

## Seasonal stability in parasite assemblages of the Brazilian flathead, *Percophis brasiliensis* (Perciformes: Percophidae): predictable tools for stock identification

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**Abstract:** A comparison of the composition and structure of parasite communities of the Brazilian flathead, *Percophis brasiliensis* Quoy et Gaimard (Perciformes: Percophidae) among seasons during one year was carried out in the Argentine Sea. A total of 195 fish specimens were examined and 25 parasite species were found. Parasite communities in seasonal samples showed a high degree of homogeneity in taxonomic composition and infection levels. Similarity analysis showed that the seasonal stability within and between samples was constant in both the composition and community structure throughout the year. Parasites can, therefore, be considered predictable markers for fish stock identification, independently of the season of capture, at least on an annual scale.

**Keywords:** parasite communities, temporal stability, biological tags, fish populations, south-west Atlantic

In recent decades parasite ecologists have searched for recurrent and predictable patterns in order to determine whether there are general rules that govern the structure of parasite assemblages (Poulin 2007). As a result, an increasing number of macroecological studies have sought to identify the key determinants of parasite community structure (Gotelli and Rohde 2002, Luque et al. 2004, Poulin 2004, Mouillot et al. 2005, Luque and Poulin 2008) and a variety of ecological and evolutionary processes, historical events and geographical contingencies have been proposed as causal factors of the observed patterns in parasite species diversity (Poulin 2004). However, much available evidence derives from studies without replication in both space and time (Poulin 2001), and the spatial and temporal variations in community structure, and thus the detection of relevant local or short-term processes, have generally been ignored in efforts to identify patterns in fish parasite assemblages (Díaz and George-Nascimento 2002, Poulin and Valtonen 2002, Vidal-Martínez and Poulin 2003, González and Poulin 2005).

In contrast, the spatial variability in the composition and abundance of parasite assemblages makes possible the use of parasites as biological tags for identifying fish stocks. The use of parasites to provide information on the fish stock discreteness is a well-established and broadly accepted tool in fisheries management (MacKenzie and Abaunza 1998, Begg and Waldman 1999, MacKenzie

2002, Power et al. 2005): however, its implementation requires a high degree of temporal repeatability in the composition and structure of parasite communities to allow comparative studies. Nevertheless, most studies using parasites as indicators have analyzed just a single sample at each locality and thus the potential temporal variability of parasite communities, and how this may affect their use in identifying fish stocks, have been largely ignored (Chavez et al. 2007).

In the south-west Atlantic, few studies have attempted to use parasites to delineate marine fish populations (Timi 2007). However, this approach has proved to be successful in discriminating stocks of all fish species to which it has been applied (Cremonte and Sardella 1997, Timi 2003, Sardella and Timi 2004, Timi et al. 2005, 2008, 2009), including the host of interest in the present study, the Brazilian flathead, *Percophis brasiliensis* Quoy et Gaimard (Perciformes: Percophidae) (Braicovich and Timi 2008).

Parasites have been used to identify three stocks of *P. brasiliensis* off the coast of Argentina and Uruguay (Braicovich and Timi 2008). In these flathead populations, the authors also confirmed the existence of a subset of parasite species that could be used as regional biological tags, which allowed not only fish populations but also fish assemblages to be identified. The use of subsets of parasites as biological tags had been predicted by Timi (2007), and was later corroborated by Timi et al. (2008),

but this prediction also relies on the assumption of temporally repeatable parasite burdens. There are few studies on seasonal repeatability of population and community attributes of fish parasites in the south-west Atlantic. Despite this, some evidence does support their occurrence: recently, Timi et al. (2009) showed that parasites of the Brazilian sandperch *Pinguipes brasiliensis* Cuvier were seasonally stable and that locality effects exceeded temporal variation in determining the composition and structure in parasite assemblages. However, these authors did not present data for a complete annual cycle within each locality.

Seasonal variations in abiotic conditions can exert strong pressures on parasite populations, playing an important role in shaping population fluctuations (Altizer et al. 2006). For example, the transmission and survival of free-living stages are influenced by environmental conditions, either directly or through the effects on other hosts involved in their life cycles (Pietroock and Marcogliese 2003). Seasonally induced annual changes in host and parasite biology are known to fluctuate cyclically, but there is a growing awareness of the importance of multi-year oscillations and even chaotic dynamics (Altizer et al. 2006). In short, because of temporal variability, a parasite species identified as a suitable biological tag in a given place and time could prove to be an unreliable marker in other seasons or in future studies. It is therefore desirable to assess the seasonal repeatability of fish-parasite systems in order to establish their usefulness as predictable tools not only for delineation of host populations, but also the identification of harvest locations.

The aim of this study was to determine whether parasite populations and communities of *P. brasiliensis* caught at a single locality display seasonal variations along a complete annual cycle.

## MATERIALS AND METHODS

To assess the effect of seasonality on parasite burdens, a total of 195 specimens of *P. brasiliensis* were collected in four different seasons during a one-year period: Winter 2005,  $n = 49$ , mean total length (TL) (range): 55.2 (42–73) cm; Spring 2005,  $n = 51$ , mean TL (range): 56.6 (44–71) cm; Summer 2006,  $n = 50$ , mean TL (range): 55.3 (46–67) cm; Autumn 2006,  $n = 45$ , mean TL (range): 56.8 (49–64) cm. Data of Spring samples were taken from a previous study by Braicovich and Timi (2008). Fish were caught by trawling 30 miles off the coast of the city of Mar del Plata, Argentina (38°S; 57°W) and either kept fresh or frozen in plastic bags at  $-18^{\circ}\text{C}$  until examination. After defrosting, the TL of each flathead was measured to the nearest cm and a necropsy was conducted under a stereoscopic microscope. Fish length was compared among samples by means of a one-way Anova test. Prevalence and mean abundance (*sensu* Bush et al. 1997) were calculated for each parasite species in each sample. Chi square analyses and *a posteriori* multiple comparisons for proportions were used to test for significant differences in prevalence between seasons. Kruskal-Wallis and *a posteriori* Dunn's tests for unequal samples were used to analyse the effects of seasons on abundance of each parasite species. Both

analyses were performed for species with prevalence  $>10\%$  in at least one of the seasons (component species; Bush et al. 1990). Larval cestodes designated in the present study as *Scolex polymorphus* represent a complex of species (Chambers et al. 2000), each of which may display different temporal dynamics and/or geographical distribution. They are therefore not a reliable indicator of similarity among host populations (Braicovich and Timi 2008) and were excluded from all comparisons and multivariate analyses.

Similarity percentage (SIMPER, Clarke 1993) analyses based on Bray-Curtis similarity were conducted to determine which parasite species were consistently important to similarities within and between parasite assemblages. Typical species were identified as those that made substantial contributions to average within-assemblage similarity and doing it consistently by displaying a high ratio between that contribution and its standard deviation. Discriminator species were defined as those making high contributions to the average dissimilarity of parasite assemblages in different seasons. Consistently discriminating species displayed a high ratio between their contribution to average dissimilarity and its standard deviation (Clarke and Gorley 2006).

Parasite community composition was compared among sampling periods in a permutation-based one-way analysis of similarity based on Bray-Curtis similarities (ANOSIM, Clarke 1993). The statistical significance of the differences among seasons was assessed after 10,000 permutations on abundance data.

A discriminant analysis (DA), based on Mahalanobis distances, was used to reveal differences between seasons and to identify which parasite species were responsible for these differences. Analyses were computed on square root-transformed abundance data using the Brodgar 1.8 package (Brodgar 2000). All multivariate analyses included only parasites reaching the status of component species in at least one of the samples.

## RESULTS

Mean host TL did not vary significantly across the four seasons ( $F_{50,3} = 0.76, P > 0.05$ ). All Brazilian flatheads were parasitized by at least one of the 25 species of parasites listed in Table 1. A total of 227,575 metazoan parasites were found in the total sample (total mean abundance  $\pm$  standard deviation:  $1,167 \pm 946$ ). Larval endoparasites accounted for the 99.7% of all individuals found and dominated all infracommunities. The larval cestode *Grillotia carvajalregorum* (= *Progrillotia dollfusi* Carvajal et Rego, 1983) was particularly common, accounting for 60% of all parasites and dominating in 98.5% of infracommunities. Adult endoparasites accounted for 40% of species richness, and were represented mainly by hemiuroid digeneans, but their relative abundance was exceedingly low (0.3% of all individuals). Ectoparasites were represented only by gnathiid larvae (praniza and zuphea).

Parasite communities in seasonal samples of *P. brasiliensis* showed a high degree of homogeneity in taxonomic composition and infection levels. Only those parasites not reaching the status of component species (mainly those at adult stages) showed seasonal variability in their occurrence. Indeed, no significant differences were observed

**Table 1.** Taxonomic composition, prevalence (P) and mean abundance  $\pm$  standard deviation (MA  $\pm$  S.D.) of parasites of *Percophis brasiliensis* from the coast of Mar del Plata, Argentina.

	Stage	Winter 2005		Spring 2005		Summer 2005/06		Autumn 2006	
		P	MA $\pm$ S.D.	P	MA $\pm$ S.D.	P	MA $\pm$ S.D.	P	MA $\pm$ S.D.
DIGENEA									
<i>Prosorhynchus</i> sp.	Metacercaria	14.3	0.2 $\pm$ 0.5	9.8	0.2 $\pm$ 0.5	10.0	0.1 $\pm$ 0.4	6.7	0.1 $\pm$ 0.9
<i>Cardicola ambrosioi</i> Braicovich, Etchegoin, Timi et Sardella, 2006	Adult	4.1	0.2 $\pm$ 1.1	2.0	0.02 $\pm$ 0.1	2.0	0.06 $\pm$ 0.4	2.2	0.02 $\pm$ 0.2
<i>Aponurus laguncula</i> Looss, 1905	Adult	0.0	0.0	0.0	0.0	6.0	0.2 $\pm$ 1.0	2.2	0.02 $\pm$ 0.2
<i>Derogenes varicus</i> (Müller, 1784)	Adult	4.1	0.06 $\pm$ 0.3	0.0	0.0	0.0	0.0	2.2	0.09 $\pm$ 0.8
<i>Ectenurus virgulus</i> Linton, 1910	Adult	0.0	0.0	3.9	0.1 $\pm$ 0.3	4.0	0.08 $\pm$ 0.4	0.0	0.0
<i>Elytrophalloides oatesi</i> (Leiper et Atkinson, 1914)	Adult	6.1	0.7 $\pm$ 3.1	0.0	0.0	0.0	0.0	2.2	0.02 $\pm$ 0.2
<i>Lecithochirium microstomum</i> Chandler, 1935	Adult	18.4	1.0 $\pm$ 3.3	13.7	0.4 $\pm$ 1.5	36.0	2.2 $\pm$ 4.0	35.6	3.1 $\pm$ 21.4
<i>Lecithocladium cristatum</i> (Rudolphi, 1819)	Adult	8.2	1.1 $\pm$ 5.2	3.9	0.6 $\pm$ 3.4	0.0	0.0	0.0	0.0
<i>Parahemiurus merus</i> (Linton, 1910)	Adult	2.0	0.02 $\pm$ 0.1	0.0	0.0	0.0	0.0	2.2	0.02 $\pm$ 0.2
Hemiuridae	Metacercaria	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.02 $\pm$ 0.2
CESTODA									
<i>Scolex polymorphus</i> Müller, 1784	Plerocercoid	81.6	151.2 $\pm$ 220.4	76.5	76.8 $\pm$ 101.6	92.0	135.6 $\pm$ 146.9	73.3	76.0 $\pm$ 501.2
<i>Grillotia carvajalregorum</i> Menoret et Ivanov, 2009	Plerocercus	100	668.2 $\pm$ 492.1	100	957.9 $\pm$ 949.0	100	844.2 $\pm$ 775.8	100	739.7 $\pm$ 537.5
<i>Callitetrarhynchus gracilis</i> (Rudolphi, 1819)	Plerocercus	12.2	0.2 $\pm$ 0.5	33.3	0.5 $\pm$ 1.4	32.0	0.5 $\pm$ 0.8	15.6	0.16 $\pm$ 1.4
<i>Nybelinia</i> sp.	Plerocercoid	24.5	0.3 $\pm$ 0.6	39.2	2.03 $\pm$ 8.7	40.0	0.6 $\pm$ 1.0	46.7	1.0 $\pm$ 7.0
Bothriocephalidea	Plerocercoid	2.0	0.02 $\pm$ 0.1	7.8	0.08 $\pm$ 0.3	4.0	0.04 $\pm$ 0.2	0.0	0.0
NEMATODA									
<i>Anisakis simplex</i> s.l. (Rudolphi, 1809)	3rd-stage larva	44.9	1.1 $\pm$ 1.9	43.1	1.3 $\pm$ 2.5	40.0	0.9 $\pm$ 1.7	57.8	2.8 $\pm$ 18.8
<i>Contraecacum</i> sp.	3rd-stage larva	2.0	0.02 $\pm$ 0.1	3.9	0.06 $\pm$ 0.3	0.0	0.0	2.2	0.04 $\pm$ 0.4
<i>Cucullanus</i> sp.	Larva	2.0	0.04 $\pm$ 0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hysterothylacium</i> sp.	3rd-stage larva	98.0	38.7 $\pm$ 54.6	100	75.6 $\pm$ 104.7	100	124.9 $\pm$ 124.3	100	67.4 $\pm$ 437.1
<i>Terranova galeocerdonis</i> (Thwaite, 1927)	3rd-stage larva	0.0	0.0	5.9	0.1 $\pm$ 0.6	0.0	0.0	2.2	0.02 $\pm$ 0.3
<i>Moravecia argentinensis</i> Braicovich, Moravec et Timi, 2007	Adult	38.8	0.9 $\pm$ 1.8	52.9	1.2 $\pm$ 1.5	52.0	1.1 $\pm$ 1.5	40.0	0.7 $\pm$ 5.0
ACANTHOCEPHALA									
<i>Corynosoma australe</i> Johnston, 1937	Cystacanth	100	115.8 $\pm$ 115.5	100	196.3 $\pm$ 250.2	100	170.1 $\pm$ 135.7	100	174.7 $\pm$ 165.8
<i>Corynosoma cetaceum</i> Johnston et Best, 1942	Cystacanth	63.3	3.1 $\pm$ 4.7	64.7	3.3 $\pm$ 5.8	78.0	2.2 $\pm$ 2.7	73.3	2.6 $\pm$ 3.2
<i>Bolbosoma</i> sp.	Cystacanth	0.0	0.0	0.0	0.0	2.0	0.04 $\pm$ 0.3	0.0	0.0
ISOPODA									
Gnathiidae gen. sp.	Praniza	4.1	0.06 $\pm$ 0.3	15.7	0.2 $\pm$ 0.5	22.0	0.6 $\pm$ 1.4	15.6	0.4 $\pm$ 2.8

**Table 2.** Breakdown of average similarity of parasite infracommunities of *Percophis brasiliensis* within sampling seasons into contributions from each parasite species. Only those with a cumulative contribution >90% are included.

Average similarity	Winter		Spring		Summer		Autumn	
	56.27		56.68		59.29		57.75	
	AS/SD <sup>a</sup>	% <sup>b</sup>	AS/SD	%	AS/SD	%	AS/SD	%
<i>Grillotia carvajalregorum</i>	2.23	85.38	2.37	83.22	2.61	75.17	2.76	78.49
<i>Corynosoma australe</i>	1.53	11.00	1.32	11.36	1.70	14.83	1.50	14.35

<sup>a</sup> Average contribution to the total average similarity/standard deviation; <sup>b</sup> percentage of total similarity contributed by each species.

**Table 3.** Breakdown of average dissimilarity of parasite infracommunities of *Percophis brasiliensis* between sampling seasons into contributions from each parasite species. Species are ordered in decreasing contribution to winter-spring comparison. Only those with a cumulative contribution >90% are included.

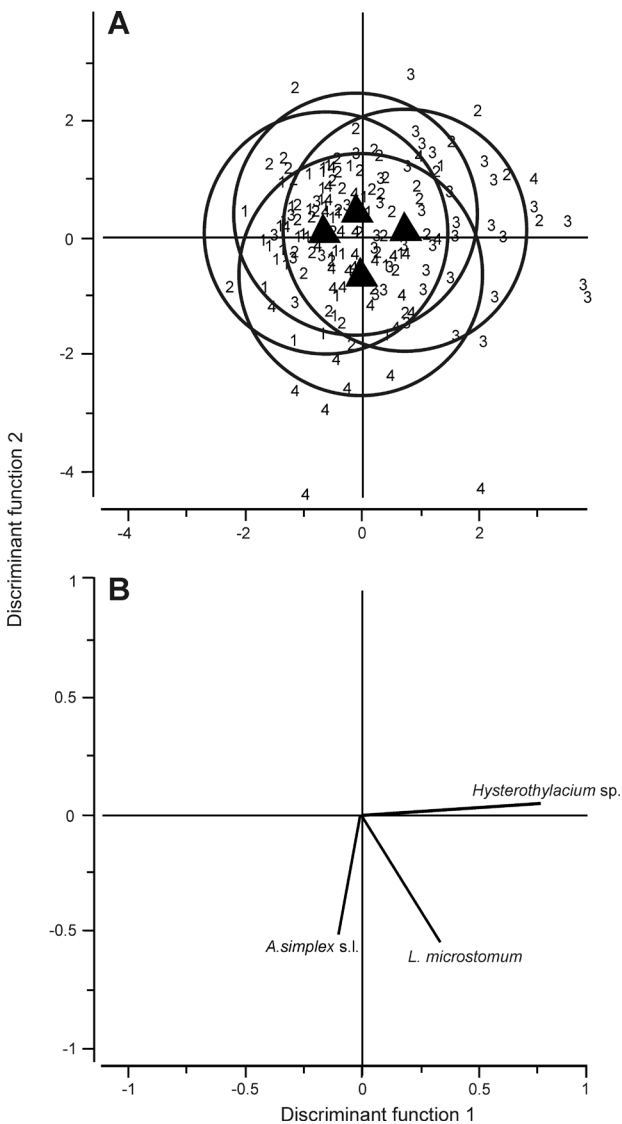
Average dissimilarity	Winter-Spring		Winter-Summer		Winter-Autumn		Spring-Summer		Spring-Autumn		Summer-Autumn	
	43.68		43.64		42.01		42.13		41.20		40.10	
	AS/SD <sup>a</sup>	% <sup>b</sup>	AS/SD	%	AS/SD	%	AS/SD	%	AS/SD	%	AS/SD	%
<i>Grillotia carvajalregorum</i>	1.58	72.97	1.52	67.72	1.54	70.36	1.52	67.86	1.54	69.56	1.47	66.48
<i>Corynosoma australe</i>	1.27	17.56	1.39	16.40	1.28	19.06	1.31	17.72	1.19	20.18	1.36	18.36
<i>Hysterothylacium</i> sp.	–	–	0.95	14.25	1.04	8.49	1.00	12.94	1.07	8.37	1.00	13.19

<sup>a</sup> Average contribution to the total average dissimilarity/standard deviation; <sup>b</sup> percentage of total dissimilarity contributed by each species.

**Table 4.** Discriminant analysis classification showing the numbers and percentages of *Percophis brasiliensis* classified in each season (rows correspond to group memberships, number of correctly classified fish in each sample in bold).

	Winter	Spring	Summer	Autumn	%*
Winter	<b>26</b>	12	4	7	53.06
Spring	12	<b>19</b>	12	8	37.25
Summer	12	6	<b>24</b>	8	48.00
Autumn	10	10	4	<b>21</b>	46.67

\*Percentage of correctly classified fish per season.



**Fig. 1.** **A.** Samples scores of the first two discriminant functions for specimens of *Percophis brasiliensis* from four seasons from Mar del Plata cost. Triangles are group means; the circle around group means are the 90% tolerance regions (i.e., 90% of the observations in a group are expected to lie in this region). 1, winter; 2, spring; 3, summer; 4, autumn. **B.** Canonical correlations between the first two discriminant functions and the parasites and species scores as variables of *Percophis brasiliensis*.

for prevalence among seasons in any component parasite species (all  $P > 0.05$ ). Mean abundance was also similar among seasons for most of these species. The only component species showing significant seasonal variations was *Hysterothylacium* sp., which was less abundant in winter than in summer and autumn ( $H_3 = 27.13$ ,  $P < 0.01$ ).

Average similarity within seasonal samples was nearly constant throughout the year (Table 2). *Grillotia carvajalregorum* and *Corynosoma australe* were typical species that contributed substantially (>90%) to the average similarity in all seasons. Average dissimilarity values between pairs of seasons were low and also showed little seasonal variation (Table 3), therefore, pairwise average similarity between seasons (calculated as 100 minus average dissimilarity) and ranging between 56.32 and 59.90) were similar to those within season. The most important and consistent discriminators among all samples were the typical *G. carvajalregorum* and *C. australe*. *Hysterothylacium* sp. also made important contributions to dissimilarity but did so less consistently.

Parasite communities varied less between seasons than within seasons. Similarity-based multivariate analysis showed that the four samples did not differ significantly in their parasite species composition (Global  $R_{ANOSIM}$ : 0.001,  $P = 0.40$ ), indicating that within-season similarity did not exceed among-seasons similarity in parasite assemblages. In effect, parasite communities in individual fish caught during any given season were as similar to one other as to those in fish caught in different seasons.

Similarly, DA showed that the samples collected in different seasons were highly homogeneous. The first two discriminant functions explained 87.2% of the variance, contributing 53.3% (eigenvalue = 0.252) and 33.9% (eigenvalue = 0.160), respectively. Although a significant group effect was observed (Wilks'  $\lambda = 0.649$ ,  $F_{(33,534.03)} = 2.56$ ,  $P < 0.01$ ), the dimensionality test showed significant group separation in only one dimension ( $\chi^2_{(20)} = 38.8$ ,  $P < 0.01$ ). Individual fish from all seasons clumped together in the bi-dimensional space (Fig. 1.A) and only 47% of hosts were correctly classified with respect to season (Table 4). The importance of each parasite species with respect to discrimination between seasons, evaluated as canonical correlations between discriminant functions and species scores as variables, showed that *Hysterothylacium* sp. was the most important species in determining the position of samples, its exclusion from the analysis producing a decrease of the total sum of Mahalanobis distances of 26.2%. *Hysterothylacium* sp. was clearly related to fish from summer, and was followed in importance by *Lecithochirium microstomum* (14.5%) and *Anisakis simplex* s.l. (14.4%), both related to summer and autumn samples (Fig. 1.B). Contributions of the remaining parasite taxa were all lower than 10%.



## DISCUSSION

At present, the parasite fauna of *Percophis brasiliensis* along its distributional range is known to contain 27 species of metazoans (Braicovich et al. 2009). However, artifacts such as sampling effort can affect richness estimates because both the number of hosts examined and the number of surveys conducted tend to co-vary with the number of species found in a community (Walther et al. 1995). Sampling over several seasons can increase the likelihood of detecting rare parasites (Zander 2005). Indeed, three previously unrecorded parasite species were found in 144 flatheads newly collected, namely Hemiuridae metacercariae, *Cucullanus* sp. and *Bolbosoma* sp. All these species can be considered as rare or accidental in flatheads, which were represented by 1, 2 and 2 individuals, respectively.

It is known that temporal variability in local environmental factors can regulate the survival and transmission success of infective stages, causing variations in parasite burdens (Pietroock and Marcogliese 2003), particularly for ectoparasitic species with monoxenous life cycles, but also for endoparasites either directly or via their effects on other host species. Temporal variability in the composition and structure of a parasite community are often caused by changes in either abiotic conditions (Zander 2005) and/or biological processes, such as migratory behaviour of definitive hosts. In the present study, seasonal variability was only observed in the occurrence of those parasites not reaching the status of component species. Although the low prevalence and abundance of these rare taxa precluded reliable statistical comparisons, most were adult stages living in the digestive tract. As such, seasonal oscillations of these parasites may result from changes in host diet. Many of these rare species could be considered as accidental infestations instead of members of the parasite fauna of *P. brasiliensis*.

On the other hand, almost all component species were long-lived stages, the exception being the ectoparasitic isopods and the endoparasites *Lecithochirium microstomum* and *Moravecchia argentinensis* found at the adult stages in the gut and blood vessels, respectively. Component species showed fairly constant prevalence throughout the annual cycle and, with the exception of *Hysterothylacium* sp., the abundance of most parasites was also stable. Anisakid larvae, found in the body cavity of fishes, are known to be long-lived in fish hosts, and although their prevalence and abundance may vary over longer time scales, they remain stable for several years (McClelland and Marcogliese 1994). Therefore, seasonal changes should not be expected among fish of the same size or age. Hence, seasonality cannot account for the lower abundance of *Hysterothylacium* sp. in the winter sample, and other causes should be considered.

One explanation for the changing abundance of *Hysterothylacium* sp. in Mar del Plata fish could be a tem-

porary immigration of flatheads from a neighbouring population. Infection levels of this parasite vary spatially among flathead populations. For example, the mean abundance of *Hysterothylacium* sp. in flatheads from El Rincón (2.7 worms per fish) (Braicovich and Timi 2008) is much lower than in fish from Mar del Plata (77.6 worms per fish in the whole sample). However, it seems unlikely that a neighbouring population of flatheads would be alike with respect to all parasite species except one. There are other helminths in flatheads that differ in abundance between El Rincón and Mar del Plata (e.g., *Corynosoma australe*, *Anisakis simplex*), but all showed constant values along the four seasons.

Certainly, the existence of variable oceanographic conditions in the study area is not in question. There are seasonal latitudinal oscillations of different water masses over the continental shelf of Buenos Aires province. This is particularly so in the coastal area between Necochea and Mar del Plata, which is alternately influenced by estuarine waters from El Rincón or the Río de la Plata and highly saline waters from San Matías Gulf, or continental shelf waters (Lucas et al. 2005), each with characteristic conditions of temperature and salinity, the two main determinants of the abundance and distribution of marine parasites (Esch and Fernández 1993). The latter water mass occupies the central portion of the shelf, with the exception of the coast between Necochea and Mar del Plata (38°30'S and 37°30'S), where it reaches the coast due to the proximity of the 50 m isobath to the coast and the lack of locally formed coastal water (Lucas et al. 2005). Thus, the existence of a different population of *P. brasiliensis* inhabiting this water mass cannot be discounted. Further studies including samples from continental shelf waters are necessary to assess if this region is the source of immigrants and even to estimate the extent of the possible mixing among populations.

Although the causes of the seasonal variability in the abundance of *Hysterothylacium* sp. cannot be established, the fact that only one of the component species varied across seasons, and the absence of differences in prevalence for all of them, constitute strong evidence of the temporal persistence in species composition and abundance of parasite communities throughout an annual cycle. The seasonal stability observed in the parasite communities of *P. brasiliensis* was mainly determined by the contribution of the most abundant and prevalent species, *Grillotia* sp. and *C. australe*, to the average similarity both within and between seasons. The importance of both species as drivers of the structure of parasite assemblages is also reflected in their contribution to the dissimilarity values between pairs of seasons, which was, as expected, also determined by *Hysterothylacium* sp., although less consistently.

The overall seasonal stability of parasite communities of flathead in the study area was strongly in evi-

dence in the convergent results of several multivariate analyses. Non-parametric similarity-based tests showed that within-season resemblance of parasite assemblages was comparable to between-season resemblance. Operating from very different assumptions, discriminant analyses showed the same basic trend. Although samples could be discriminated along the first discriminant function, this was a consequence of the seasonal variations in abundance of *Hysterothylacium* sp., which differentiated winter and summer samples along this axis. Two other important species, *L. microstomum* and *A. simplex*, were associated with the less important second discriminant function, which did not distinguish between seasons. Despite the distinguishing effects of these parasites, parasite communities of individual fish from all seasons clumped together in the bi-dimensional space and relatively few hosts could be correctly assigned to their season of capture, again showing the temporal homogeneity of parasite assemblages.

Since geographic distribution and community dynamics of marine parasites depend largely on environmental conditions (Esch and Fernández 1993, Rohde and Heap 1998, Luque et al. 2004), the seasonal stability of parasite assemblages of *P. brasiliensis* could be a consequence of constant oceanographic conditions in the study area. Fish assemblages in the northern Argentine coastal system show a remarkable degree of temporal persistence in species composition and geographical location, which has been attributed to the stability of factors such as temperature, depth and type of sediment (Jaureguizar et al. 2006). Furthermore, the dominance of larval stages in the parasite communities of flatheads, as well as in other fish species in the region (Timi 2007, Timi and Lanfranchi 2009, Lanfranchi et al. 2009), which can persist for long periods

in their hosts, provides a certain degree of temporal inertia to these assemblages (Holmes 1990), increasing the effects of environmental homogeneity on the temporal stability of parasite community structure.

We have shown that the composition and structure of parasite communities of *P. brasiliensis* is seasonally repeatable, which is a prerequisite for spatial comparative studies. Although some degree of seasonal variability was observed in particular parasite species (such as *Hysterothylacium* sp.), these variations were vastly exceeded by the effect of the locality of capture, which also surpassed the influence of host size on the population attributes of parasite species. The discriminator species were the same as those found in a previous study of flatheads (Braicovich and Timi 2008), and have been also successfully used as biological tags for other host species in this region (Timi 2003, 2007, Sardella and Timi 2004, Timi et al. 2005, 2008, 2009). Consequently, seasonal predictability is also expected to occur in these parasites in other host species in the area, such as was recently observed for *Pinguipes brasiliensis* (Timi et al. 2009). Thus, the parasites identified as suitable biological tags in the study area can be considered reliable and predictable markers for stock assessment, independently of the season of capture, at least on an annual scale.

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