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Parasite communities in three sympatric flounder species (Pleuronectiformes: Paralichthyidae)

Similar ecological filters driving toward repeatable assemblages

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Abstract The relative role of host phylogeny and ecology on parasite community structure is analyzed in three sympatric paralichthyids from Argentine waters: the carcinophagous *Xystreureys rasile* and the piscivorous *Paralichthys isosceles* and *P. patagonicus*. Their relatedness, inherited ecological and physiological traits and shared past histories should result in certain similarities in their parasite assemblages. With this as our null hypothesis, we focused on the effects of measurable traits (size, age and diet) across fish species, with departures from a general pattern being interpreted as a consequence of ecological filters preventing homogeneous infections. The percentage of individuals/species that host-specific parasites contributed to each component community, as well as their effect on similarity of assemblages within/across host species, showed that they were not important contributors to abundance, richness and similarity, being irrelevant for the repeatability within component communities and across fish species as a phylogenetically related group. To minimize the effect of variables other than diet or trophic level only trophically transmitted nonspecific parasites were included in further analyses. After controlling for fish size, the congeneric host species harboured assemblages significantly different from those found in *X. rasile*, but were similar to each other because of their shared high trophic levels. Assemblages of equivalent structure harboured by fish with different age–size relationships showed that these variables seem to act at dissimilar

rates on different features of the parasites assemblages. Indeed, age affected mainly the parasite abundance, whereas body size influenced mostly species richness. In conclusion, similar ecological filters produce analogous infections across host species driving towards homogeneous parasite communities.

Introduction

Fish parasite assemblages are highly complex and dynamic ecological systems resulting from the interaction of evolutionary and ecological processes acting together at multiple levels. The discernment between these factors is not always straightforward (Desdevises et al. 2003), and these characteristics make the recognition of recurrent patterns in community structure difficult (Poulin 2007).

The relative role of phylogeny and host ecology as drivers of parasite community structure has been a matter of debate for many years among parasite ecologists (Poulin 1995; Poulin and Rohde 1997; Morand and Poulin 2003; Poulin et al. 2011). The host phylogeny is expected to have an influence on the structure of parasite assemblages since related host species can harbour related parasites inherited from their common ancestors through cospeciation (Vickery and Poulin 1998; Poulin and Morand 2004). For this reason, many researchers have applied comparative methods that control for host phylogeny to disentangle both variables and uncover the importance of host ecology (Poulin 1995; Poulin and Rohde 1997; Sasal et al. 1997; Luque et al. 2004; Luque and Poulin 2008). However, it has been argued recently that the phylogenetic position of a species encompasses much of its history, as well as its ecological and immunological features, and is therefore a much better predictor of species richness acquired

A. J. Alarcos (✉) · J. T. Timi
Laboratorio de Parasitología,
Instituto de Investigaciones Marinas y Costeras (IIMyC),
Consejo Nacional de Investigaciones Científicas y Técnicas
(CONICET), Facultad de Ciencias Exactas y Naturales,
Universidad Nacional de Mar del Plata,
Funes 3350,
7600 Mar del Plata, Argentina
e-mail: anajulia_alarcos@yahoo.com.ar

over evolutionary time by a particular host lineage than any ecological variable (Poulin et al. 2011).

The present study on the parasites of three sympatric and closely related species, was chosen from this perspective in order to “neutralize” phylogenetically inherited ecological (i.e., habitat, general shape) and physiological characteristics as well as shared past history (i.e., biogeographic area of origin). A certain degree of similarity in their parasite assemblages should be expected for related host species (Poulin and Rohde 1997; Luque et al. 2004; Luque and Poulin 2008), especially for those hosts with similar ecology (Muñoz et al. 2006; Marques et al. 2011), constituting a null hypothesis through which to focus on the effect of measurable differences, such as size, age and diet between fish species. Thus, any departure from a general pattern could be interpreted as the consequence of ecological filters preventing a homogeneous infection across host species.

Among host ecological traits that have been identified as key determinants of species assembly rules in fish parasite communities are size and age, habitat, diet, trophic level, schooling behavior, population size and density, depth distribution and geographical range (Poulin and Morand 2000; Luque et al. 2004; Bagge et al. 2004; Pérez-del Olmo et al. 2008; Luque and Poulin 2008; Timi et al. 2011). However, the available knowledge about the relative magnitude of different fish characteristics as drivers of the structure of parasite assemblages shows little consistency (Poulin and Morand 2004), with contingent, rather than recurrent, patterns being the general rule (Poulin 2007; Luque and Poulin 2008). This fact should be a consequence of the effect of environmental characteristics and trophic webs at local scales, regardless of the traits of the host species (Marcogliese 2001, 2002; Luque et al. 2004; Luque and Poulin 2008; Aguirre-Macedo et al. 2007), as well as to the parasite guild under study, because ecto- or endoparasites can respond differently to either environmental or host related variability (Luque and Poulin 2008; Timi et al. 2010a; Marques et al. 2011).

In shelf waters off Buenos Aires Province, Argentina, fish parasite assemblages are dominated by trophically transmitted larval helminths in all host species so far studied, with a suit of species of low host specificity being widely distributed and ubiquitous among fish hosts (Timi 2007; Lanfranchi et al. 2009; Timi and Lanfranchi 2009; Rossin and Timi 2010; Vales et al. 2011). These parasites indiscriminately infect paratenic hosts, in which they can live for long periods, and some of them can be transmitted from one paratenic host (prey) to others (predators), thus persisting in the food web. These characteristics make them potentially available for any fish host, independently of its trophic level. However, Timi et al. (2011) recently demonstrated that not all host species in this study area harbour the same number and type of parasites, reflecting the existing differences in their ecological characteristics, among which the trophic level featured as the main

explanatory factor for the similarity of parasite assemblages across fish species. Among the species studied, two sympatric paralichthyids, *Xystreurys rasile* (Jordan, 1891) and *Paralichthys isosceles* Jordan, 1891 varied in the species composition of their parasite assemblages, attributable to their different trophic levels (Timi et al. 2011). These two species differ in their feeding habits, with *X. rasile* preying exclusively on benthic invertebrates and *P. isosceles* also including a high proportion of fishes (Díaz de Astarloa and Munroe 1998; Cousseau and Perrotta 2004). Here, we include a third paralichthyid, *Paralichthys patagonicus* Jordan, 1889, caught in the same region, a species with similar trophic habits to those of *P. isosceles* (Díaz de Astarloa and Munroe 1998), to test whether two sympatric species with similar habitat and diet display similar assemblages of nonspecific parasites in terms of both abundance and species composition, as well as in relation to their infracommunity descriptors. Previous studies on parasites of these flounders were mainly taxonomic and focused on particular parasite groups in Argentina (Szidat 1961; Incorvaia and Díaz de Astarloa 1998; Suriano and Labriola 1998, 1999; Alarcos and Timi 2011) and Brazil (Luque and Tavares 2007; Felizardo et al. 2009a, b, 2010, 2011).

The aim of this paper is, therefore, two-fold: first, to describe for the first time the parasite communities of three sympatric paralichthyids, *X. rasile*, *P. isosceles* and *P. patagonicus*, and second, to analyze their relationships with the feeding habits and trophic levels of the fishes, in order to determine if similar ecological filters produce analogous infections across host species driving towards homogeneous parasite communities.

Materials and methods

A total of 150 paralichthyid flounders were examined for parasites. Fish were caught by trawl in waters off Necochea, Argentina (38°52'S, 58°10'W) and landed at Puerto Quequén by commercial fishermen (Table 1). Fish were either kept fresh or deep frozen at -18°C until examination. After thawing flounders were measured for total length (cm) and sexed. Body surface, gills, branchial and body cavities, viscera (stomach, intestine, liver, gall bladder, spleen, heart, gonads and mesenteries), swim bladder, kidneys and musculature were examined with the aid of a stereomicroscope. Fins were examined only for specimens of *P. patagonicus*.

Fish lengths were compared between samples by means of a one-way ANOVA (Zar 1996). The prevalence and mean abundance were calculated for each parasite species in each sample following Bush et al. (1997).

Host-specific parasites and those belonging to general known to display a certain degree of host specificity (those described from the host species examined and not reported from other fishes) were identified with reference to the

Table 1 Composition of samples of three species of parichthyid flounders, caught off Necochea Argentina

Species	<i>N</i>	Date of capture	Total length±SD	Maximum size (cm) ^a	Mean % of maximum size±SD
<i>Xystreureys rasile</i>	48	22 May 2009	29.26±2.64	Males: 39, females: 43	70.84±6.91
<i>Paralichthys isosceles</i>	51	22 May 2009	27.95±2.11	Males: 32, females: 38	80.95±7.44
<i>Paralichthys patagonicus</i>	51	29 September 2010	35.20±2.64	Males: 48, females: 62	65.50±9.43

^aMaximum size recorded for the species, taken from Cousseau and Perrotta (2004) and Froese and Pauly (2010)

relevant bibliography. Their numerical importance was measured as the percentage of individuals and species they contributed to the total abundance and species richness, respectively, of each component community, as well as their contribution to similarity in parasite assemblages within and across host species. For the last analyses, similarity percentages (SIMPER; Clarke 1993) between parasite assemblages were calculated on values of abundance among all possible pairs of individual fish (infracommunities) within and between host species and expressed as averaged similarity, for all parasite species, and after excluding sequentially the host-specific and the nonspecific gut parasites. SIMPER and subsequent multivariate statistical procedures on community data were implemented in PRIMER package V6 (Clarke and Gorley 2006; Clarke and Warwick 2001) and PERMANOVA+ for PRIMER package (Anderson et al. 2008).

In order to minimize the effect of variables other than diet or trophic level, the following restrictions were made to the data set, to avoid the effect of host phylogeny, if any, on parasite communities. Only nonspecific parasites were included in comparative analyses, focusing on the guild of trophically transmitted helminths, i.e., metacercariae of actively penetrating trematodes were excluded. As samples of *X. rasile* and *P. isosceles* were obtained in a single catch, it is assumed that both species are exposed to the same set of infective stages. Samples of *P. patagonicus* were caught 1 year later and during a different season (spring). As endohelminths of the gut lumen are frequently relatively short-lived (Lester and MacKenzie 2009), this guild of parasites was excluded prior to comparative analyses. The same geographical origin of samples also precludes any possible spatial heterogeneity in the distribution of infective stages. The possible effect of host size was taken into account by including this factor as a covariable in comparative analyses.

In the case of host-specific parasites, similarity percentages (SIMPER) were calculated to identify *typical* and *discriminator species* of trophically transmitted and long-lived larval helminths. This analysis was made to determine if host-specific parasites characterized or distinguished between parasites assemblages: “characterized” if they were “typical species” contributing substantially to the average similarity and doing it consistently by displaying a high ratio between that contribution and its standard deviation, and “distinguished” if

they were “discriminator species” contributing largely to the average dissimilarity and displaying a high ratio between that contribution and its standard deviation (Clarke and Gorley 2006). The Bray–Curtis index, which takes into account differences in abundance of each shared parasite species (Magurran 1988) was used as a similarity measure.

The differences in community structure were tested by means of a one-way permutational multivariate analysis of the variance (PERMANOVA) on parasite abundances. The structure of parasite infracommunities between samples (1×3 factorial design, host species as fixed factors) was compared, testing for main effects after 9,999 permutations. Where differences were detected by PERMANOVA, pair-wise comparisons were used to determine which samples differed. Following Anderson et al. (2008) a permutation of residuals under a reduced model was used as the method of permutation. A sequential sum of squares (Type I SS) was applied because samples were unbalanced (different numbers of fish examined per sample) and because host size was introduced as a covariable (ANCOVA model). Fish length was included as a covariable because of the known effect of size/age on parasite burdens of fish. The Bray–Curtis index was used as a similarity measure. These procedures were repeated applying the Jaccard index as a similarity measurement, an index that uses binary presence–absence data (Magurran 1988) to compare species composition between samples. Since PERMANOVA is sensitive to differences in multivariate dispersion between groups (sensu homogeneity of variances, which can inflate Type I error even when centroids have identical locations), the same models were tested for differences in dispersion using the routine PERMDISP (Anderson et al. 2008). Dispersions were measured as distances to the centroids and each term in the analysis was tested using 9,999 permutations, with significant terms investigated using a posteriori pair-wise comparison with *t*-statistic (Anderson et al. 2008) between those pairs of samples showing significant differences with PERMANOVA.

For each individual fish the following community descriptors were calculated at infracommunity level: total abundance (the number of parasites per host, *N*), species richness (*S*), Brillouin’s index of diversity (HB) and Berger–Parker’s index of dominance (BP) (Magurran 1988); the latter two indices were calculated only for those flounders harbouring two or more species. Infracommunity descriptors

were compared between host species with univariate PERMANOVA and PERMDISP analyses, using Euclidean distances for the construction of similarity matrices.

Results

Mean host body lengths were significantly different between flounder species ($F_{2,146}=123.7$; $P<0.01$), with all pairs of

species showing differences in size ($X. rasile$ – $P. isosceles$, $0.01<P<0.05$; both comparisons involving $P. patagonicus$, $P<0.01$).

Only one specimen of $X. rasile$ was found unparasitized, the rest of the hosts were parasitized by at least one of 26 parasite species (Table 2). Of these, metacercariae of *Proso-rhynchus australis* found in the fins of $P. patagonicus$ were excluded from further analyses because the fins of the other two host species were not examined.

Table 2 Prevalence (P) and mean abundance (Ma \pm SD) of metazoan parasites in three species of parichthiid flounders from the southwestern Atlantic

Parasite species	Stage	Site	<i>Xystreureys rasile</i>		<i>Paralichthys isosceles</i>		<i>Paralichthys patagonicus</i>	
			P	Ma \pm SD	P	Ma \pm SD	P	Ma \pm SD
Monogenea								
<i>Neoheterobothrium paralichthyi</i> Suriano et Labriola, 1999	Ad	Gi	–	–	–	–	17.65	0.24 \pm 0.59
Digenea								
Hemiuroidea gen. sp.	Me	St	–	–	–	–	56.86	2.20 \pm 3.49
<i>Proso-rhynchus</i> sp.	Me	Gi	–	–	–	–	13.73	0.47 \pm 2.02
<i>Proso-rhynchus australis</i> Szidat 1961	Me	Fi	Ne	Ne	Ne	Ne	64.71	5.53 \pm 7.33
<i>Derogenes varicus</i> (Müller, 1784)	Ad	St–In	37.50	1.29 \pm 2.29	11.76	0.22 \pm 0.70	–	–
<i>Lecithochirium microstomum</i> Chandler, 1935	Ad	St	10.42	0.17 \pm 0.56	–	–	–	–
<i>Aponurus laguncula</i> Loos, 1907	Ad	St	–	–	–	–	23.53	0.94 \pm 0.28
<i>Paralichthyrema patagonicum</i> Szidat, 1960	Ad	GI	–	–	–	–	7.84	0.08 \pm 0.27
Cestoda								
<i>Scolex polymorphus</i> Müller, 1784	Pl	St–In	45.83	4.42 \pm 9.39	7.84	6.47 \pm 24.61	54.90	10.35 \pm 27.08
<i>Nybelinia</i> sp.	Pl	St–In	50.00	1.60 \pm 2.18	58.82	6.08 \pm 9.02	88.23	5.02 \pm 4.28
<i>Grillotia carvajalregororum</i> (Carvajal et Rego, 1983)	Pc	Me	56.25	5.04 \pm 9.75	100	332.39 \pm 314.13	100	167.22 \pm 198.00
Unidentified larva	Pl	Me	2.08	0.02 \pm 0.14	–	–	–	–
<i>Anonchocephalus argentinensis</i> Szidat 1961	Ad	In	14.58	0.23 \pm 0.79	–	–	–	–
Nematoda								
<i>Anisakis simplex</i> (Rudolphi, 1809) s.l.	LIII	Me	–	–	–	–	9.80	0.18 \pm 0.59
<i>Terranova galeocerdonis</i> (Thwaite, 1927)	LIII	Me	–	–	–	–	1.96	0.02 \pm 0.14
<i>Contra-caecum</i> sp.	LIII	Me	12.77	0.21 \pm 0.62	50.98	1.37 \pm 1.94	39.22	0.61 \pm 1.15
<i>Pseudoterranova</i> sp.	LIII	Me–Mu	2.08	0.06 \pm 0.43	1.96	0.02 \pm 0.14	17.65	0.25–0.63
<i>Hysterothylacium</i> sp.	LIII	Me	33.33	0.69 \pm 1.36	37.25	0.63 \pm 0.92	27.45	0.49 \pm 1.10
<i>Hysterothylacium aduncum</i> (Rudolphi, 1802)	LIII	Me	2.08	0.02 \pm 0.14	11.76	0.12 \pm 0.33	–	–
<i>Ascarophis marina</i> (Szidat 1961)	Ad	In	2.08	0.02 \pm 0.14	–	–	–	–
<i>Cucullanus</i> sp.	Ad	In	27.08	0.50 \pm 0.92	–	–	–	–
<i>Cucullanus bonaerensis</i> Lanfranchi, Timi et Sardella, 2004	Ad	In	39.58	0.73 \pm 1.22	–	–	–	–
<i>Dichelyne pleuronectidis</i> Yamaguti 1935	Ad	In	–	–	11.76	0.16 \pm 0.46	60.78	2.06 \pm 3.15
Acanthocephala								
<i>Corynosoma australe</i> Johnston, 1937	Ju	Me	89.58	9.23 \pm 9.38	92.16	14.69 \pm 20.55	94.12	6.35 \pm 4.30
<i>Corynosoma cetaceum</i> Johnston et Best, 1942	Ju	Me	2.08	0.04 \pm 0.29	–	–	74.51	2.55 \pm 2.71
Copepoda								
<i>Brasilochondria riograndensis</i> Tatcher et Pereira, 2004	Ad	Op	–	–	–	–	5.88	0.06 \pm 0.24
<i>Acanthochondria sagitta</i> Alarcos et Timi, 2011	Ad	Gi	2.08	0.06 \pm 0.43	–	–	–	–

Stages: *Ad* adult, *Ju* juvenile, *LIII* third-stage larva, *Pc* plerocercus, *Pl* plerocercoid; sites: *Fi* fins, *GI* gills, *IN* intestine, *Me* mesenteries, *MU* musculature, *OP* operculum, *St* stomach; *Ne* not examined

Parasites were unevenly distributed among flounder species, with *P. patagonicus*, *X. rasile* and *P. isosceles* harbouring 17, 17 and ten species, respectively (*P. australis* excluded). Only six species were common to all three flounders, with *Grillotia carvajalregorum*, *Contraecaecum* sp., *Hysterothylacium* sp. and *Corynosoma australe* reaching high values of prevalence in all of them. Eight (excluding *P. australis*) species were found parasitizing exclusively *P. patagonicus* and seven exclusively in *X. rasile*, while all species found in *P. isosceles* were shared with one or both other species.

Parasites identified as host-specific were all at the adult stage, and comprised the copepod *Acanthochondria sagitta*, the cestode *Anonchocephalus argentinensis* and the nematodes *Cucullanus bonaerensis* and *Cucullanus* sp. in *X. rasile*, the nematode *Dichelyne pleuronectidis* in both *Paralichthys* spp. and the copepod *Brasilochondria riograndensis*, the monogenean *Neoheterobothrium paralichthyi* and the digenean *Paralichthytrema patagonicum* in *P. patagonicus*. This group made a small contribution to both total abundance (Fig. 1a) and species richness (Fig. 1b) in all three flounder species, while nonspecific parasites, especially

non-gut larval ones, were the dominant guild, especially in terms of abundance.

The influence of host-specific and gut parasites on similarity within (Fig. 2a) and between (Fig. 2b) host species was negligible when compared with that based on all species, similarities being mainly determined by non-gut nonspecific helminths. It is also noteworthy that host-specific parasites diminished similarity between infracommunities within host species.

The contribution of individual species of host-specific parasites, as well as of all of them together had little influence on the within host species infracommunity average similarity when compared with nonspecific parasites (Table 3). Also their effect on dissimilarity between host species was unimportant. Furthermore, *D. pleuronectidis*, the only host-specific parasite shared by two host species contributed more to dissimilarity between them than other species present in only one flounder (Table 3).

When only long-lived larval endohelminths were considered, species richness was more homogeneous across flounder species, being 10, 9 and 6 for *P. patagonicus*, *X. rasile* and *P. isosceles*, respectively. Excluding parasites with

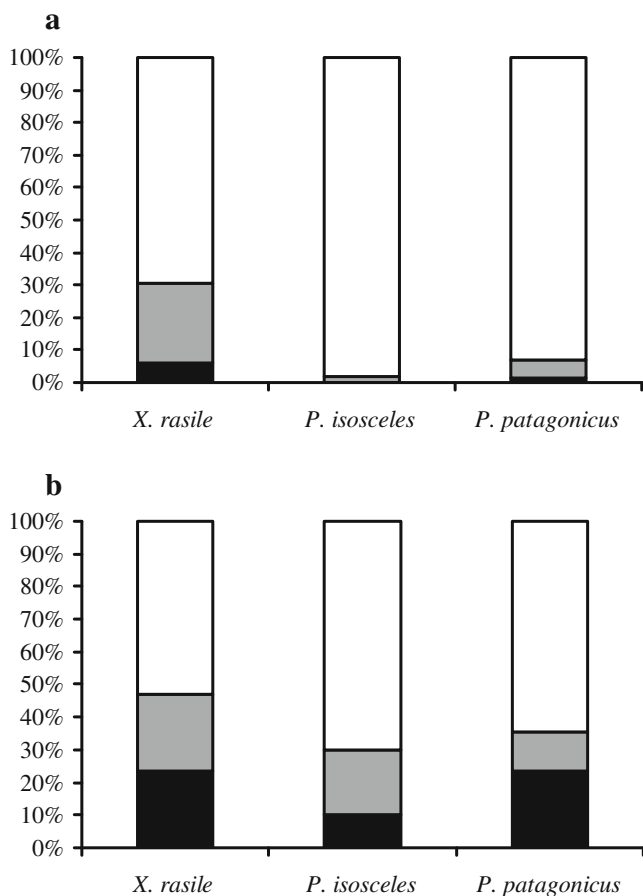


Fig. 1 Contributions of parasite guilds, expressed as percentages, to total abundance and (a) species richness (b) of parasite assemblages of three species of paralichthyid flounders. Black specific parasites, grey unspecific intestinal parasites, white unspecific larval non-intestinal parasites

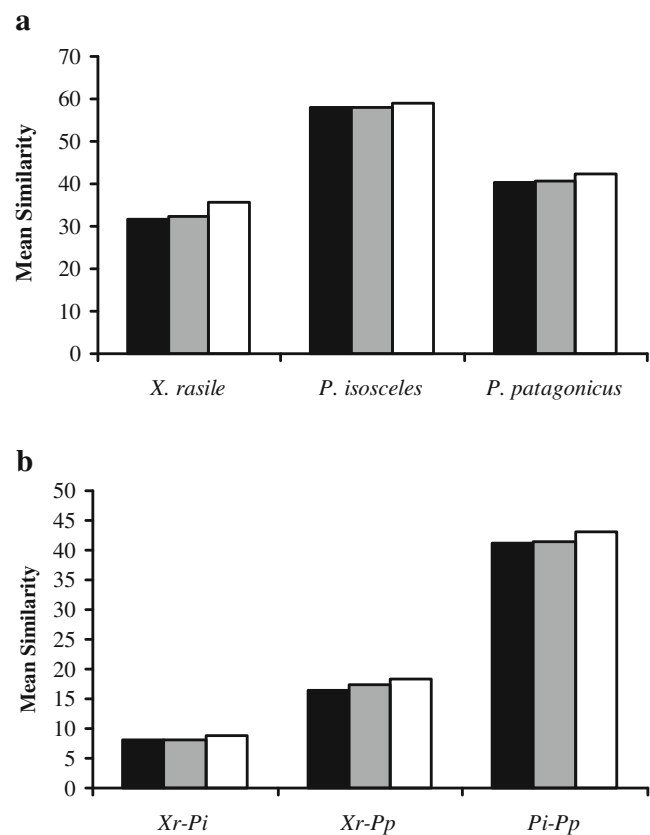


Fig. 2 Averaged Bray-Curtis similarity between pairs of infracommunities within (a) and between (b) three species of paralichthyid flounders. Black all parasites included, grey specific parasites excluded, white specific parasites and nonspecific intestinal parasites excluded. *Xr* *Xysteuryx rasile*, *Pi* *Paralichthys isosceles*, *Pp* *Paralichthys patagonicus*

Table 3 Breakdown of average similarity and dissimilarity of infracommunities of individual host-specific parasites and of species grouped in: total specific parasites, total nonspecific intestinal parasites

and total nonspecific extra-intestinal parasites within and between three sympatric flounders into contributions from each species/group expressed as percentages

	<i>X. rasile</i>	<i>P. isosceles</i>	<i>P. patagonicus</i>	<i>Xr–Pi</i>	<i>Xr–Pp</i>	<i>Pi–Pp</i>
<i>C. bonaerensis</i>	3.15	–	–	0.35	0.81	–
<i>Cucullanus</i> sp.	1.02	–	–	0.22	0.49	–
<i>A. argentinensis</i>	0.37	–	–	0.11	0.25	–
<i>A. sagitta</i>	–	–	–	0.03	0.06	–
<i>D. pleuronectidis</i>	–	0.01	1.73	0.07	2.6	1.02
<i>N. paralichthyi</i>	–	–	0.06	–	0.27	0.11
<i>P. patagonicus</i>	–	–	0.01	–	0.05	0.03
<i>B. riograndensis</i>	–	–	0	–	0.07	0.03
Total specific parasites	4.54	0.01	1.8	0.78	4.6	1.19
Total nonspecific intestinal parasites	14.64	0.23	2.24	5.36	9.22	6.38
Total nonspecific non-intestinal parasites	80.82	99.76	95.96	93.86	86.18	92.43

Xr *Xysteurys rasile*, *Pi* *Paralichthys isosceles*, *Pp* *Paralichthys patagonicus*

very low prevalence (<5%) and probably accidental in some hosts different, these values were reduced to 9, 5 and 5.

SIMPER results on abundances of this group showed that *P. isosceles* was the most homogeneous species in terms of parasite community structure with both measurements of similarity, followed by *P. patagonicus* and finally *X. rasile* (Fig. 3a). The main contributor to similarity for *X. rasile* was *C. australe* and it did so consistently in inter-comparisons, as shown by the ratios between their contributions and standard deviations >1 (Table 4), although *G. carvajalregorum* and *Nybelinia* sp. were also important in contributing to similarity within this sample. On the other hand, *G. carvajalregorum* was the only typical species for both species of *Paralichthys*; this species, despite being a relevant contributor to within samples similarity, was also an important and consistent discriminator among all of them (Table 4).

Comparisons across host species showed the highest similarities between the two *Paralichthys* spp. when the quantitative Bray–Curtis was used as similarity measurement, but more equivalent values of similarity between species when presence only of parasite species was compared by means of the Jaccard index (Fig. 3b).

Results of both PERMANOVA analyses (Table 5) showed a strong effect of host size on the response variables, and therefore on the parasite community structure. The interaction of host length with host species shows that the nature of the relationship between the covariate and the multivariate response differs within different levels of the factor. Furthermore, taking into account the variations among samples due to host size, significant variability was detected among the parasite assemblages. Pair-wise tests between host species showed that there were significant differences between most pairs of samples (all $P < 0.001$), except for both congeneric species when Bray–Curtis similarity was used ($P > 0.05$).

Dispersion of parasite infracommunities varied between flounder species in terms of their deviations from centroids, with significant variability observed for Bray–Curtis similarity

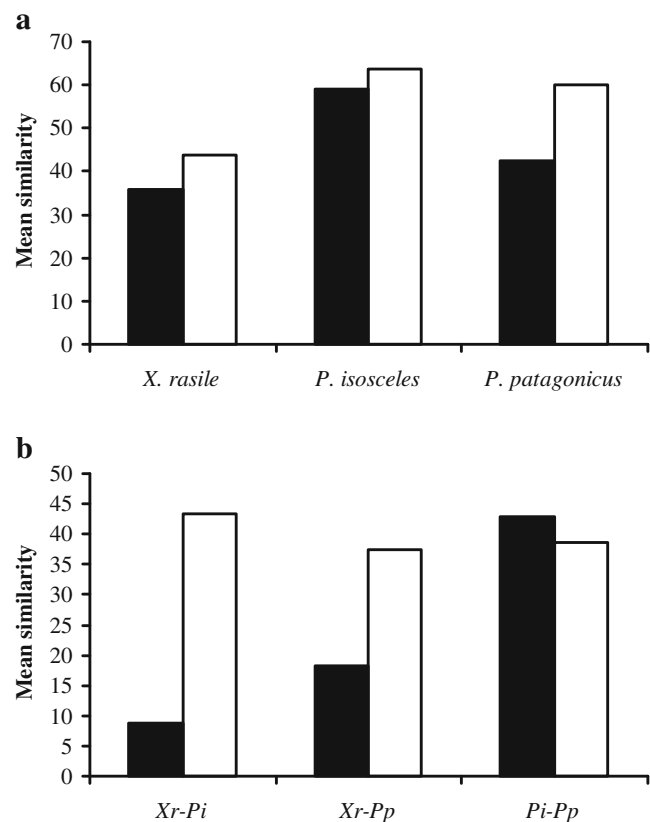


Fig. 3 Averaged similarity between pairs of infracommunities of nonspecific non-intestinal parasites within (a) and between (b) three species of paralichthyid flounders. Black Bray–Curtis similarity, white Jaccard similarity. *Xr* *Xysteurys rasile*, *Pi* *Paralichthys isosceles*, *Pp* *Paralichthys patagonicus*

Table 4 Breakdown of average similarity and dissimilarity of infracommunities of individual host-specific parasites and of species grouped in: total specific parasites, total nonspecific intestinal parasites and total nonspecific extra-intestinal parasites within and between three sympatric flounders into contributions from each species/group expressed as percentages

	<i>X. rasile</i>	<i>P. isosceles</i>	<i>P. patagonicus</i>	<i>Xr–Pi</i>	<i>Xr–Pp</i>	<i>Pi–Pp</i>
<i>C. australe</i>	66.87	3.71	8.19	91.28	75.74	87.81
<i>G. carvajalregorum</i>	20.63	95.93	87.92	6.52	9.25	5.7
<i>Nybelinia</i> sp.	10.39	–	7.15	0.92	6.18	2.72
<i>Hysterothylacium</i> sp.	1.93	0.09	0.21	0.57	1.16	0.71
<i>Contracaecum</i> sp.	0.17	0.26	0.49	0.48	1.46	0.45
<i>H. aduncum</i>	–	0.01	–	0.15	0.03	0.08
<i>C. cetaceum</i>	–	–	2.32	0.05	0.45	0.15
Hemiuroidea gen. sp.	–	–	1.79	0.02	2.64	1.18
Unidentified plerocercoid	–	–	0.09	0.01	0.03	–
<i>Pseudoterranova</i> sp.	–	–	0.03	–	2.79	1.09
<i>A. simplex</i> s.l.	–	–	–	–	0.27	0.1

Values for typical (average contribution to the total average similarity/standard deviation >1) and discriminator (average contribution to the total average dissimilarity/standard deviation >1); species are in bold

Xr *Xystreurus rasile*, *Pi* *Paralichthys isosceles*, *Pp* *Paralichthys patagonicus*

($F_{2,146}=19.03$; $P_{(perm)}<0.0001$) and Jaccard similarity ($F_{2,146}=21.78$; $P_{(perm)}<0.0001$). A posteriori tests underlined significant differences for most comparisons (all $P<0.001$); except for the pairs *X. rasile*–*P. patagonicus* using Bray–Curtis index and *P. isosceles*–*P. patagonicus* using Jaccard index (both $P>0.05$).

Comparisons of the averaged infracommunity descriptors showed that *P. isosceles* harboured a higher number of parasites (Fig. 4a), but also a higher value of dominance (Fig. 4b) and the lowest diversity (Fig. 4c), whereas the species richness of *P. patagonicus* was notably higher than those of the other two host species (Fig. 4d).

After correcting for host size, all indices were significantly different between flounder species (Table 6), however pairwise tests showed that both *Paralichthys* species harboured similar values for all infracommunity descriptors, with *P. patagonicus* and *X. rasile* displaying also marginal differences in diversity. Multivariate dispersion of data could have an

important influence on the significance of differences in total mean abundance involving *X. rasile* and, to a lesser extent, those of diversity between *P. patagonicus* and *X. rasile* (Table 6).

Discussion

Given the phylogenetic relatedness among the host species, the presence of shared parasites, either conspecific or phylogenetically related to each other, was expected as a result of their inheritance from their common ancestors. However, the identification of host-specific parasites showed that only *D. pleuronectidis* was shared by two flounders (the two *Paralichthys* spp.). This species was originally described from *Paralichthys olivaceus* (Temminck et Schlegel, 1846) in Toyama Bay in Japanese waters (Yamaguti 1935), although taking into account the geographical distance it is probably

Table 5 One-factor PERMANOVA results of infracommunity data of parasites of three species of flounders based on Bray–Curtis (for abundance) or Jaccard (for presence–absence) dissimilarity measures with host length as covariable

Similarity measurement	Source	df	SS	MS	F	$P_{(perm)}$
Bray–Curtis	Host length	1	15,790	15,790	9.11	<0.0001
	Host species	2	1.3181×10^5	65,904	38.03	<0.0001
	Host length × species	2	10,620	5,310.1	3.06	<0.01
	Residual	143	2.4779×10^5	1,732.8		
	Total	148	4.0601×10^5			
Jaccard	Host length	1	45,589	45,589	39.01	<0.0001
	Host species	2	35,661	17,831	15.26	<0.0001
	Host length × species	2	7,104.9	3,552.4	3.04	<0.01
	Residual	143	1.6714×10^5	1,168.8		
	Total	148	2.5549×10^5			

P values obtained after 9,999 permutations

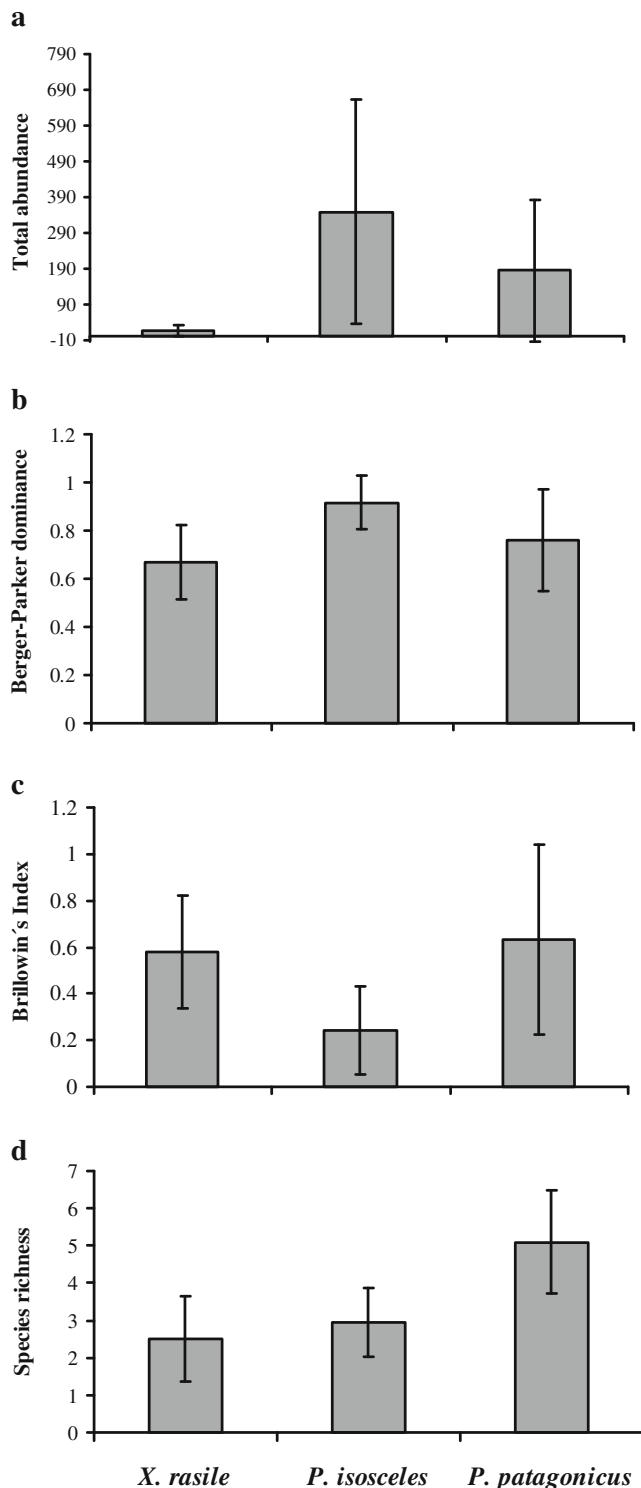


Fig. 4 Mean infracommunity descriptors in three species of paralicthyid flounders. **a** Total abundance, **b** dominance, **c** diversity, **d** richness

that they represent sibling species. *Cucullanus bonaerensis* was described from the Brazilian codling *Urophycis brasiliensis* (Gadiformes) in the same region (Lanfranchi et al. 2004), but none of the adult females from codling was found to be

gravid suggesting the presence of this parasite constituted an accidental infection in an unsuitable host (Lanfranchi et al. 2004). The presence of gravid females of *C. bonaerensis* in *X. rasile* suggests that this is the definitive host for this nematode. The second species of *Cucullanus* found in this host was not identified, so no conclusions can be made on their specificity. *Brasilochondria riograndensis*, found on *P. patagonicus*, has also been recorded on the sympatric congener *P. orbignyanus* (Braicovich and Alarcos 2007), but not in *P. isosceles*. However, all host-specific parasites were of little importance as contributors to abundance and species richness in all three flounder species, as well as to similarity within and between host species. This group was not only irrelevant in delineating the repeatability of communities in each flounder species, but also in the structuring of parasite assemblages of all three species as a phylogenetically related group. Indeed, host-specific parasites diminished similarity between infracommunities within host species and the only species shared by two flounder species contributed more to dissimilarity between them than other species present in only one of them.

Poulin et al. (2011), based on analyses of species richness, stressed that host phylogeny may often outweigh specific host ecological traits as a predictor of parasite species richness. This conclusion was based on extensive datasets, gathered at broad spatial scales and including both related and unrelated host species. On the other hand, the present study is in agreement with others dealing with phylogenetically related hosts, in which analyses of either species richness or multivariate abundance data (Lile 1998; Muñoz et al. 2006; Marques et al. 2011) provide strong evidence that host phylogeny has only a weak influence on parasite diversity and community structure. Studies carried out at intermediate scales (unrelated hosts caught at short temporal and spatial scales) have concluded that both phylogeny and host ecology influence the composition of the parasite fauna of fishes (Aguirre-Macedo et al. 2007; Luque et al. 2004; Takemoto et al. 2005). The quantification of the relative influence of both host phylogeny and ecology as drivers of parasite diversity, as in many other fields of parasite ecology (see Poulin and Mouritsen 2003; Fredensborg et al. 2006; Krasnov et al. 2011), seems to be a matter of scale.

Similarity analyses based on abundances of nonspecific larval parasites showed that the highest homogeneity of infracommunities was displayed by the two congeneric host species. This pattern could be a consequence of their similar and high trophic level. It has been shown recently that fish species at a low trophic level harbour more variable and stochastic parasite assemblages than hosts at a higher trophic level, which display higher values of similarity between infracommunities (Timi et al. 2011). Indeed, flounders at a high trophic level harbour higher numbers of parasites, especially those that largely dominate the assemblages, homogenizing and increasing the quantitative similarities among conspecifics.

Table 6 Comparisons of infracommunity descriptors (PERMANOVA) and their dispersions (PERMDISP) of unspecific non-intestinal parasite species in three sympatric paralichthyid flounders

Infracommunity Descriptors	PERMANOVA					PERMDISP				
	Main test		Pair-wise test (<i>P</i>)			Main test		Pair-wise test (<i>P</i>)		
	Pseudo- <i>F</i>	<i>P</i>	<i>X_r-P_i</i>	<i>X_r-P_p</i>	<i>P_i-P_p</i>	<i>F</i>	<i>P</i>	<i>X_r-P_i</i>	<i>X_r-P_p</i>	<i>P_i-P_p</i>
Total abundance	28.37	<0.0001	<0.0001	<0.0001	>0.05	23.73	<0.0001	<0.0001	<0.0001	–
Species richness	16.27	<0.0001	0.013	<0.0001	>0.05	6.07	<0.01	>0.05	>0.05	–
Diversity	11.59	<0.0001	<0.0001	0.041	>0.05	19.82	<0.0001	>0.05	<0.001	–
Dominance	24.16	<0.0001	<0.0001	<0.001	>0.05	16.76	<0.0001	0.017	0.013	–

The higher similarity within samples of both *Paralichthys* spp., which occupy a higher position in the food web because of their ichthyophagous habits, can be due to the accumulation of larger numbers of infective stages acquired as packets of helminth species that travel together in paratenic fish hosts along food chains (Bush et al. 1993; Poulin and Valtonen 2001; Marcogliese 2002). *X. rasile*, on the other hand, displays impoverished assemblages, resulting from stochastic encounter events at low densities, which in turn decrease intraspecific similarity, reflecting the dilute nature of parasite distribution in previous intermediate invertebrate hosts (Marcogliese 1995, 2002).

It has been also postulated that juvenile fish harbour more variable and stochastic parasite communities than older fish (Timi et al. 2010b), which could explain the higher homogeneity between infracommunities of *P. isosceles* in comparison with *P. patagonicus*. It could be due to young fish beginning their lives free of parasites, followed by small differences in exposure to different parasites generating substantial differences between individuals. Over time, parasite communities become homogenized by repeated exposure. This pattern of increasing predictability in older fish has been observed in experimental fish, initially uninfected, and exposed to natural infections (Vidal-Martinez et al. 1998) as well as in wild fish (Timi et al. 2010b).

Comparisons across host species showed the highest quantitative similarity between *P. isosceles* and *P. patagonicus*, an expected result given the prevalence of 100% in both host species shown by *G. carvajalregorum*, the typical parasite of both *Paralichthys* spp., and the main contributor to within species similarity, although its abundance was also the main factor responsible for the differences between them. For *X. rasile*, on the other hand, this role was played by *C. australe*.

PERMANOVA analyses, after correcting for fish size, confirmed statistically that both *Paralichthys* spp. species harbour assemblages of similar structure, but that they also showed significant differences in composition when binary data were compared between infracommunities across host

species. This is not surprising, as the Bray–Curtis index incorporates more information about each community, i.e., the abundance of each species as opposed to the binary data only, and is less subject to the vagaries of rare species than the Jaccard index.

Fish parasite communities in the northern Argentinean Sea are dominated by trophically transmitted larval parasites of low host-specificity (Timi 2007). Given the high abundances and broad distributions of these parasites in the regional compound community (Timi 2007; Timi and Lanfranchi 2009), which are obtained via passive sampling of available infective stages by feeding on previous intermediate hosts, the assemblages they form predictable subsets of the species available regionally. This applies to parasite assemblages in all host species so far examined in this region, with a non-random composition and a structure determined mainly by ecological filters, such as fish habitat or diet (Lanfranchi et al. 2009; Timi and Lanfranchi 2009; Rossin and Timi 2010; Timi et al. 2011). These parasites have such an influence that the infracommunities they form are governed by their abundances (Timi and Lanfranchi 2009). In fact, if a PERMANOVA is run including all parasite species found in the three flounder species, even the host-specific ones, and after correcting for flounder size, infracommunities of *P. isosceles* and *P. patagonicus* do not differ in their structure (unpublished data).

In the present study, the sympatry of the three flounder species and their benthic habits reduce the ecological filters and only the host traits can constrain the number of both species and individuals in their parasite assemblages to produce differences between fish species. Two fish species with different size, but exposed to the same pool of infective stages, should acquire qualitatively or quantitatively different parasite assemblages depending of the amount and type of prey they eat. Increasing differences in interspecific host characteristics should, therefore, lead to being exposed to increasingly different subsets of the total assemblage of parasite species, and similarity in parasite assemblages should decay as a function of trophic or size differences between fish species (Timi et al. 2010b).

The sample of *P. patagonicus* was caught 16 months later than those of the other two flounders. However, and in despite temporal differences in the accumulation of larval helminths that can generate differences between fish species, the life spans of the selected larval parasites diminished the possible variability of community structure at this temporal scale. Host trophic level, therefore, emerged as the main explanatory variable for the differences observed at host generic level. Although it seems obvious, the present data explicitly show that two sympatric hosts with similar diets and habitats harbour parasite communities with identical structure. On the other hand, the size of flounders was the factor responsible for variation in parasite assemblages between congeneric hosts.

The effect of host size on the discrimination between the two *Paralichthys* spp. was clearly observed when the infracommunity descriptors were analyzed. Values of diversity depended on the balance between dominance and species richness. In fact, the higher number of parasites displayed by *P. isosceles* was almost exclusively due to the abundance of *G. carvajalregorum* (which represented near 92% of all parasite individuals found in this host); this parasite was also responsible for the higher dominance which, combined with the intermediate values of species richness produced the lowest diversity. The opposite trend was observed for *P. patagonicus*, which by displaying the highest species richness and intermediate values of dominance reached the maximum diversity. Finally, *X. rasile* with the lowest values of both species richness and dominance, displayed an intermediate diversity. These differences were confirmed by PERMANOVA analyses, but the correction for fish size showed that both *Paralichthys* species, if they were of comparable sizes, should harbour similar infracommunities. This similarity is a clear reflection of both the influence of fish size in drawing the differences between them and their shared trophic habits by comparison with *X. rasile*.

The higher species richness in *P. patagonicus* may be attributed to the larger size of specimens compared with the other two flounder species. Host size is a key determinant of parasite community structure across fish species (Luque and Poulin 2008) by affecting parasite diversity through its influence on the rates of parasite speciation and colonization by new parasites in evolutionary and ecological time scales, respectively. An increase in the number of species in larger hosts is a common feature of fish–parasite systems, because larger bodied hosts should be able to accommodate more parasite species and to sustain a greater absolute number of parasites than small ones. They also display larger surface areas for parasite attachment and ingest larger quantities of food with a concomitant higher exposure to infective stages (Guégan et al. 1992; Poulin 2000; Valtonen et al. 2010). Furthermore, large fish can also feed on larger prey, broadening the set of potential parasites (Timi et al. 2011). These

results, therefore, imply that if specimens of *P. isosceles* were larger, they should harbour richer infracommunities.

On the other hand, the higher abundance observed in *P. isosceles* should imply that, if these fishes were larger they should have lower abundances than they actually have, an unexpected situation given the cumulative effect of host size on parasite burdens. This contradictory fact is, however, attributable to the age of specimens of *P. isosceles*, which were comparatively the oldest, judging by the percentage of the maximum length the species reached, and is a consequence of the dominance of long-lived larval stages in the assemblages. The intensity of parasite infections is known to increase with the age of fish hosts (Dogiel et al. 1958; Poulin 2000); therefore, older fish have had longer to accumulate parasites, by being exposed to parasites for longer periods than younger hosts.

In synthesis, both size and age act together as drivers of parasite community structure. This is a well-known feature of fish–parasite systems (Poulin 2000), which has been largely based on evidence from studies based on a single fish species. Because of the logical relationship between age and size, it has been generally assumed that both variables act synergistically, and the distinction between their individual outcomes is not undemanding. The present study, by analyzing comparatively two species harbouring parasite assemblages of equivalent structure, but with different age–size relationships, showed that both variables seem to act at dissimilar rates on different characteristics of parasite assemblages. Indeed, fish age affects mainly the parasite abundance, whereas body size influences mainly the species richness, through its relationship with the trophic level. The discernment between these variables is essential not only for understanding how parasite community structure is mediated by size-dependent trophic interactions, but also for assessing how much this structure is affected by the host age.

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