

INFRACOMMUNITY STRUCTURE OF PARASITES OF *HEMIGYMNUS MELAPTERUS* (PISCES: LABRIDAE) FROM LIZARD ISLAND, AUSTRALIA: THE IMPORTANCE OF HABITAT AND PARASITE BODY SIZE

Gabriela Muñoz and Thomas H. Cribb

School of Molecular and Microbial Sciences, Department of Microbiology and Parasitology, University of Queensland, Brisbane 4072, Queensland, Australia. e-mail: s4005684@student.uq.edu.au

ABSTRACT: This study describes the community of all metazoan parasites from 14 individuals of thicklip wrasse, *Hemigymnus melapterus*, from Lizard Island, Australia. All fish were parasitized, and 4,649 parasite individuals were found. Twenty-six parasite species were identified although only 6 species were abundant and prevalent: gnathiid isopods, the copepod *Hatschekia hemigymmi*, the digenean *Callohelminis pichelinae*, and 3 morphotypes of tetraphyllidean cestode larvae. We analyzed whether the body size and microhabitat of the parasites and size of the host affected understanding of the structure of the parasite community. We related the abundance, biovolume, and density of parasites with the host body size and analyzed the abundances and volumetric densities of some parasite species within microhabitats. Although the 2 most abundant species comprised 75% of all parasite individuals, 4 species, each in similar proportion, comprised 85% of the total biovolume. Although larger host individuals had higher richness, abundance, and biovolume of parasites than smaller individuals, overall parasite volumetric density actually decreased with the host body size. Moreover, parasites exhibited abundances and densities significantly different among microhabitats; some parasite species depended on the area available, whereas others selected a specific microhabitat. Parasite and habitat size exhibited interesting relationships that should be considered more frequently. Considerations of these parameters improve understanding of parasite community structure and how the parasites use their habitats.

To understand the structure of a community, we need to identify the species present and determine their abundances. Other complementary parameters such as body size, biomass, and density of the species allow better descriptions of the community structure. In parasite communities, as well as free-living species, different kinds of variables have been studied to determine which of them influence the community structure. For example, many studies focused on infracommunities have assessed the importance of body size of hosts (Guégan and Hugueny, 1994; Lo et al., 1998), habitat and diet (Sasal et al., 1999; Muñoz et al., 2002), and social behavior (Bartoli et al., 2000). Aspects of parasites such as their microhabitats, body sizes, and associations between species have also been considered (e.g., Holmes, 1973; Lotz and Font, 1985; Adamson and Noble, 1993; Rohde et al., 1994; Sasal et al., 1999; George-Nascimento et al., 2002).

Consideration of parasite body size may be important to help understand the structure of parasite communities because, in general, the abundance or density of a parasite species shows some relationship with its body size (e.g., Tompkins and Hudson, 1999). However, parasite body size has only recently been taken into account in analyzing infracommunities (Rohde et al., 1994; George-Nascimento et al., 2002) or component communities of parasites (Arneberg et al., 1998; Poulin, 1999; Poulin et al., 2003; George-Nascimento et al., 2004). According to George-Nascimento et al. (2002), analyses based only on numbers of parasites may fail to identify important patterns when there are substantial differences in body size of hosts and parasites as well as in the number of parasites.

This study is focused principally on the significance of parasite body size and habitat size on the structure of parasite infracommunities of a fish species. If there are significant differences in body sizes among parasite species, this variable will translate into differences in relative parasite biomasses and densities, which would lead to a different understanding than if the analysis was based just on numbers of individuals. In addition,

the habitat size (host weight or microhabitat area) may also affect the understanding of parasite communities in abundances and densities because, in general, a large habitat may have more resources than small habitats and may support more individuals and species.

The objective of this study is to identify and analyze the community structure of metazoan parasites of the thicklip wrasse, *Hemigymnus melapterus* (Bloch, 1791), and to consider the importance of parasite body size, microhabitat areas, and host body weight. We analyze the data in 2 ways; first, we relate the abundance, biovolume, and densities of parasites, considering the whole community per fish individual with the host body size; second, we compare the abundances and densities of some parasite species in different microhabitats. To date, there has been no study of all metazoan parasites of this species, although several studies have focused on ectoparasites specifically (Grutter, 1994, 1998, 1999; Grutter and Poulin, 1998).

MATERIALS AND METHODS

Fourteen specimens of *H. melapterus* were collected from Lizard Island, Australia (14°40'S, 154°28'E) in August 2002 and September 2003 (late winter). Fish were caught using a spear gun while snorkeling and put into a plastic bag to minimize loss of ectoparasites during handling. Each host individual was weighed, and its sex was determined.

Parasites were sought for from the body surface, gills, gut, body cavity, and muscles. They were identified according to Kabata (1991) and Vervoort (1969) for copepods, Cannon and Lester (1988) for turbellarians, Chambers et al. (2000) for cestode larvae, Pichelin and Cribb (2001) for acanthocephalans, Cribb and Bray (1999) for digeneans, and Hartwich (1974) for nematodes.

Each parasite species was measured for length and width to estimate its body size. The body size was estimated using a geometric formula according to parasite body shape. Thus, gnathiids, copepods, and digeneans resemble ellipsoids; nematodes, acanthocephalans, and cestodes resemble a cylinder.

The area of the gills was estimated by drawing the outline of each fish on graph paper. We estimated the area for each site and arch. Only 1 face of each gill was considered. Because gill arches 1–3 are double, and the fourth arch is simple, the areas of gill arches were multiplied by 2 for the first 3 gill arches. Then, we multiplied each gill microhabitat by 2 because we used the ectoparasites from both sides of the fish (left and right).

The microhabitat area of the digestive tract was calculated by taking

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TABLE I. Parasites of *Hemigymmus melapterus* (n = 14) collected from Lizard Island (NP = number of parasites, P = prevalence, \bar{x} = mean abundance, SD = standard deviation, PBV = mean parasite body volume, n = number of parasites measured to determine body volume, and BIO = mean biovolume of parasites).

Parasite group	NP	P (%)	\bar{x}	SD	PBV (mm ³)	n	BIO (mm ³)
Ectoparasites							
Turbellaria							
<i>Ichthyophaga</i> sp. and/or <i>Paravortex</i> sp.	17	64.3	1.21	1.31	0.042	12	0.051
Isopoda							
Gnathiidae gen. spp. (larvae)	301	100	21.50	17.84	0.158	63	3.397
Copepoda							
<i>Hatschekia hemigymni</i>	1,179	92.9	84.21	84.41	0.058	40	4.884
<i>Orbitacolax</i> sp.	2	14.3	0.14	0.36	0.112	2	0.016
Endoparasites							
Trematoda							
<i>Callohelms pichelinae</i>	228	64.3	16.29	20.00	0.208	37	3.388
Hemiuridae (metacercaria)	75	78.6	5.35	8.65	0.064	12	0.342
Cestoda (larvae)							
Tetraphyllidea type 1	123	64.3	8.79	12.96	0.018	41	0.158
Tetraphyllidea type 4	2,334	100	166.71	190.31	0.016	82	2.667
Tetraphyllidea type 6	275	93.9	19.64	35.10	0.006	48	0.118
Tetraphyllidea type 8	2	14.3	0.14	0.36	0.018	1	0.002
Tetraphyllidea type 10	7	35.7	0.50	0.76	0.033	4	0.016
Tetraphyllidea type 12*	2	7.1	0.14	0.53	0.031	1	0.004
Tetraphyllidea type 13*	3	14.3	0.21	0.58	0.024	1	0.005
Tetraphyllidea type 14*	1	7.1	0.07	0.27	0.035	1	0.002
Tetraphyllidea type 22*	2	7.1	0.14	0.53	0.002	2	<0.001
Tetraphyllidea type 26*	1	7.1	0.07	0.27	0.002	1	<0.001
Tetraphyllidea type 30*	82	21.4	5.86	13.78	0.009	12	0.053
Pseudophyllidea gen. sp.	1	6.7	0.07	0.27	0.177	1	0.012
Trypanorhyncha type 1	1	7.1	0.07	0.27	5.690	1	0.398
Trypanorhyncha type 2	1	7.1	0.07	0.27	2.610	1	0.183
Metacestode unidentified	1	7.1	0.07	0.27	0.016	1	0.001
Nematoda							
Ascaridoidea larva type 1	1	7.1	0.07	0.27	0.176	1	0.012
Ascaridoidea larva type 2	3	7.1	0.21	0.80	0.033	1	0.007
Ascaridoidea larva type 3	1	7.1	0.07	0.27	0.045	1	0.003
Spirurida gen. sp.	1	7.1	0.07	0.27	0.005	1	<0.001
Acanthocephala							
<i>Transvena annulospinosa</i>	5	28.6	0.36	0.63	2.020	5	0.727
Total	4,649		332.07	301.97			16.447

* Types of larva different from those described by Chambers et al. (2000).

the length and width of each portion. Each digestive tract portion resembled a rectangle so that the area was calculated as length \times width. The areas of microhabitats (arch and site in gills, and portion of the digestive tract) were all measured in square centimeter.

The parasitological descriptors of richness, abundance, and prevalence were calculated according to Bush et al. (1997). Diversity was calculated using Hill's index because this gives importance to both abundant and rare species (Hill, 1973). Three other parameters were included: biovolume, as a measurement of biomass (abundance \times mean of parasite body volume of a species [in mm³] of parasites, see George-Nascimento et al., 2002; Poulin et al., 2003); numerical density of parasites, which was considered in 2 ways, for a whole infracommunity (numerical abundance/individual host weight) and per microhabitat area (numerical abundance/cm² of microhabitat); and volumetric density of parasites considered per infracommunity (biovolume/individual host weight) and per microhabitat (biovolume/cm² of microhabitat).

The host body weight was compared between sexes using a Kruskal–Wallis test and Dunnett test (post hoc). Most parameters were transformed to $\log_{10}(x + 1)$ to reduce the data biases (Zar, 1984). Pearson

correlations were applied to relate the parasitological parameters with host body weight. To compare the parasitological descriptors for parasites among microhabitats and parasite body sizes, 1- and 2-way analysis of variance were applied according to the number of factors to be compared (Zar, 1984). The Scheffé post hoc test for multiple comparison was used. Pearson correlations were applied for logarithmic transformed data to relate parasitological parameters with host and parasite body sizes. A significance level of 0.05 was used for all statistical analyses.

RESULTS

General parasite community structure

Five male, 4 female, and 5 juvenile individuals were examined. The body weight of juveniles was smaller (\bar{x} = 73.9 \pm 21.1 g) than that of adults, and no significant difference was detected for body weight between males (\bar{x} = 446.8 \pm 274.7

TABLE II. Percentage of total abundance and total biovolume of parasites. Bold values indicate the highest percentages in both parameters.

Parasite species	% Abundance	% Biovolume
Tetraphyllidea type 4	50.20	16.19
<i>Hatschekia hemigygni</i>	25.36	29.66
<i>Callohelms pichelinae</i>	4.90	20.57
Tetraphyllidea type 6	5.92	0.72
Gnathiidae	6.47	20.63
Tetraphyllidea type 1	2.65	0.96
Hemiuridae	1.61	2.08
<i>Transvena annulospinosa</i>	0.11	4.38
Trypanorhyncha type 2	0.02	2.47
All other 17 parasite species	2.76	2.34
Total percentage	100	100
Total abundances	4,649	230.3

g) and females ($\bar{x} = 317.1 \pm 277.5$ g) (Kruskal–Wallis test: $H = 6.5$, $n = 14$, $P = 0.038$ and Dunnett test: juveniles < males = females). All the analyses were done for the whole sample without regard to sex of the host because body size of fish was considered in all analyses of this study (i.e., body weight and microhabitat area).

All specimens of *H. melapterus* examined ($n = 14$) were parasitized with at least 5 parasite taxa each. Twenty-six taxa were found: 4 ectoparasites and 22 endoparasites. However, only 6 species were abundant and frequent: larval gnathiid isopods, the copepod *Hatschekia hemigygni*, the digenean *Callohelms pichelinae*, and cestode tetraphyllidean larvae types 1, 4, and 6 (Table I).

The body volume of parasites varied from 0.002 to 5.7 mm³ (Table I). Averages of parasite body sizes were compared among parasite species with enough numbers to be analyzed statistically. Body volume differed among ectoparasite species (turbellarians, gnathiids, and *H. hemigygni*: $F_{(2,112)} = 6.7$, $P = 0.002$); the gnathiids were the biggest (Table I). The endoparasites also differed in body size (tetraphyllidean types 1, 4, and 6 and *C. pichelinae*: $F_{(3,204)} = 161.9$, $P < 0.001$). Of these, the digenean was the biggest and the tetraphyllidean type 6 was the smallest (Table I). When abundance and parasite body size were considered together, the digenean had a higher biovolume than tetraphyllidean type 4, despite the fact that the cestode was 10 times more abundant than the digenean (Table I). The tetraphyllidean type 4 and the copepod *H. hemigygni* represent approximately 75% of the total abundance of parasites (Table II). However, 4 species each in similar proportions (16–29%, Table II) comprised more than 85% of the total biovolume.

The total body weight of the host varied between 47 and 801 g (body lengths of 14 and 37 cm, respectively). In general, the parasite-based parameters of richness, abundance, and biovolume increased with the host body weight, whereas parasite diversity and numerical density did not have any significant relationship with host body weight. Volumetric density of parasites was inversely related to host body weight (Fig. 1). In general, correlations of data subsets (ectoparasites and endoparasites) showed similar tendencies, although some relationships were significant or nonsignificant with host body weight (Fig. 1).

Parasitological parameters and parasite body volume did not

show any significant correlation when all parasite species were considered or when the species with the lowest prevalence and abundance were removed in case they were introducing noise into the relationship (Tables I, III).

Microhabitats and densities of parasites

The areas of gill microhabitats differed among gill arches ($F_{(3,156)} = 24.79$, $P = 0.0001$) because the fourth gill arch was the smallest, and between sites ($F_{(2,156)} = 6.83$, $P = 0.001$) where the midsite was the biggest. However, there was no significant difference in the gill area when both categories, gill arch and site, were considered ($F_{(6,156)} = 0.12$, $P = 0.99$). The areas of microhabitats in the digestive tract did not differ significantly ($F_{(3,52)} = 0.92$, $P = 0.437$).

The abundances of gnathiids and *H. hemigygni* on the gills did not differ between the left and right sides of the host (gnathiids: $t_{(26)} = -0.21$, $P = 0.83$; and *H. hemigygni*: $t_{(26)} = 0.50$, $P = 0.67$). Thus, parasites from both sides were combined for statistical comparisons. There were significant differences in abundances of ectoparasites among gill arches and among sites (Table IV). However, volumetric densities did not differ for gnathiids by microhabitats, but *H. hemigygni* had higher volumetric density in the middle site on the gills (Fig. 2).

The most common endoparasite species (Tetraphyllidea types 1, 4, and 6 and the digenean *C. pichelinae*, Table I) were found along the whole digestive tract, thus they were considered for abundance and volumetric density comparisons. The 4 species exhibited abundances and volumetric densities significantly different among microhabitats ($P < 0.01$ for all species and comparisons, Fig. 3). Tetraphyllidea types 1 and 6 had high abundances and volumetric densities in the rectum, whereas Tetraphyllidea type 4 were significantly less abundant in the rectum but without significant difference in the intestine (Scheffé test [post hoc], $P \leq 0.001$ rectum vs. each intestine portions, Fig. 3). The digeneans were more abundant and denser in the midintestine (Fig. 3). The total abundance (considering just these 4 species) was similar among microhabitats unlike the total volumetric density (Fig. 3).

DISCUSSION

Parasite community structure

This is the first study of all the metazoan parasites of *H. melapterus*. We found 26 metazoan species in 14 individuals of *H. melapterus*. The richness and abundance were higher than has been reported for some other wrasses with a larger sample size (Campos and Carbonell, 1994; Treasurer, 1997; Bartoli et al., 2000), although few studies have considered all metazoan parasites in wrasses.

The larger hosts had higher richness, abundance, and biovolume of parasites than the smaller ones (Fig. 1). This pattern may be explained by the combination of resources, time, and prey. In general, large hosts have more space, more flux of energy (i.e., food), and more microhabitats for parasites than small hosts. Also, large fish are, in general, older than smaller individuals of the same species so that they have been in contact with the environment for longer and they have had more opportunities to become infected (Rohde, 1993; Muñoz et al., 2002). For endoparasites, the change of host diet with ontogeny

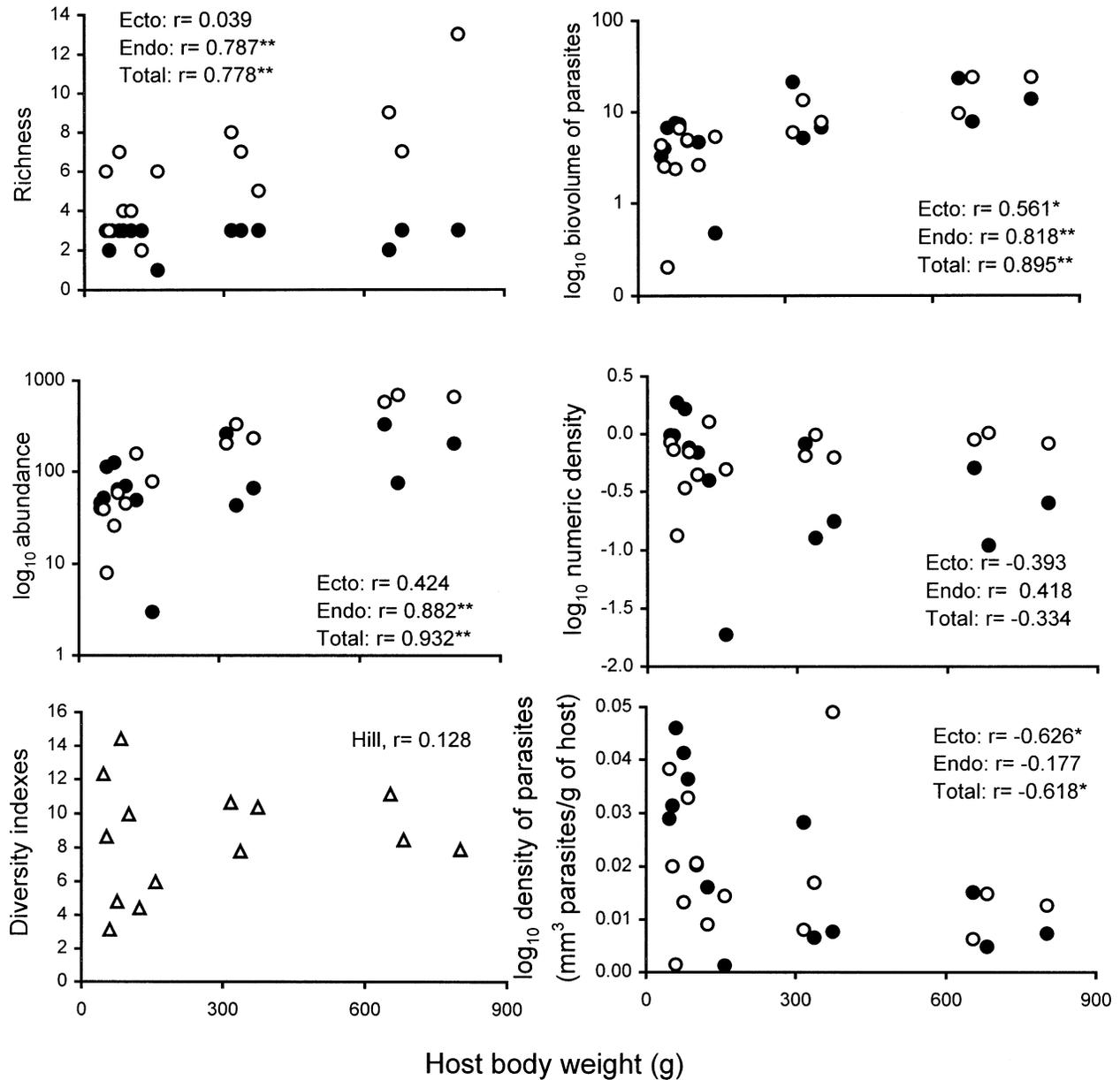


FIGURE 1. Pearson correlations between richness, abundance, diversity, biovolume, and density of ectoparasites (black circles) and endoparasites (white circles) with host body weight of 14 specimens of *Hemigymnus melapterus*. r = correlation coefficient; significant probability (*) $P < 0.05$ and (**) $P < 0.001$. Diversity was calculated per infracommunity (triangles) but not per ecto- or endoparasites.

TABLE III. Pearson correlations of mean abundance, biovolume, numerical density, and volumetric density of parasites with the parasite body size.

Parameter	All parasite species (n = 26)		Prevalent parasite species (n = 14)	
	r	P	r	P
\log_{10} abundance	-0.208	0.307	-0.251	0.386
\log_{10} biovolume	0.072	0.726	0.117	0.689
\log_{10} numerical density	-0.032	0.875	0.118	0.866
\log_{10} volumetric density	-0.136	0.509	-0.154	0.589

could affect the accumulation of parasites. The diet of *H. melapterus* changes during its ontogeny and older fish consume a more varied and greater quantity of prey (Gottlieb, 1992; data not shown), so there are progressively increasing chances of eating infected prey and become parasitized.

George-Nascimento et al. (2004) found that in component communities the numerical density of parasites decreased with the host body size, but that the volumetric density was similar in different host sizes. These relationships were different from those found in this study (Fig. 1). The general hypothesis is that parasite numerical density would decrease as host body weight increases because a large host has lower specific metabolic rate (i.e., flux of energy per gram), so there would be a smaller number of parasites per gram of host (George-Nasci-

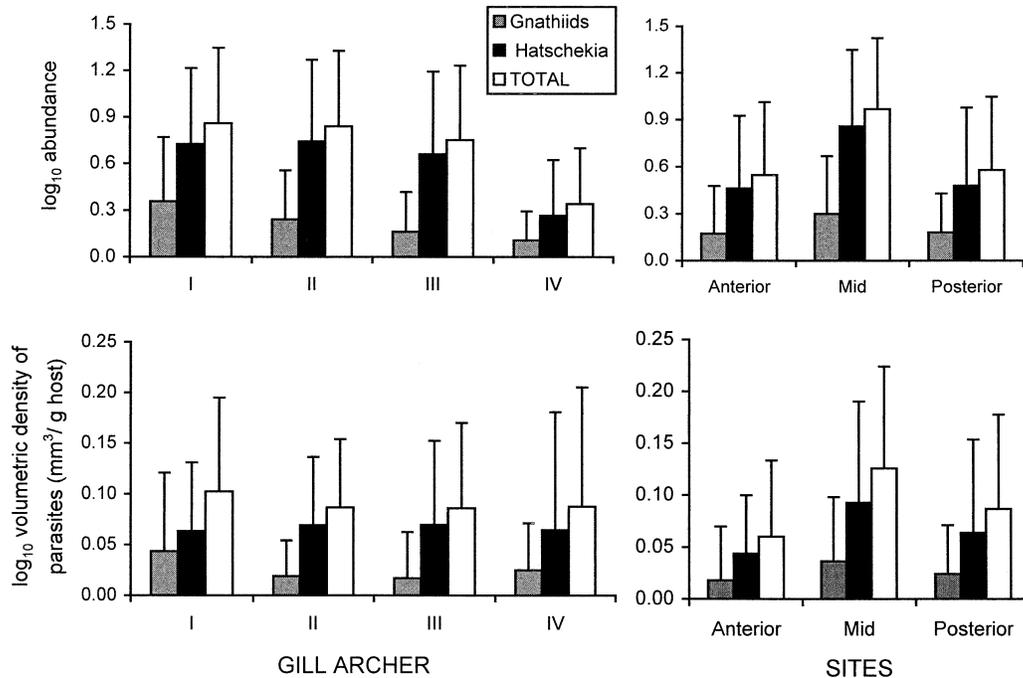


FIGURE 2. Abundance and volumetric density of 2 species of ectoparasites on gill arches (I = the most external to IV = the most internal) and sites on gills. Lines over bars indicate standard deviation.

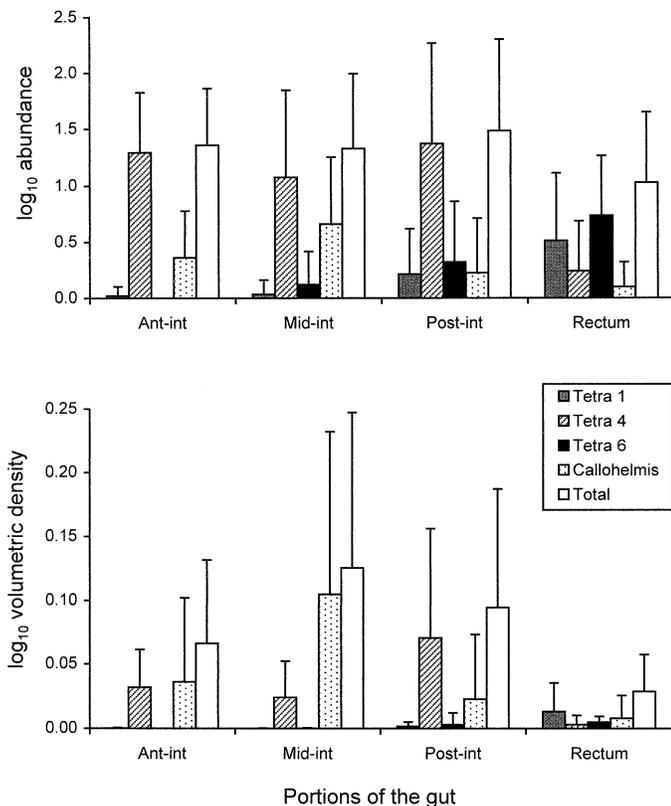


FIGURE 3. Abundance and volumetric density of endoparasites in different portions of the gut: ant-int = anterior intestine, mid-int = mid intestine, post-int = posterior intestine, and rectum. Lines over bars indicate standard deviation.

mento et al., 2004). There is no study about parasite density and host body size in infracommunities; however, it is possible that these relationships of densities, numerical or volumetric, and host body size vary among host species, which may depend on the kind of parasites (ecto or endo, larval or mature) and their body sizes.

It is clear in our results that parasite body size and abundance differ significantly among species and that the parasites with the highest abundance are not the biggest. Previous studies have found no significant relationship between parasite body sizes and their abundances or densities in the infracommunities (Rohde et al., 1994; George-Nascimento et al., 2002; Table III). However, the parasite body size was clearly important in the general composition of infracommunities (Table II), meaning that some species were important in number, whereas others

TABLE IV. Two-way analysis of variance results that compare abundances and volumetric densities of gnathiids and *Hatschekia hemigymini*, in different gill arches (n = 4) and sites (n = 3). df = degree freedom, F = Fisher's ratio, P = probability.

Effect	df	\log_{10} abundance		\log_{10} density	
		F	P	F	P
Gnathiids					
Arches	3, 156	5.29	0.001	2.19	0.091
Site	2, 156	3.07	0.049	2.21	0.112
Arches × site	6, 156	0.14	0.989	0.33	0.919
<i>H. hemigymini</i>					
Arches	3, 156	10.40	<0.001	1.08	0.360
Site	2, 156	13.79	<0.001	6.10	0.003
Arches × site	6, 156	0.58	0.744	0.47	0.475

were important in biovolume, which may be connected with the stage of maturity and the resources that each species needs.

Microhabitat, abundance, and density of parasites

Differential distributions of parasites on or inside the host were observed (Figs. 2, 3), but different results were obtained using numerical abundance and volumetric density.

For the gnathiids we found that the numbers of parasites were proportional to the surface area of the gills. For *H. hemigymini*, surface area was important in explaining the differences among gill arches, but we found higher volumetric density on the middle and distal sites even when the area was controlled for this parameter (Table IV). We conclude that *H. hemigymini* probably selects these specific sites on the gills because of better physical conditions of the habitat that affect ectoparasites, such as water currents (see Suydam, 1971).

Many studies have reported that gill ectoparasites inhabit different microhabitats (Suydam, 1971; Ramasamy et al., 1985; Rohde, 1994; Lo and Morand, 2001). The divisions of these microhabitats tend to be arbitrary, so that the actual areas under consideration may be significantly different. Gnathiids and *H. hemigymini* presented distinct relationships with the microhabitat, which may relate to their vagility and ontogenetic stage. The gnathiids are parasites only in their juvenile phases, and they move actively on and off the host (Grutter, 1999). Larval and adult stages of *H. hemigymini* live permanently on the host, and their movements are restricted to the gills only (Kabata, 1991).

Differential distribution of parasites along the gut may be the result of niche selectivity or niche segregation (Holmes, 1973). Tetracanthellid types 1 and 6 mainly live in the rectum in *H. melapterus* (Fig. 3) as well as in other wrasse species (data not shown). We interpret this distribution as niche selectivity because they choose a favorable habitat for themselves. Specimens of *C. pichelinae* were large adult parasites, unlike most of the other enteric parasite species, so its energetic requirements may be higher than those of the other species. This species was localized mainly in the midintestine, where there may be more food to support high densities of this parasite. On the other hand, Tetracanthellid type 4, larval stage, was in similar abundance along the intestine, but its highest volumetric density was in the posterior intestine (Fig. 3). This differential distribution could be interpreted as niche segregation between Tetracanthellid type 4 and the digenean. In this way these species could coexist even though both have high abundances and different body sizes (see Holmes, 1973).

This is a general view about how host and parasite body sizes affect parasite communities. Parasite communities have generally been considered to be unsaturated by species and without an upper limit in the productivity of their parasites (Poulin et al., 2003). If this is a rule, parasite communities may be restricted by the body sizes of the hosts and the parasites and the relationship between the energy requirements of both. If this kind of relationship is true and strong, then physiological and energetic relationships may determine the community structure of parasite more than interactions between parasite species as has frequently been concluded in the past (see Holmes, 1973; Lotz and Font, 1985; Adamson and Noble, 1993).

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