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The relationship between species richness and productivity in metazoan parasite communities

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Abstract Biodiversity is not distributed homogeneously in space, and it often covaries with productivity. The shape of the relationship between diversity and productivity, however, varies from a monotonic linear increase to a hump-shaped curve with maximum diversity values corresponding to intermediate productivity. The system studied and the spatial scale of study may affect this relationship. Parasite communities are useful models to test the productivity-diversity relationship because they consist of species belonging to a restricted set of higher taxa common to all host species. Using total parasite biovolume per host individual as a surrogate for community productivity, we tested the relationship between productivity and species richness among assemblages of metazoan parasites in 131 vertebrate host species. Across all host species, we found a linear relationship between total parasite biovolume and parasite species richness, with no trace of a hump-shaped curve. This result remained after corrections for the potential confounding effect of the number of host individuals examined per host species, host body mass, and phylogenetic relationships among host species. Although weaker, the linear relationship remained when the analyses were performed within the five vertebrate groups (fish, amphibians, reptiles, mammals and birds) instead of across all host species. These findings agree with the classic isolationist-interactive continuum of parasite communities that has become widely accepted in parasite ecology. They also suggest that parasite communities are not saturated with species, and that the addition of new species will result in increased total parasite biovolume per host. If the number of parasite species exploiting a host population is not regulated by processes arising from within the parasite community, external factors such as host characteristics may be the main determinants of parasite diversity.

Keywords Helminths · Host body mass · Parasite diversity · Phylogeny · Sampling effort

Introduction

The relationship between species richness and productivity (rate of energy flow through an ecosystem) remains controversial in ecology despite the large number of ecological studies focused on this problem. In heterotrophs, productivity is the rate of organic matter accumulation, and is often difficult to measure; for this reason, biomass (or standing stock) is often used as a surrogate measure, one that is particularly adequate for systems with rapid turnover of individuals. At low values of productivity or biomass, there can only be few species in an area or community. Species richness is often argued to increase and then decrease with productivity to produce a hump-shaped or unimodal relationship (Grime 1973; Huston 1979; Huston and DeAngelis 1994). This relationship has been observed in numerous empirical studies, and generated in several modelling studies (see Huston and DeAngelis 1994; Rosenzweig 1995; Leibold 1999; Dodson et al. 2000). However, some studies have pointed out that hump-shaped relationships between diversity and productivity are not the universal rule in natural communities. Recent syntheses of published results have showed that there is often no relationship at all between productivity and diversity (Mackey and Currie 2001; Mittelbach et al. 2001). When it exists, the kind of relationship between diversity and productivity depends on the scale of observation, on whether the data are from animal or

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plant species, and on whether the community sampled is from terrestrial or aquatic ecosystems (Grace 1999; Waide et al. 1999; Mackey and Currie 2000, 2001; Mittelbach et al. 2001; Chase and Leibold 2002). The other pattern often observed instead of a hump-shaped relationship is a monotonic increase in species diversity with increasing productivity, a result expected if species are complementary and have additive effects on productivity, with negative interspecific interactions playing no major role (e.g. Loreau and Hector 2001).

The most popular explanation for hump-shaped curves is the intermediate-disturbance hypothesis (Grime 1973; Connell 1978; Huston and DeAngelis 1994). The hypothesis stipulates that at high levels of biomass or productivity and low levels of disturbance, only a few species of top competitors persist, preventing the establishment of other species, whereas at low levels of productivity and high levels of disturbance, only few specialist or opportunistic species can exist. Only at intermediate levels of both productivity and disturbance is coexistence of several species possible. Rosenzweig and Abramsky (1993) summarized a series of other explanations for hump-shaped curves, but either rejected or cast suspicion on all of them. More recently, Van der Meulen et al. (2001) proposed evolutionary scenarios that would cause diversity to be higher at intermediate productivities. All these explanations, however, require the existence of a hump-shaped relationship between diversity and productivity, and the ubiquity of this pattern is itself under scrutiny (Mackey and Currie 2001; Mittelbach et al. 2001).

Parasite communities may be a useful model system to test the productivity-diversity relationship. They differ from communities of free-living organisms in that new recruits arrive from outside the community (via infection of the host) and not from within (via births), but the number of species and total biomass that the community supports are nonetheless influenced by the same general factors. Parasite communities in different host species represent independent assemblages (when phylogenetic relationships between hosts are taken into account) and consist of species belonging to a restricted set of higher taxa common to all host species. Several empirical studies have investigated the determinants of species diversity in parasite communities (see reviews in Poulin 1997; Morand 2000; Poulin and Morand 2000). The majority of investigators have focused on helminths and arthropods parasitic in vertebrates, using a comparative approach in which the parasite species richness of different host species is related to one or more predictor variables. All these studies, however, have attempted to explain parasite species richness as the product of external factors. First, using arguments derived from epidemiological models, or from island biogeography theory and species-area relationships, the number of parasite species per host species has been related to a range of host ecological and life history traits, such as body size, lifespan, population density or geographical range (e.g. Gregory 1990; Poulin 1995; Watve and Sukumar 1995; Morand and Poulin 1998). Second, others have examined the impact of large-scale environmental gradients, such as latitudinal gradients, on the richness of parasite communities (Rohde and Heap 1998; Choudhury and Dick 2000). There has been no attempt to explain interspecific differences in parasite species richness among host species in terms of intrinsic features of the parasite communities themselves, via the action of processes operating among the parasite species sharing the same host resource.

The importance of different structuring processes in parasite communities is known to vary as a function of species richness (Holmes and Price 1986; Sousa 1994), however, and there exists a framework allowing predictions to be made regarding the shape of the relationship between productivity and diversity in parasite communities. Traditionally, parasite communities have been viewed as forming a continuum between two extremes. At one end of the spectrum, there are "isolationist" communities, characterised by low rates of colonization, low densities (numbers of individual parasites per host), weak interactions and low species richness. At the other extreme, "interactive" communities experience high rates of colonization, high densities, strong interspecific interactions such as competition, and higher species richness (Holmes and Price 1986; Sousa 1994). This framework suggests a monotonic increase in species richness from low-productivity (low-biomass) to high-productivity (high-biomass) parasite communities. Much field and experimental evidence, however, indicates that interspecific competition can become strong at high parasite densities, and that it is often asymmetric, with dominant species sometimes even excluding other species (Dobson 1985; Poulin 1998). Thus, in highly productive parasite communities with high densities of individuals, species richness could become limited and even drop below the richness values of communities with intermediate productivity. This pattern would mirror the hump-shaped relationship often reported or predicted for communities of free-living organisms (Mittelbach et al. 2001; Oba et al. 2001; Venterinck et al. 2001). It is at the high-biomass end of the spectrum that the monotonic increase in species richness can break down if interspecific interactions are strong enough.

Our objectives were to test the relationship between productivity and species richness among communities of metazoan parasites in vertebrate host populations. Specifically, we distinguish between a monotonic increase and a hump-shaped relationship, and determine whether confounding variables are responsible for any observed patterns. We use parasite biovolume, an equivalent of biomass, as a surrogate for community productivity, as in other studies (see Mittelbach et al. 2001). To our knowledge, this is the first large-scale, comparative analysis of patterns in parasite species richness as determined by intrinsic community properties unrelated to host traits or environmental influences.

Materials and methods

We used a large data set on communities of trophically transmitted metazoan parasites in 131 vertebrate species (Appendix 1). Data on fish were obtained from samples of different species of marine fish collected along the coast of Chile, whereas data on amphibians, reptiles, birds and mammals were obtained from the literature. We included all host species for which data could be obtained, with no other selection criteria. For each host species, we recorded: (1) number of individual hosts examined, (2) host body mass (either measured directly in the case of fish, or from the literature in the case of the other vertebrates), (3) endoparasite species richness, and (4) the mean volume of parasites per host individual. The volume of fish parasites was obtained either by water displacement in the case of large or irregularly shaped species, or by computing the body volume of an individual based on measurements of its dimensions. For instance, trematodes and cestodes have regular, almost two-dimensional shapes (oval and rectangular, respectively), whereas nematodes and acanthocephalans have cylindrical bodies. Volumes of individual parasites were multiplied by the mean number found in an individual host, and then volumes of all species were added up to obtain a mean parasite biovolume per host. For other vertebrates, parasite volumes were computed using measurements of body dimensions obtained from original species descriptions found in a comprehensive literature search. There may have been small biases in the calculation of parasite biovolumes; however, the use of logarithmic transformations of the data (see below) eliminates this small problem.

We performed an analysis across all vertebrate host species, but also separate analyses for fish, amphibians, reptiles, birds and mammals. For each group of hosts, we used both a linear regression and a statistical test developed by Mitchell-Olds and Shaw (MOS) (1987) to determine whether or not the relationship between parasite species richness and biovolume was significantly unimodal (i.e. hump-shaped). This method (hereafter the MOS test) uses a jackknife procedure and tests whether an unconstrained least-squares model with a particular intermediate maximum provides a significantly better fit to the data than a model with a maximum at either the higher or lower end of the range of values (i.e. monotonic increase or decrease). In other words, it tests whether there is evidence of a hump as opposed to simple monotonic change. In recent studies on the diversity-productivity relationship, the MOS test has been widely used and often shown to be more rigorous, though more conservative, than simply looking for a significant quadratic regression (Leibold 1999; Mackey and Currie 2001; Mittelbach et al. 2001; Chase and Leibold 2002).

Analyses were first performed using the raw data on parasite species richness and mean total parasite volume per host, although the latter required logarithmic transformation to meet the assumptions of parametric tests. Some confounding variables can influence both parasite richness and biovolume, however, in ways that may affect the shape of the relationship between the two. Sampling effort, or the number of hosts examined, is likely to explain some of the variation among host species in parasite species richness (Walther et al. 1995). Similarly, host body mass often correlates positively with parasite species richness (see Poulin 1997; Morand 2000), and it likely also correlates positively with total parasite biovolume. Therefore, corrected measures of both parasite species richness and biovolume were obtained by taking the residuals of regressions of these two variables against sampling effort and host body mass (host body mass only in the case of parasite biovolume). Both confounding variables were log transformed for these regressions. Testing for linear or hump-shaped relationships between parasite species richness and biovolume was then repeated using corrected values.

The other important confounding variable that may influence the shape of the relationship is host phylogeny. Closely related host species are likely to harbour a similar number of parasite species because these were inherited from a recent common ancestor; this means that they do not represent independent statistical observations. To control for the influence of phylogeny, we used the phylogenetically independent contrasts method (Felsenstein 1985; Harvey and Pagel 1991), implemented with the CAIC version 2.0 program (Purvis and Rambaut 1994). Contrasts were derived from a host phylogeny constructed from published studies on fish (Lauder and Liem 1983; Nelson 1994; Bargelloni et al. 2000), amphibians (Hillis and Davis 1986; Ruvinsky and Maxson 1996; Graybeal 1997), reptiles (Estes et al. 1988; Densmore et al. 1992; Butler and Losos 1997; Wiens and Reeder 1997; Bonine and Garland 1999; Jackman et al. 1999; Giannasi et al. 2000), birds (Sibley and Ahlquist 1990) and mammals (Bininda-Emonds et al. 1999; DeBry and Sagel 2001; Murphy et al. 2001; Jones et al. 2002). Contrasts were computed on log-transformed data and all regression analyses were forced through the origin (Garland et al. 1992). As before, contrasts corrected for the confounding influence of sampling effort and host body mass were obtained by taking the residuals of regressions.

Results

Our analyses included data on 13 amphibian, 35 reptilian, 20 mammalian, 20 avian and 43 teleost fish species, in which parasite species richness ranged from 1 to 35 species (see Appendix 1). Confounding variables did influence measures of both parasite species richness and parasite biovolume. Sampling effort correlated positively with parasite species richness across host species (r=0.338, n=131 species, P=0.0001), as it did among phylogenetically independent contrasts (r=0.465, n=108 sets of contrasts, P=0.0001). There was much scatter in this relationship, however (Fig. 1a). Host body mass correlated positively with parasite biovolume, both across host species (r=0.631, n=131 species, P=0.0001) and among phylogenetic contrasts (r =0.380, n=108 sets of contrasts, P=0.0001), with larger hosts clearly harbouring larger biovolumes of parasites (Fig. 1b). Host body mass correlated positively with parasite species richness across host species (r=0.381, n=131 species, P=0.0001), but not among phylogenetic contrasts (r=–0.132, n=108 sets of contrasts, P=0.176), suggesting that this relationship is an artefact of host phylogeny.

Across all host species, we found a significant linear relationship between parasite species richness and parasite biovolume (r^2=0.284, P=0.0001; Fig. 2a). The same was true after correcting parasite species richness and biovolume for the confounding influence of sampling effort and host body mass (r^2=0.174, P=0.0001; Fig. 2b). Models with an intermediate maximum did not provide a better fit to the data than the linear regressions, assuming a monotonic increase (MOS test, both P>0.05). When the five taxa of vertebrates were tested separately, positive linear relationships were still the norm, though not in mammals and, to some extent, amphibians (Table 1); all groups of hosts showed a pattern not significantly different from a monotonic increase in parasite species richness with increasing parasite biovolume (MOS test, all P>0.05).

Using phylogenetically independent contrasts, there was a strong, positive relationship between parasite biovolume and parasite species richness (r=0.345, n=108 sets of contrasts, P=0.0003), which remains when the contrasts are corrected for sampling effort and host

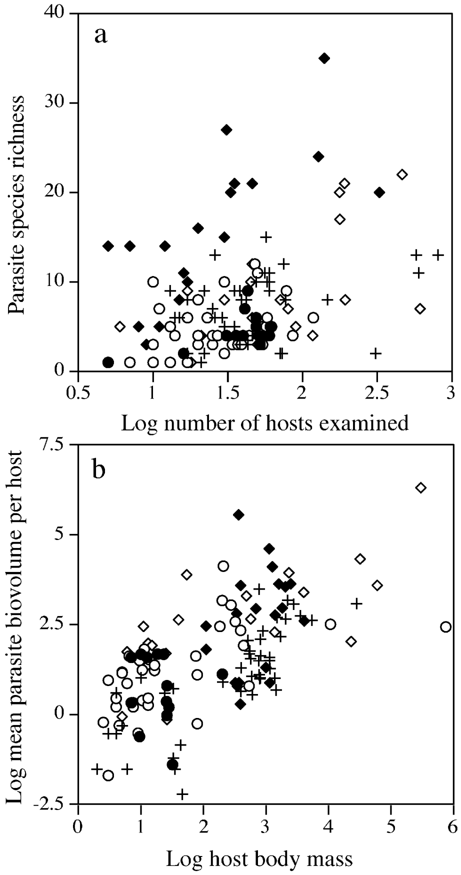

Fig. 1 Relationship between sampling effort and parasite species richness (**a**), and between host body size and the mean parasite biovolume per host (**b**), across 131 species of vertebrate hosts. Different host taxa are represented by different symbols: ✚ fish, ● amphibians, ○ reptiles, ◇ mammals, ◆ birds

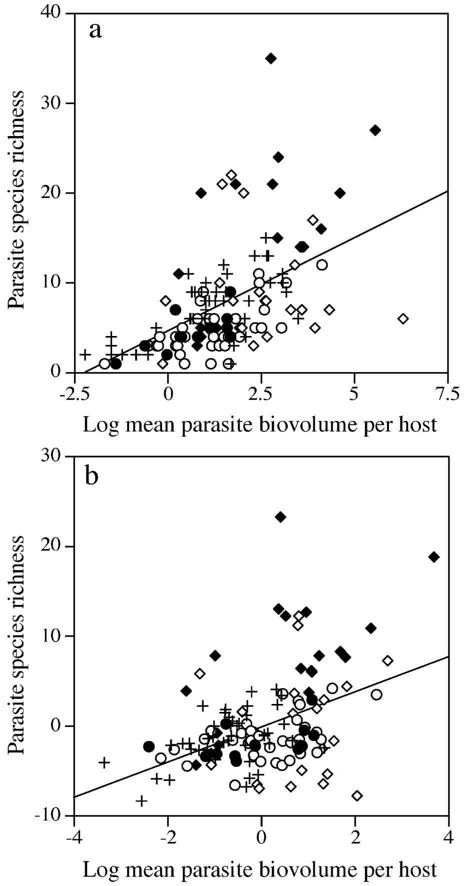

Fig. 2 Relationship between parasite species richness and parasite biovolume, across 131 species of vertebrate hosts. Plots are shown for the raw values (**a**, $y = 2.083x + 4.645$) as well as for values corrected for two confounding variables, sampling effort and host body mass (**b**, $y = 1.85x + 0.068$); see text. For symbols representing different host taxa see Fig. 1

Table 1 Relationship (linear regression) between parasite biovolume and parasite species richness across species values in different taxa of vertebrate hosts, with or without correction for confounding variables (see text)

Host taxon	*n*	No correction	After correction
		r	*r*
Fishes	43	0.663***	0.430**
Amphibians	13	0.634*	0.348
Reptiles	35	0.639***	0.466**
Mammals	20	0.063	0.044
Birds	20	0.522*	0.774***

*P <0.05, **P <0.005, ***P <0.001

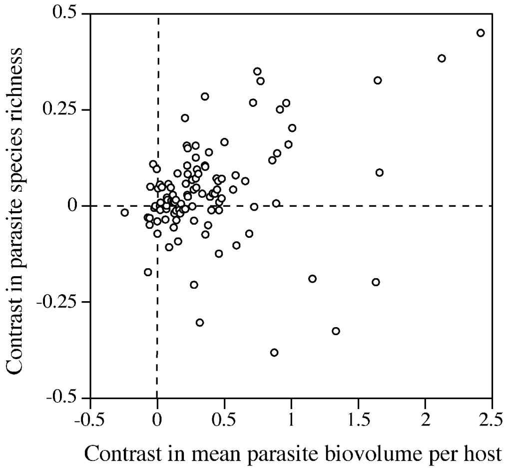

Fig. 3 Relationship between parasite species richness and parasite biovolume, among 108 phylogenetically independent contrasts derived from 131 species of vertebrate hosts

body mass (r=0.421, n=108 sets of contrasts, P=0.0001). Host taxa harbouring larger parasite biovolumes than their sister taxa were twice as likely to also harbour more parasite species, since contrasts in parasite biovolume and contrasts in parasite species richness had the same sign in two-thirds (72 out of 108) of the sets of contrasts (Fig. 3). Positive relationships between parasite biovolume and parasite species richness were found in all analyses restricted to each of the five vertebrate taxa of hosts, with

Table 2 Relationship (correlation coefficient) between parasite biovolume and parasite species richness among phylogenetically independent contrasts in different taxa of vertebrate hosts, with or without correction for confounding variables (see text)

Host taxon	*n*	No correction	After correction
		r	*r*
Fishes	30	0.062	0.306
Amphibians	12	0.963**	0.362
Reptiles	31	0.437*	0.397*
Mammals	14	0.271	0.331
Birds	17	0.141	0.459*

*P <0.05, **P <0.001

or without corrections for confounding variables (Table 2); the correlations were often non-significant, though this is likely due to the limited number of contrasts available and thus to low statistical power.

Discussion

The general form of the species richness-productivity relationship can provide strong hints about the nature of the mechanisms responsible for the coexistence of many species in certain communities. In studies where a pattern is found, both linear and hump-shaped curves are commonly reported, and the shape of the relationship for a given set of communities depends on the type of organisms or habitats, and on the scale of study (Waide et al. 1999; Mittelbach et al. 2001; Chase and Leibold 2002). Here we present the first analysis of this relationship for communities of parasitic organisms. We found that the species richness of metazoan parasites of vertebrates increases linearly with increasing productivity (i.e. parasite biovolume per host). This pattern is still discernable after parasite species richness and biovolume are corrected for the confounding influence of sampling effort, host body size, and host phylogenetic relationships.

A central assumption in our study was that biovolume (or biomass) of parasites per host is a surrogate measure of productivity. Although it would be impossible to demonstrate that the two are perfectly linked, it is more than likely that more productive hosts will harbour more parasite biomass. For instance, many parasitic helminths display considerable phenotypic plasticity in adult body size (Poulin 1998), and will achieve larger sizes if given the opportunity. Another assumption behind our approach is that, as habitats, different host species are just as comparable as are different lakes or forests, the kinds of habitats investigated in previous studies on diversity and productivity. Different host species differ with respects to many features, but then so do any group of lakes; the advantage of our system is that we were capable of taking into consideration the historical relationships (phylogeny) among our habitats, something not possible in previous studies. Our results are thus relevant to the many earlier studies on the diversity-productivity relationship.

Our main analyses were performed across all vertebrates. A look at Fig. 2 indicates that apart from birds generally having higher parasite species richness than other types of vertebrates, there is much overlap among all host taxa. They also harbour the same higher taxa of metazoan parasites, and thus represent comparable communities. This suggests that different vertebrates form a continuum rather than ecologically distinct groups. Analyses performed within each group tended to support the results found across all species. Apart from a lack of statistical power, another explanation for the lack of statistically significant relationships may be that the range of parasite species richness or biovolume values is simply too restricted within each group.

The classic isolationist-interactive continuum of parasite communities at the core of parasite community ecology (see Holmes and Price 1986; Sousa 1994) predicts a monotonic increase in parasite species richness with increasing productivity, or biomass/biovolume. Our study is the first to provide quantitative support for this prediction from a rigorous comparative analysis. Although we did not measure the intensity of interactions per se, our results do not support the view that interspecific competition intensifies as the density or biomass of different parasite species increase, with the resulting exclusion of some species (Dobson 1985). Maximum parasite diversity is apparently achieved in communities of high biomass, and not in those of intermediate biomass as expected from earlier hypotheses (Connell 1978; Grime 1973; Huston 1979). An interesting line of research to pursue in the future will be to look at the same relationship, i.e. between parasite species richness and parasite biovolume, but at a lower scale: among individual hosts from the same population. The importance of study scale in determining the shape of the relationship has already been pointed out by Chase and Leibold (2002).

Our findings also have implications for another debate in parasite ecology: whether or not parasite communities are saturated with species. In free-living communities, the relationship between local and regional species richness can provide cues regarding species saturation (Cornell and Lawton 1992; Srivastava 1999; Shurin et al. 2000). This approach has been applied to parasite communities, where the number of parasite species per individual host is the local richness, and the number of parasite species in the host population is the regional richness. In analyses across different populations or species of hosts, both linear (no saturation) and asymptotic (saturation) relationships have been reported, and there is currently no consensus regarding the existence of limits to species richness in parasite communities (Kennedy and Guégan 1996; Poulin 1998; Rohde 1998). The results of the present study provide some support to the view that there is no upper limit to parasite species richness set by the productivity (or biomass) of the community. Parasite species may be complementary (sensu Loreau and Hector 2001), with total community biomass or productivity increasing with the addition of each new species.

However, the links between the local-versus-regional richness relationship, saturation and productivity may be complex (see Abrams 1995; Shurin and Allen 2001), and it is only with caution that one may infer the absence of species saturation in parasite communities from our results.

Our study is the first to search for determinants of parasite species diversity that are *intrinsic* to parasite communities. All previous empirical studies have focused exclusively on the role of *external* factors, i.e. factors other than parasite features, such as host traits or environmental parameters (see reviews in Poulin 1997; Morand 2000). These earlier studies have identified some variables, such as host population density or geographical range, that are sometimes correlated with parasite species richness across several host species. Data on these variables are not available for the host species in our data set, and may account for some of the variation observed. Nevertheless, our results suggest that processes acting within parasite communities are not very important in determining how diverse they are, and that the search for external determinants of parasite species richness is the most promising direction to pursue.

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Appendix 1

Summary of the data set used in the analyses

Host species	No. hosts examined	Host mass (g)	Parasite richness	Log parasite biovolume/host
Genypterus maculatus	60	2,236	9	3.177
Genypterus chilensis	60	3,538	10	2.743
Genypterus blacodes	60	2,757	11	3.07
Hippoglossina macrops	25	810	7	1.017
Paralichthys adspersus	35	817	9	1.633
Paralichthys microps	35	568	9	1.55
Macruronus magellanicus	147	1,700	8	2.166
Merluccius australis	807	2,057	13	2.653
Merluccius gayi	578	890	13	2.322
Trachurus symmetricus	600	601	11	0.544
Dissostichus eleginoides	49	28,253	10	3.079
Stromateus stellatus	35	595	5	1.061
Eleginops maclovinus	75	1,136	12	1.496
Seriolella violacea	26	778	6	3.485
Scomber japonicus	77	1,372	8	1.009
Helicolenus lengerichi	56	1,136	11	1.584
Sebastes capensis	42	778	8	1.106
Brama australis	26	1,505	13	2.691
Thyrsites atun	17	1,161	8	1.27
Pinguipes chilensis	29	800	6	0.994
Prolatilus jugularis	35	400	9	1.29
Sicyases sanguineus	21	538	1	1.688
Scartichthys viridis	71	43	2	−0.854
Girella laevifrons	309	35	2	−1.523
Auchenionchus microcirrhis	22	46	2	−2.222
Graus nigra	73	33	2	−1.222
Cilus gilberti	57	5,447	15	2.623
Aplodactylus punctatus	46	814	4	2.086
Mugil cephalus	15	1,453	6	0.677
Gobiesox marmoratus	55	6	4	−1.523
Sindoscopus australis	43	2	3	−1.523
Calliclinus geniguttatus	30	5	5	−0.319
Myxodes cristatus	17	3	2	−0.538
Notothenia macrocephala	38	33	9	0.718
Epigonus crassicaudus	38	550	3	1.762
Auchenionchus variolosus	14	24	6	0.588
Myxodes viridis	15	4	6	0.602
Tripterygion chilensis	17	4	2	−0.538
Aphos porosus	22	204	9	0.9
Cheilodactylus variegatus	13	395	9	0.64
Bovichthys chilensis	14	513	6	2.056
Patagonotothen curnicola	58	10	10	1.015
Chamsocephalus gunnari	39	769	8	1.491
Bufo retiformis	49	12.5	6	1.583

Host species	No. hosts examined	Host mass (g)	Parasite richness	Log parasite biovolume/host
Bufo cognatus	36	18.5	4	1.675
Bufo debilis	49	7	5	1.583
Bufo hemiophys	40	23	4	1.672
Spea multiplicata	31	26	4	0.795
Rana catesbiana	16	26	2	−0.027
Rana clamitans	62	200	5	1.119
Rana palustris	5	32	1	−1.398
Plethodon cinereus	60	25.5	4	0.358
Desmognathus brimleyorum	41	28	7	0.199
Desmognathus fuscus	52	9.5	3	−0.62
Eurycea bislineata	51	7	4	0.322
Rana pipiens	43	10	9	1.671
Nerodia cyclopion	48	208	12	4.126
Nerodia fasciata	30	183	10	2.448
Nerodia rhombifera	11	322	7	2.581
Agkistrodon piscivorus	10	199	10	3.167
Anolis aeneus	20	4	3	0.207
Anolis extremus	10	9	3	−0.523
Anolis gingivinus	78	3	9	0.947
Anolis griseus	10	13	3	0.258
Anolis luciae	34	5	3	1.176
Anolis marmoratus	25	4.5	3	−0.31
Anolis oculatus	20	6	8	0.863
Anolis richardi	20	13	4	0.452
Anolis trinitalis	17	3	1	−1.699
Anolis wattsi	20	2.5	4	−.222
Anolis carolinensis	30	7.5	2	0.322
Cnemidophorus dixoni	58	11.3	6	1.813
Cnemidophorus exanguis	37	13.5	3	1.525
Cnemidophorus gularis	118	10.5	6	1.234
Cnemidophorus neomexi	44	7.5	4	0.207
Cnemidophorus tesselatus	27	16.5	4	1.222
Sceloporus magister	17	534	6	0.79
Sceloporus meriami	39	79.5	3	−0.26
Sceloporus marriami	23	79.5	6	1.101
Sceloporus olivaceus	61	392.5	5	2.336
Sceloporus poinsettii	13	276	5	3.043
Sceloporus serrifer	25	438	4	1.916
Sceloporus undulatus	10	75.5	1	1.622
Urosouys ornatus	86	6.5	4	1.622
Alligator mississippiensis	50	750,000	11	2.435
Cnemidophorus burtistic	57	10.5	5	0.386
Barisia imbricata	14	9.5	4	1.498
Coerrhonotus ophiurus	54	16.5	3	1.37
Liolaemus lemniscatus	13	4	1	0.442
Liolaemus tenuis	7	5	1	1.15
Caretta caretta	54	10,700	5	2.506
Spermophylus townsendii	117	570	4	2.656
Eptesiicus fuscus	464	25	22	1.697
Lasionycteris noctivagans	6	15	5	1.917
Lasiurus borealis	90	13	5	1.979
Lasiurus cinereus	18	26	1	−0.143
Myotis keenii	30	6	8	1.742
Myotis lucifurgus	191	12	21	1.453
Myotis sodalis	17	11	9	2.447
Pipistrellus subflavus	71	5	8	−0.066
Hydrochaeris hydrochaeris	41	32,000	7	4.324
Clethrionomys glarealus	193	40	8	2.63
Oryzomys palustris	178	54	17	3.883
Rattus rattus	612	485	7	3.293
Canis latrans	177	23,000	20	2.029
Tadarida brasiliensis	45	13	10	1.384
Phocoena phocoena	80	60,000	7	3.589
Didelphis virginiana	46	4,020	12	3.396
Mustela vison	50	2,325	5	3.939
Ondatra zibethicus	50	1,370	3	2.291
Otaria flavescens	46	300,000	6	6.302
Aechmophorus occidentalis	20	1,262	16	4.105
Podiceps grisegena	33	1,124	20	4.609
Podiceps nigricollis	31	366	27	5.553

Host species	No. hosts examined	Host mass (g)	Parasite richness	Log parasite biovolume/host
Podiceps auritus	7	393	14	3.583
Dendrocygna bicolor	30	688	15	2.938
Corus frugilegus	327	370	20	.886
Egretta caerulea	35	340	21	2.802
Ajaia ajaja	128	1,814	24	2.957
Edocinus albus	140	1,400	35	2.758
Accipiter striatus	8	323	5	0.88
Buteo lagopus	21	1,150	4	0.882
Buteo jamaicensis	11	995	5	1.306
Buteo platypterus	16	390	11	0.286
Falco sparverius	9	350	3	0.779
Puffinus gravis	15	4,080	8	2.601
Pandion haliaetus	5	1,600	14	3.625
Ixoreus naevius	46	110	21	1.808
Turdus migratorius	17	110	10	2.457
Phalacrocorax auritus	12	2,041	14	3.548
Phalacrocorax brasilianus	12	2,495	14	3.632

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