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ORIGINAL PAPER

The importance of the compound community on the parasite infracommunity structure in a small benthic fish

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Abstract The extent to which the structure of parasite infracommunities and component communities is determined by the composition of the compound community was assessed by determining the importance of unspecific larval parasites relative to the other guilds (ectoparasites and adult endoparasites). This was analyzed under the hypothesis that the infracommunities harbored by any fish species in coastal waters of the northern Argentine sea will be dominated by unspecific larval stages, which also will be the determinants of the infracommunity structure. These predictions were tested in the Atlantic sea robin, *Prionotus nudigula*. A total of 1,570 metazoans belonging to 11 species were found in the overall sample (total prevalence=98%). Larval endoparasites, especially *Corynosoma australe* and *Grillotia* sp., were the best represented species, with a deep influence on the infracommunity structure, accounting for the highest proportion of individuals, dominating about 60% of the infracommunities, greatly determining all infracommunity descriptors, and producing marked changes in the similarity among infracommunities. Given the abundance and broad distribution of unspecific larval parasites in the compound community, infracommunities can be considered as subsets of the species available regionally. They are obtained by passive sampling of infective stages as fish feed, and lead to predictable assemblages, with a non-random composition and structure modeled mainly by ecological filters.

Introduction

During the last few decades, an increasing amount of meta-analyses and macroecological studies have been accumulated by parasite ecologists in an attempt to identify the key determinants of parasite community structure (Gotelli and Rohde 2002; Luque et al. 2004; Poulin 2004, 2007; Mouillot et al. 2005; Luque and Poulin 2008) searching for recurrent and predictable patterns to determine whether general rules determine the structure of parasite assemblages (Poulin 2007).

At such large macroecological scales, patterns in species diversity are caused by a variety of ecological and evolutionary processes, as well as historical events and geographical contingencies (Poulin 2004), and distinguishing among these factors is not always straightforward (Desdevises et al. 2003). Host ecological traits have received much attention as drivers of species assembly rules in fish parasite communities. Among them, size and age, habitat and diet, schooling behavior, and population size and density have been suggested as key determinants (Bagge et al. 2004; Pérez-del Olmo et al. 2008; Luque and Poulin 2008). However, it is at this intermediate scale that contingent, rather than recurrent, patterns are generally the rule, and no general answers have been found about the linkage between diversity of parasites and host ecological traits (Poulin 2007; Luque and Poulin 2008).

Several methodological problems have been pointed as a cause of the inconsistency of results, such the use of species richness as a sole measurement of diversity of parasite communities in most of these studies and the influence of

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phylogenetic relationships among both fish and parasite species (Poulin and Morand 2004; Luque and Poulin 2008).

Species richness may be the single most important feature of a community (Poulin and Rohde 1997); however, it does not include all aspects of diversity (Luque et al. 2004) and other features of parasitism, such as parasite abundance, measured either as number or biomass of parasites per host (George-Nascimento et al. 2004; Mouillot et al. 2005; Poulin and George-Nascimento 2007) as well as the use of average taxonomic distances between parasite species in an assemblage (Luque et al. 2004) have been thus considered as an alternative measurement of diversity in parasite communities.

A common feature of all these previous comparative studies is that they do not take into account the identity of the parasites involved in the comparisons. Despite many parasite species being quite specific, many others often exploit more than a single host species at any given stage of their life cycles (Poulin 2005). The extent to which different host species are exploited by a given parasite species can shed some light on some features shared by these hosts, especially ecological ones when non-specific parasites are considered; on the other hand, an uneven use of host species could indicate which ecological traits govern the distribution of parasites among potential hosts in an ecosystem.

An interesting theoretical framework was proposed by Holmes (1996); it relates the structure of the different hierarchical levels of parasite communities (e.g., compound community, component community, and infracommunity; see Bush et al. 1997) and predicts that component communities and infracommunities may be either restricted subsets or random samples of the compound community. According to Holmes (1996), if the component community is determined by phylogenetic, ecological, or physiological specificity of the parasites, then it will be essentially a restricted subset of the compound community, and infracommunities are likely to represent random samples of that subset. On the other hand, if infracommunities depend upon ecological or physiological traits acting at the level of individual hosts, then infracommunities will be random samples of the compound community, the component community essentially being an artificial construct. Both situations are the opposite ends of a continuum, rather than exclusive alternatives.

The position of any parasite assemblage along this continuum relies on the numerical importance of non-specific species in the compound community; therefore, the identity of parasite species shared by several host species has a great relevance in comparative analyses aiming to determine the influence of the composition of the compound community on that of both component communities and infracommunities at a regional scale.

The distribution patterns of marine parasites are mainly determined by temperature–salinity profiles and their association with specific masses of water (Esch and Fernández 1993). Furthermore, as geographic and oceanographic conditions are far from uniform throughout the oceans, especially in coastal systems, the composition and structure of fish, and therefore of parasite assemblages, can vary greatly among regions. In each particular environment, the structure of the food chain, through its influence on the transmission rates of some parasite species (Marcogliese 2002), as well as certain host features, such as feeding habits, can influence the number of parasite species exploiting a host species (Luque et al. 2004) and therefore a host community.

The number of parasitological studies on fish species inhabiting the Argentine sea is still scarce; however, in the north zone (coastal waters of Buenos Aires Province), the dominance, in terms of prevalence and abundance, of larval parasites (mainly nematodes, cestodes, and acanthocephalans) seems to be the rule. Numerical dominance of members of this guild has been documented for all fish species so far examined (Sardella and Timi 1996, 2004; Cremonte and Sardella 1997; Timi 2003, Timi and Poulin 2003, Timi et al. 2005, 2008; Braicovich and Timi 2008).

Despite the numerous studies on the community ecology of fish parasites, larval helminths in intermediate or paratenic hosts have received little attention (Poulin and Valtonen 2001; Luque and Poulin 2004). Recently, Timi (2007) identified in the Argentine sea a group of trophically transmitted parasite species shared by different fish species, which are all at the larval stage. This group comprises species with extremely low specificity (such as juvenile acanthocephalans of the genus *Corynosoma*, plerocerci larvae of the genus *Grillotia*, and anisaskid nematodes of the genus *Hysterothylacium*). And, more importantly, this group displays similar latitudinal patterns in all hosts. Based upon this evidence, Timi (2007) predicted that these species could be sufficient for identifying populations of all fishes inhabiting this region. Consequently, fish populations, but also fish assemblages, might be identified according to the occurrence of this group of parasites, characteristic of the region, making them suitable as regional biological tags. This prediction was later corroborated for two fish species (Timi et al. 2008; Braicovich and Timi 2008), indicating that infracommunities are, to a certain degree, random subsets of the species available in the compound community.

Based on previous evidence, it can by hypothesized that the parasite communities harbored by any fish species in coastal waters off the northern Argentine sea will be dominated by non-specific larval stages (mainly *Grillotia* sp., *Corynosoma australe*, and *Hysterothylacium* spp.), which also will be the determinants of the infracommunity structure.

These predictions are tested by analyzing the composition and structure of parasite communities of a small benthic fish, the Atlantic sea robin, *Prionotus nudigula* (Ginsburg 1950) (Triglidae). This fish is distributed in coastal waters from Rio de Janeiro (Brazil) to near 43°S in Argentina and feeds on small benthic organisms, mainly crustaceans (Cousseau and Perrotta 2004). At present, only their ectoparasites have been studied (Euzet and Suriano 1975; Cressey and Cressey 1989; Rohde 1991; Timi et al. 2004).

Materials and methods

A total of 101 specimens of *P. nudigula* (TL 19.7±3.0 cm) were examined for parasites. Fish were caught by trawl off the coast of Buenos Aires Province (Bonaerense region) as bycatch by the commercial fleet operating at Mar del Plata port (38°27′S, 57°90′W) between March and December, 2004. Fish were either kept fresh or deep frozen in plastic bags at −18°C until examination. After defrosting, each sea robin was measured for total length (cm). Parasites were recovered from the body surface, gills, branchial and body cavities, and viscera (stomach, intestine, liver, gonads, and mesenteries) after examination under a stereoscopic microscope.

Prevalence and mean abundance were calculated for each parasite species in each area following Bush et al. (1997). For each individual fish, the species richness was calculated; also, the following community descriptors were calculated at infracommunity level (*sensu* Bush et al. 1997) for those sea robins harboring two or more species (infracommunities): number of parasites in each infracommunity (N), species richness (S), Brillouin's index of diversity (HB), evenness associated to Brillouin's index of diversity (E), and the percentage of infracommunities in which each parasite species was either dominant or codominant (Magurran 1988).

The importance of each parasite guild (by pooling parasites in the following categories=ectoparasites, adult endoparasites, and larval endoparasites) within each infracommunity was evaluated by calculating the proportion of individual parasites that it contributes to the assemblage and their effect on the number of parasitized fish. Their contribution to the structure of each infracommunity was assessed by means of a backward selection, by leaving out one guild in turn and then re-calculating species richness, diversity, and evenness. The underlying idea is that the exclusion of an important category will result in a greater change in the value of the descriptor, compared to a less important guild. The same analyses were carried out for each particular parasite species. The effect of parasite guilds on the whole parasite infracommunities was also analyzed by means of Spearman rank correlations between infracommunity descriptors for these fish harboring more than one species in each guild.

To determine the importance of each species to the similarity among infracommunities, Jaccard's (qualitative) and Sørensen (quantitative) indices (Magurran 1988) were calculated among all infracommunities first including all parasite species, and then after applying the same backward selection procedure. The sequential exclusion of different species produced different numbers of communities harboring two or more parasite species.

To determine whether co-occurrences of larval species living in the body cavity were more or less frequent than expected by chance in a same host, a null model of expected frequencies based on the actual prevalence of parasites was generated according to Janovy et al. (1995).

To assess the pairwise relationship between the intensity of pairs of species of larval parasites across individual hosts, Spearman's rank correlation coefficients (R_s) were calculated, excluding double zeros and species with prevalence <10%.

Results

Ninety-nine of out 101 fish were found to be parasitized by at least one of 11 parasite species (Table 1) (total prevalence 98%). A total of 1,570 metazoan parasites were found in the overall sample (total mean abundance 15.5).

Larval endoparasites, especially *C. australe* and *Grillotia* sp., accounted for the highest percentage of all individuals, whereas adult endoparasites represented almost 5% of the total abundance (Table 2). About 60% of the infracommunities were dominated or co-dominated by larval endoparasites, mainly by *C. australe* and *Grillotia* sp.; they were followed in importance by ectoparasites, whereas adult endoparasites were hardly represented as dominant in the assemblages (Table 2).

Mean infracommunity species richness when all hosts were considered was 2.41±1.4. This value was greatly affected when *C. australe* was excluded from its calculation, producing also the highest increment of the percentage of uninfected fish; these variations were reflected in the values of larval endoparasites. A marked decrease in species richness was also observed when either *O. marplatensis* or *Grillotia* sp. were excluded. Comparing among categories, values after removing ectoparasites were always intermediate between adult and larval endoparasites, but more similar to those of the former (Table 2).

Mean values of infracommunity descriptors, when only fish harboring two or more parasite species were considered, are given in Table 3. Values obtained for larval endoparasites (37 infracommunities) were more similar to

Table 1 Taxonomic composition, microhabitat, prevalence (P), and mean abundance±S.D. (MA) of parasites of *Prionotus nudigula* from the coasts of Mar del Plata, Argentina

	Stage	Site	P	MA
Ectoparasites				
Monogenea				
Orbocotyle marplatensis Euzet and Suriano 1975	Adult	Gills	42.6	1.0±1.7
Copepoda				
Orbitacolax haplogenyos (Yamaguti & Yamasu 1959)	Adult	Gills	18.8	0.3±0.8
Blias marplatensis Timi et al. 2004	Adult	Operculum	17.8	0.3±0.7
Adult endoparasites				
Nematoda				
Cucullanus sp.	Adult	Intestine	1.0	0.01±0.1
Hysterothylacium aduncum (Rudolphi 1802)	4th stage larva/adult	Intestine	2.0	0.1±0.2
Ascarophis marina (Szidat 1961)	Adult	Intestine	20.8	0.6±2.3
Larval endoparasites				
Digenea				
Unidentified	Metacercaria	Eye	2.0	0.02±0.1
Cestoda				
Grillotia sp.	Plerocercus	Mesenteries	32.7	3.9±10.9
Nematoda				
Hysterothylacium sp.	3rd stage larva	Mesenteries	6.9	0.03±0.5
Acanthocephala				
Corynosoma australe Johnston 1937	Juvenile	Mesenteries	85.1	9.2±10.9
Corynosoma cetaceum Johnston and Best 1942	Juvenile	Mesenteries	10.9	0.1±0.4

those of the whole sample than values of ectoparasites (22 infracommunities), whereas no hosts with more than one adult endoparasites species (to be considered as infracommunities) were observed. Unfortunately, only six sea robins harbored infracommunities of ectoparasites and larval endoparasites simultaneously (more than two species in each guild), to allow reliable comparisons. However, infracommunity descriptors in these 37 infracommunities of larval helminths were significantly correlated with the values of the whole sample in these fish (S—R_s=0.46; N—Rs=0.79; HB—R_s=0.61; E—R_s=0.80, all $P<0.01$), whereas in the 22 fish harboring ectoparasitic infracommunities, no relationships were observed between their infracommunity estimates and those including all guilds (S—R_s=−0.17; N—R_s=0.43; HB—R_s=0.15; E—R_s=0.25, all $P>0.05$). When categories were excluded in turn from the analyses, the highest variations with respect to the total sample (a decrease of N, S, and HB and increase of E) were observed after removing larval endoparasites, with adult endoparasites having only a minor effect.

Table 2 Effect of parasite categories and species on the composition of parasite communities of *Prionotus nudigula* from the coasts of Mar del Plata, Argentina

	% of total number of individuals	% of dominance+co-dominance	% of uninfected fish[a]	Species richness[a]
All ectoparasites	10.06	16.67	10.89	1.61±1.02
All adult endoparasites	4.65	3.92	11.88	1.38±0.87
All larval endoparasites	85.29	59.80	31.68	1.01±0.87
O. marplatensis	6.24	12.74	6.93	1.98±1.10
O. haplogenyos	2.04	0.98	1.98	2.22±1.21
B. marplatensis	1.78	2.94	2.97	2.23±1.19
Cucullanus sp.	0.06	0	1.98	2.40±1.23
H. aduncum	0.76	0	1.98	2.39±1.23
A. marina	3.82	3.92	1.98	2.20±1.13
Unidentified metacercaria	0.13	0	1.98	2.39±1.20
Grillotia sp.	25.14	15.69	2.97	2.08±1.07
Hysterothylacium sp.	0.19	0	1.98	2.34±1.15
C. australe	58.94	44.12	21.78	1.55±1.19
C. cetaceum	0.89	0	1.98	2.30±1.19

[a] After eliminating in turn each category or species

Table 3 Effect of parasite categories on the descriptors of parasite infracommunities of *Prionotus nudigula* from the coasts of Mar del Plata, Argentina

	Samples		S[c]	HB[d]	E[e]
	n[a]	N[b]			
All species included	72	18.69±19.03	3.0±0.95	0.57±0.25	0.72±0.24
Ectoparasites	22	4.44±2.70	2.06±0.24	0.40±0.10	0.93±0.18
Adult endoparasites	0	–	–	–	–
Larval endoparasites	37	23.19±23.14	2.35±0.54	0.45±0.19	0.67±0.23
Ectoparasites excluded	49	20.55±21.45	2.49±0.68	0.46±0.20	0.68±0.23
Adult endoparasites excluded	68	18.60±19.11	2.76±0.83	0.52±0.24	0.71±0.25
Larval endoparasites excluded	29	4.63±2.82	2.30±0.46	0.44±0.12	0.93±0.14

[a] Number of infracommunities
[b] Total number of parasites±S.D.
[c] Species richness±S.D.
[d] Brillouin's diversity index±S.D.
[e] Evenness±S.D.

Small changes of infracommunity descriptors were obtained after removing most individual species from the analyses (Table 4), with the exception of *C. australe* (whose exclusion produced an important decrease of N, S, and HB, but an increment of E), *Grillotia* sp. (which displayed similar variations, except for E), and *O. marplatensis* (leading a decrease in both S and HB). Changes of both total sample and the guild of larval helminths followed mainly those of *C. australe.*

Little variations with respect to the total sample were observed in qualitative similarity among infracommunities, when most parasite species as well as all ectoparasites and all adult endoparasites were excluded, although small increases of similarity were produced, especially without ectoparasites. The exception was *C. australe*, whose elimination produced a decrease of similarity of about 60%, influencing the effect of total larval endoparasites (Fig. 1). The same picture was observed when Sørensen indices were calculated.

The co-occurrence of larval species did not deviate significantly from a null model based on random occurrences (χ^2=17.22, P=0.31) (Fig. 2). The pairwise correlations between the intensity of infection of those larval species with prevalence >10%, *C. australe*–*C. cetaceum* (R_s 0.16), *C. australe*–*Grillotia* sp. (R_s −0.03), and *C. cetaceum*–*Grillotia* sp. (R_s 0.11) were not significant (all P>0.05).

Table 4 Effect of parasite species on the descriptors of parasite infracommunities of *Prionotus nudigula* from the coasts of Mar del Plata, Argentina

Species removed	Samples		S[c]	HB[d]	E[e]
	n[a]	N[b]			
O. marplatensis	65	19.03±19.67	2.63±0.78	0.48±0.21	0.70±0.25
O. haplogenyos	66	18.66±19.60	2.89±0.95	0.55±0.24	0.72±0.24
B. marplatensis	67	18.49±19.56	2.89±0.87	0.55±0.23	0.74±0.23
Cucullanus sp.	72	18.68±19.01	2.99±0.94	0.57±0.25	0.72±0.24
H. aduncum	72	18.65±19.05	2.97±0.95	0.56±0.25	0.72±0.24
A. marina	68	18.66±19.12	2.81±0.85	0.53±0.24	0.71±0.25
Unidentified metacercaria	72	18.67±19.03	2.97±0.89	0.56±0.25	0.72±0.24
Grillotia sp.	67	14.03±12.10	2.67±0.80	0.47±0.23	0.70±0.29
Hysterothylacium sp.	71	18.77±18.99	2.93±0.82	0.56±0.24	0.72±0.24
C. australe	48	11.33±14.59	2.62±0.70	0.47±0.19	0.78±0.26
C. cetaceum	72	18.50±18.87	2.85±0.94	0.55±0.25	0.73±0.25

[a] Number of infracommunities
[b] Total number of parasites±S.D.
[c] Species richness±S.D.
[d] Brillouin's diversity index±S.D.
[e] Evenness±S.D.

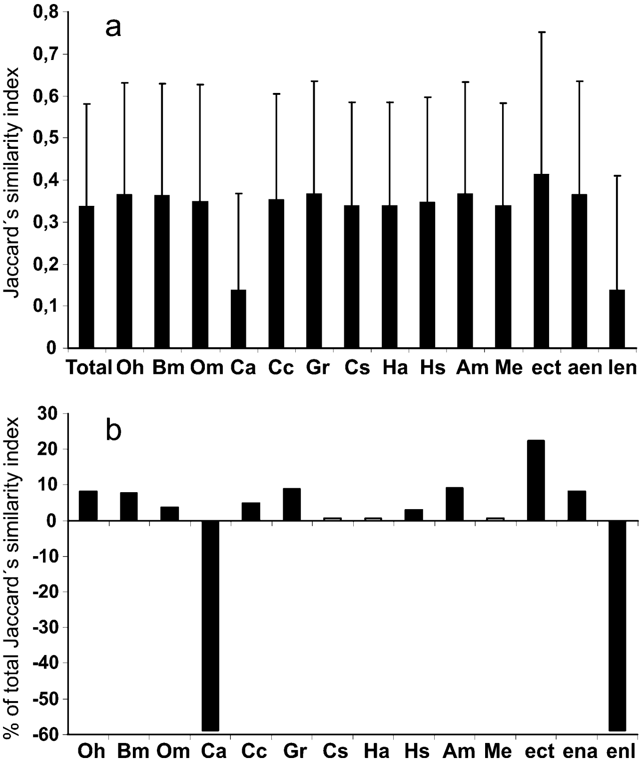

Fig. 1 Similarity values among infracommunities of parasites of *Prionotus nudigula* from the coasts of Mar del Plata, Argentina. **a** Average values and standard deviations for the total sample, and after excluding each parasite species or category. **b** Variations of similarity in relation of total sample after excluding each parasite species or category. Total: all species included; *Oh*: *Orbitacolax haplogenyos*; *Bm*: *Blias marplatensis*; *Om*: *Orbocotyle marplatensis*; *Ca*: *Corynosoma australe*; *Cc*: *Corynosoma cetaceum*; *Gr*: *Grillotia* sp.; *Cs*: *Cucullanus* sp.; *Ha*: *Hysterothylacium aduncum*; *Hs*: *Hysterothylacium* sp.; *Am*: *Ascarophis marina*; *Me*: metacercariae unidentified; *ect*: ectoparasites; *aen*: adult endoparasites; *len*: larval endoparasites

Discussion

In the Argentine Sea, *P. nudigula* harbors 11 parasite species, with the exception of the ectoparasites all of them constituting new host records. However, some species could be considered as accidental in this host, especially *Cucullanus* sp. and *H. aduncum* which were found in the digestive tract of one and two hosts, respectively, but the unidentified metacercariae were also uncommon.

Because the sea bottom is an exchange zone of infective stages of parasites among hosts inhabiting different bathymetric layers, parasite assemblages of benthic fishes display high levels of diversity (Marcogliese 2002). However, sea robins, despite having benthic habits (Texeira and Haimovici 1989), showed low species richness and abundance in relation to other fish species from the same zone, such as *Cynoscion guatucuapa* (Timi et al. 2005), *Merluccius hubbsi* (Sardella and Timi 1996, 2004), *Scomber japonicus* (Cremonte and Sardella 1997), *Engraulis anchoita* (Timi 2003, Timi and Poulin 2003), *Pinguipes brasilianus* (Timi et al. 2008), and *Percophis brasiliensis* (Braicovich and Timi 2008). Fish size is a key determinant of parasite species richness, with large species harboring more parasites (Guégan et al. 1992; Luque et al. 2004); the low species richness of *P. nudigula*, therefore, could be due to the small size of this fish species, together with its low level in the food chain (Poulin and Morand 2004).

The structure and dynamics of food webs (Marcogliese 2001, 2002) as well as the oceanographic conditions in this area (Timi 2007) can also determine the number of potentially available parasite species at a regional scale. In fact, a congeneric species, *P. punctatus* (Bloch, 1793), sympatric with *P. nudigula* in the Argentine Sea, harbors 23 parasite species in another region, the coastal waters of the State of Rio de Janeiro, Brazil (Bicudo et al. 2005).

The dominant species in the parasite assemblages of *P. nudigula* were, as expected, the non-specific larval stages of *C. australe* and *Grillotia* sp., although *Hysterothylacium* sp. was little represented in the sample. The importance of both parasite species in particular, especially *C. australe*, and of all larval endoparasites in general goes beyond their high values of prevalence and abundance. Both parasites have a deep influence on the infracommunity structure, accounting for the highest percentage of all individuals, greatly affecting all infracommunity descriptors whose values were governed by larval parasites, and producing marked changes in the similarity among infracommunities, and thus on the predictability of this system. On the other hand, neither ectoparasites nor adult endoparasites have an effect on the structure of the assemblages to which they belong.

The determination of infracommunity structure by trophically transmitted larval parasites is apparently the general pattern among fish species so far examined in this

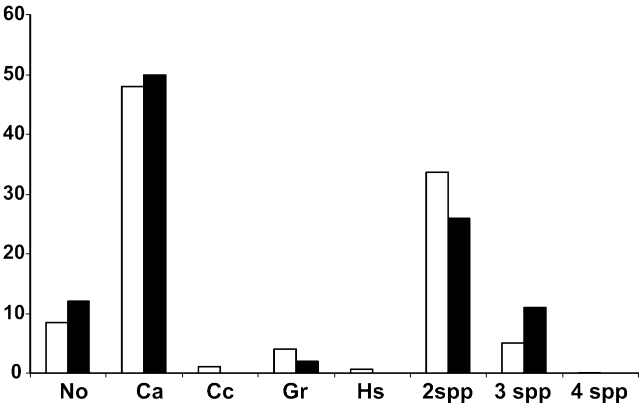

Fig. 2 Frequencies of expected (*white bars*) and observed (*black bars*) co-occurrence of larval parasites in individual specimens *Prionotus nudigula* from the coasts of Mar del Plata, Argentina. *No*: No parasites; *Ca*: *Corynosoma australe*; *Cc*: *Corynosoma cetaceum*; *Gr*: *Grillotia* sp.; *Hs*: *Hysterothylacium* sp.

region. This guild comprises mainly species with extremely low specificity whose life cycles and transmission seem to be favored by the regional environmental conditions (Timi 2007). Given the abundance and broad distribution of non-specific larval parasites in the compound community, infracommunities can be considered as subsets of the species available in the compound community, reflecting the structure of this higher-level assemblage instead of being randomly assorted. They are obtained by passive sampling of available infective stages as fish feed on previous intermediate hosts, leading to predictable assemblages, with a non-random composition and structure modeled mainly by ecological filters (such as fish habitat or diet). Host ecological traits constrain the number of both species and individuals in the component communities to produce differences in parasite assemblages among fish species. A clear example of the effect of ecological filters is the low number of *Hysterothylacium* sp. in *P. nudigula*, whereas in other sympatric species (i.e., *C. guatucupa* and *P. brasiliensis*) this parasite attains high abundance values.

On the other hand, close phylogenetic relationships among host species increase the possibility that hosts share similar parasite abundances or species richness because these were inherited from a common ancestor, therefore, they do not provide statistically independent observations in comparative studies, needing corrections when the effect of host features on the evolution of parasite assemblages is evaluated (Poulin and Rohde 1997). However, given the low specificity of these larval parasites and the fact that speciation over evolutionary time is unlikely to occur in intermediate or paratenic hosts, historical reasons should have no effect on the structure of these larval communities.

Many members of the guild of larval parasites have complex multiple-host life cycles that are embedded in food webs, and larval helminths can travel together along common transmission ways by sharing the same intermediate hosts, which harbor packets of infective stages that not only transmit individuals but also the structure of these assemblages to target communities harbored by their predators (Bush et al. 1993; Lotz et al. 1995; Poulin and Valtonen 2001). No evidence of significant co-occurrence of larval species was found in *P. nudigula*, which is probably a consequence of the carcinophagous habits of the fish, with larval parasites not sharing crustacean intermediate hosts. However, the structured assemblages of larval parasites harbored by sea robins can be transferred to ichthyophagous fish, at least those species using paratenic hosts in their life cycles (such as anisakids and probably *Corynosoma* sp.). Vickery and Poulin (2002) showed that patterns of association between helminth species cannot only be transferred up the food chain but also amplified in definitive hosts. It is also probable that amplification of community patterns also occurs in other paratenic hosts of higher trophic levels. This possibility should be studied in other fish species of this region to corroborate the reciprocal influence exerted between infracommunities and the regional compound community of non-specific larval parasites.

Further studies on this guild of parasites at a regional scale are promising to evaluate the extent of the influence of ecological filters on the structure of parasite communities, with the advantages of the independence of possible effect of the inheritance of similar assemblages by phylogenetically related hosts as well as of the evolutionary relationships among the parasites.

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All experiments comply with Argentinean laws.

References

Bagge AM, Poulin R, Valtonen ET (2004) Fish population size, and not density, as the determining factor of parasite infection: a case study. Parasitology 128:305–313

Bicudo AJA, Tavares LER, Luque JL (2005) Metazoarios parasitos da cabrinha *Prionotus punctatus* (Bloch, 1793) (Osteichthyes: Triglidae) do litoral do Estado do Rio de Janeiro, Brasil. Rev Bras Parasitol Vet 14:27–33

Braicovich PE, Timi JT (2008) Parasites as biological tags for stock discrimination of the Brazilian flathead in the South West Atlantic. J Fish Biol 73:557–571

Bush AO, Heard RW, Overstreet RM (1993) Intermediate hosts as source communities. Can J Zool 71:1358–1363

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Cousseau MB, Perrotta RG (2004) Peces marinos de Argentina. Biología, distribución, pesca. Publicaciones especiales INIDEP, Mar del Plata, Argentina

Cremonte F, Sardella NH (1997) The parasitofauna of *Scomber japonicus* Houttuyn, 1782 (Pisces: Scombridae) in two zones of the Argentine Sea. Fish Res 31:1–9

Cressey R, Cressey HB (1989) A new species of *Orbitacolax* (Copepoda: Bomolochidae) and redescriptions of two additional species. Can J Zool 67:1902–2909

Desdevises Y, Legendre P, Azouzi L, Morand S (2003) Quantifying phylogenetically structured environmental variation. Evolution 57:2647–2652

Esch GW, Fernández JC (1993) A functional biology of parasitism, 1st edn. Chapman & Hall, London

Euzet L, Suriano DM (1975) *Orbocotyle marplatensis* n. g., n. sp. (Diclidophoridae) Monogène parasite branchial de Téléostéens marins du genre *Prionotus* (Triglidae) en Argentine. Bull Mus Natl Hist Nat Zool 192:11–22

George-Nascimento M, Muñoz G, Marquet PA, Poulin R (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. Ecol Lett 7:527–531

Gotelli NJ, Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model analysis. Ecol Lett 5:86–94

Guégan J-F, Lambert A, Lévêque C, Combes C, Euzet L (1992) Can host body size explain the parasite species richness in tropical freshwater fishes. Oecologia 90:197–204

Holmes JC (1996) Helminth communities in marine fishes. In: Esch G, Bush A, Aho J (eds) Parasite communities: patterns and processes. Chapman & Hall, London

Janovy Jr J, Clopton RE, Clopton DA, Snyder SD, Efting A, Krebs L (1995) Species density distributions as null models for ecologically significant interactions of parasite species in an assemblage. Ecol Modell 77:189–196

Lotz JM, Bush AO, Font WF (1995) Recruitment-driven, spatially discontinuous communities: a null model for transferred patterns in target communities of intestinal helminths. J Parasitol 81:12–24

Luque JL, Poulin R (2004) Use of fish as intermediate hosts by helminth parasites: a comparative analysis. Acta Parasitol 49:353–361

Luque JL, Poulin R (2008) Linking ecology with parasite diversity in Neotropical fishes. J Fish Biol 72:189–204

Luque JL, Mouillot D, Poulin R (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. Parasitology 128:671–682

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton

Marcogliese DJ (2001) Pursuing parasites up the food chain: implications of food web structure and function on parasite communities in aquatic systems. Acta Parasitol 46:82–93

Marcogliese DJ (2002) Food webs and the transmission of parasites to marine fish. Parasitology 124:S83–S99

Mouillot D, George-Nascimento M, Poulin R (2005) Richness, structure and functioning in metazoan parasite communities. Oikos 109:447–460

Pérez-del Olmo A, Fernández M, Raga JA, Kostadinova A, Poulin R (2008) Halfway up the trophic chain: development of parasite communities in the sparid fish *Boops boops*. Parasitology 135:257–268

Poulin R (2004) Macroecological patterns of species richness in parasite assemblages. Basic Appl Ecol 5:423–434

Poulin R (2005) Relative infection levels and taxonomic distances among the host species used by a parasite: insights into parasite specialization. Parasitology 130:109–115

Poulin R (2007) Are there general laws in parasite ecology. Parasitology 134:763–776

Poulin R, Morand S (2004) Parasite Biodiversity. Smithsonian Institution Press, Washington, DC

Poulin R, Rohde K (1997) Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. Oecologia 110:279–283

Poulin R, Valtonen ET (2001) Interspecific associations among larval helminths in fish. Int J Parasitol 31:1589–1596

Poulin R, George-Nascimento M (2007) The scaling of total parasite biomass with host body mass. Int J Parasitol 37:359–364

Rohde K (1991) Intra- and interspecific interactions in low density populations in resource-rich habitats. Oikos 60:91–104

Sardella NH, Timi JT (1996) Parasite communities of *Merluccius hubbsi* from the Argentinean–Uruguayan common fishing zone. Fish Res 27:81–88

Sardella NH, Timi JT (2004) Parasites of Argentine hake in the Argentine Sea: population and infracommunity structure as evidences for host stock discrimination. J Fish Biol 65:1472–1488

Texeira RL, Haimovici M (1989) Distribução, reprodução e hábitos alimentares de *Prionotus punctatus* e *P. nudigula* (Pisces: Triglidae) no litoral do Rio Grande do Sul, Brasil. Atlântica Rio Grande 11:13–45

Timi JT (2003) Parasites of Argentine anchovy in the Southwest Atlantic: latitudinal patterns and their use for discrimination of host populations. J Fish Biol 63:90–107

Timi JT (2007) Parasites as biological tags for stock discrimination in marine fish from South American Atlantic waters. J Helminthol 81:107–111

Timi JT, Poulin R (2003) Parasite community structure within and across host populations of a marine pelagic fish: how repeatable is it. Int J Parasitol 33:1353–1362

Timi JT, Etchegoin JA, Lanfranchi AL (2004) *Blias marplatensis* sp. nov. (Copepoda, Chondracanthidae) parasitizing *Prionotus nudigula* (Pisces, Triglidae) from Mar del Plata, Argentina. Acta Parasitol 49:332–335

Timi JT, Luque JL, Sardella NH (2005) Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination. J Fish Biol 67:1603–1618

Timi JT, Lanfranchi AL, Etchegoin JA, Cremonte F (2008) Parasites of the Brazilian sandperch, *Pinguipes brasilianus:* a tool for stock discrimination in the Argentine Sea. J Fish Biol 72:1332–1342

Vickery WL, Poulin R (2002) Can helminth community patterns be amplified when transferred by predation from intermediate to definitive hosts. J Parasitol 88:650–656