factor PERMANOVA results of untransformed and square-root transformed abundance data of parasites of *Trachurus lathami*, based on Bray-Curtis dissimilarity measures for localities (fixed, three levels), with host length as covariable. The P-values were obtained using 9,999 permutations.

| Source	df	Raw data of all parasites				Raw data of long-lived parasites				Square-root transformed data of long-lived parasites			
		SS	MS	F	P (perm)	SS	MS	F	P (perm)	SS	MS	F	P (perm)
Host length	1	42,145	42,145	44.92	<0.0001	44,250	44,250	46.83	<0.0001	30,585	30,585	67.70	<0.0001
Locality	2	$2.452\,e^5$	$1.226\,e^5$	130.68	<0.0001	$2.424\,e^5$	$1.212\,e^5$	128.26	<0.0001	$2.059\,e^5$	$1.030\,e^5$	227.90	<0.0001
Host length × locality	2	6,578.8	3,289.4	3.51	<0.001	8,111.6	4,055.8	4.29	<0.001	3,287.4	1,643.7	3.64	<0.001
Residual	267	$2.505\,e^5$	938.3			$2.523\,e^5$	944.8			$1,206\,e^5$	451.8		
Total	272	$5.445\,e^5$				$5.470\,e^5$				$3.606\,e^5$			
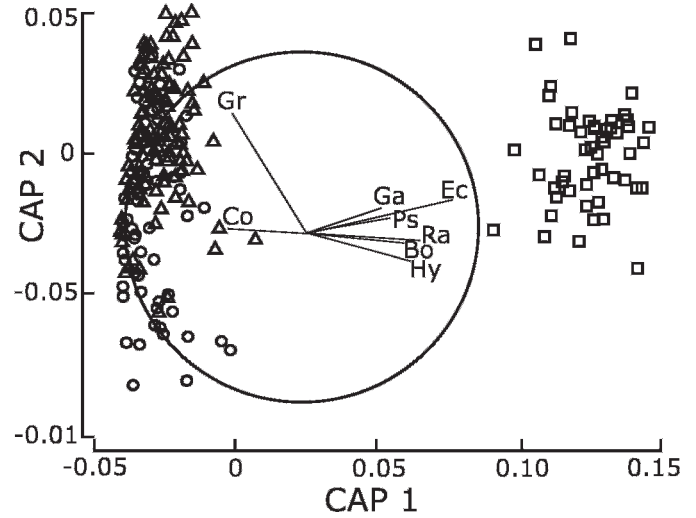
FIGURE 2. Canonical analysis of principal coordinates (CAP) bi-plot of parasite abundance in 3 samples of *Trachurus lathami* from the Brazilian and Argentinean coasts. Vector overlays are Spearman correlations of individual species with the CAP axis (restricted to those 0.4 having correlation coefficients >0.4). Triangles, Miramar; circles, Villa Gesell; squares, Cabo Frio. Bo, *Bolbosoma turbinella*; Co, *Corynosoma australe*; Ec, *Ectenurus virgulus*; Ga, *Gastrocotyle trachuri*; Gr, *Grillotia carvajalregorum*; Hy, *Hysterothylacium* sp.; Ps, *Pseudoaxine trachuri*; Ra, *Raphidascaris* sp.

prevalence between MIP and VGP. Both species also showed significant differences in abundance between sites. The difference of abundance for *E. virgulus* ($P < 0.05$) seems to be influenced by the highly significant differences in their dispersions ($P < 0.01$) which, in turn, could reflect differences in the aggregation of parasites between zones as a consequence of variations in the availability of infective stages; the same picture was observed for *B. turbinella*. In contrast, *G. carvajalregorum* was the only long-lived parasite differing significantly among both samples, with no influence by data dispersion. This species has proven to be a suitable marker for other host species in this region (Timi, 2007); it was mainly responsible for the differences found between samples of *T. lathami* from both Argentinean localities. Differences in both fish diet and oceanographic conditions were identified as causes of the inter-population variations of parasite burdens between Villa Gesell and Miramar in other host species such as *Pinguipes brasilianus* and *Pseudopercis semifasciata* (Timi et al., 2009; Timi and Lanfranchi, 2009), and this could account for the differences showed by *G. carvajalregorum* infecting *T. lathami*. The temporal homogeneity of parasite assemblages in each zone, and the significant differences in their structure between zones, indicate that different stocks of rough scad could

TABLE VII. Discriminant analysis classification showing the numbers and percentages of *Trachurus lathami* classified in each zone (number of correctly classified fish in each sample appears in bold).*

Zone	MIP	VGP	CF	%
MIP	**110**	35	0	75.9
VGP	32	**46**	0	59.0
CF	0	0	**50**	100

* MIP, Miramar, pooled sample; VGP, Villa Gesell, pooled sample; CF, Cabo Frio; %, percentage of correctly classified fish per zone.

be identified in waters of Buenos Aires Province during warmer seasons. However, owing to the similarity of most parasite species and the high percentage of misclassified fish between localities in the CAP results, the possibility of migration along the coast in this period, and the consequent interchange of fishes, cannot be disregarded. What remains unknown is whether the observed differences are a consequence of the differential availability of infective stages in the coastal zones, as has been observed for other fish species (Timi, 2007; Timi et al., 2010), or if both stocks came from different winter territories. Parasite data from samples of *T. lathami* caught in winter at different latitudes could help resolve this issue.

Here, we provide evidence to consider that parasites of *T. lathami* can be used as biological tags for stock discrimination in the southwestern Atlantic. Furthermore, and based on the differential parasite burdens found at different latitudes and their temporal persistence, they also have the potential for tracing seasonal migrations of this fish host. Sampling over different seasons, as well as increasing the number of study areas along South American coasts, will allow us to determine their migratory processes and how patterns of movement correlate with spatial and temporal changes in the environment, issues critical to understanding the stock structure of fish and its dynamics (Rijnsdorp and Pastoors, 1995).

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