Parasitol Res (2008) 103:187–193
DOI 10.1007/s00436-008-0953-0

ORIGINAL PAPER

Linking species abundance distributions and body size in monogenean communities

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Received: 9 December 2007 / Accepted: 4 March 2008 / Published online: 31 March 2008

Abstract Parasite communities are characterised by one or a few numerically dominant species and many rare species. Although this pattern is well recognised, its underlying causes remain unknown. In this study, we tested whether variation in abundance among species within parasite communities can be explained by interspecific variation in body size. We used data on nine fish species (families Serranidae and Lethrinidae) from New Caledonia, each harbouring strictly host-specific diplectanid monogenean species with very uneven abundances. On each fish species, the most abundant monogenean species accounted for between one half and two thirds of all individuals recovered from the community, and its abundance was between 2 and 114 times greater than that of the second-most abundant species. However, there was no convincing evidence that the ratio of abundance values between the two most abundant species in a community co-varied with the ratio in their body sizes; thus, size differences cannot explain these differences in abundances between common species. It is surprising to note that in two of the three communities with enough species for an analysis to be performed, body size tended to correlate positively with abundance among all species of diplectanid monogeneans. Thus, although body size variation on its own cannot account for the pronounced differences in abundance among monogenean species within the same community, body size remains an important determinant of abundance as it relates to life-history traits underpinning reproductive rates and population growth in these unsaturated communities.

Introduction

One of the most obvious patterns observed in animal communities is that a few species are very abundant whereas most other species are less common, some even being rare (Gaston 1994; Gaston and Blackburn 2000). The same is true in parasite communities where one or very few species account for the vast majority of individuals in the community (Poulin 2007). The concept of numerical dominance has been widely used in parasite community ecology (e.g. Salgado-Maldonado and Kennedy 1997; Gutiérrez 2001; Sures and Streit 2001; Schabuss et al. 2005). However, it is applied mainly as a descriptive tool to classify some species as dominant and others as rare based on arbitrary threshold values of prevalence or intensity of infection. What mechanisms cause a few species to be so abundant and most other species to be represented by only a few individuals? This is the fundamental question regarding the relative abundance of different parasite species in a community, and it remains unanswered.

In the majority of animal taxa, the most important correlate of abundance seems to be body size. Among species in a community, abundance almost invariably decreases as body size increases, such that small-bodied species occur at higher densities than larger species (Damuth 1981; Marquet et al. 1990; Blackburn and Gaston 1997; Gaston and Blackburn 2000). This relationship is one of the most robust known patterns in macroecology; it has been reported for communities involving all kinds of taxa,

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and it seems to exist in parasite communities as well, although there are exceptions (Arneberg et al. 1998; Poulin 1999). Larger species require more resources per capita than smaller species, and with the finite amount of space and energy available in a given habitat, large-bodied species cannot exist at high abundance. Therefore, we might expect that differences in body sizes among parasite species in a community are the fundamental reason underlying the great variation in abundance typically observed.

The most powerful way to illustrate and compare the relative abundance of different species in natural communities is to plot species abundance distributions (May 1975; Gaston and Blackburn 2000; Gray et al. 2006; McGill et al. 2007). Species abundance distributions are widely used in ecology but have only been applied to parasite communities on rare occasions (Norton et al. 2003; Poulin 2007). Numerous theoretical models have been proposed to explain observed species abundance distributions; they make similar predictions, and there is no consensus as to which is the most realistic or useful (McGill et al. 2007). From a graphical perspective, their use is simple and visual inspection of the plots remains the best method to evaluate existing patterns (McGill et al. 2007). When species in a community are ranked based on how many individuals they contribute to the community, and their relative abundance, expressed as the percentage of individuals they contribute to the total, is plotted against their rank, we typically obtain a curve on which relative abundance shows a steep drop among species of high rank before levelling off for species of intermediate rank. In other words, there is often a large difference in the relative abundance of the most and second-most abundant species, whereas the abundances of other species tend to be more similar. If body size is an important determinant of abundance, then we would expect substantial differences in body sizes between the two most abundant species, and the magnitude of this difference in body size should relate to the steepness of the drop in relative abundance seen on the abundance-versus-rank plots.

In this study, we examine the patterns of variation in abundance among species within monogenean communities on the gills of fish and determine whether they can be explained by interspecific variation in body size. The data come from several species of coral reef fish (families Serranidae and Lethrinidae) from New Caledonia characterised by monogenean species with very uneven abundances. More importantly, the monogeneans at the centre of our analyses (family Diplectanidae) are strictly host-specific; the fact that they occur on only single host species makes them a better model than many other parasites because they are expected to display body sizes and abundances adapted to a single community. Specifically, we aim to (1) determine the shape of the species abundance distribution in these monogenean communities; (2) quantify the relationship between abundance and body size among species within each community; and (3) assess whether the difference in abundance between the two most common species in a community is explained by the magnitude of the difference in their body sizes.

Materials and methods

Data on monogenean abundance come from nine coral-associated fish species caught off New Caledonia with hand-lines or by spear-fishing (see Table 1). Gills were removed from each fish and placed in seawater, and live monogeneans were then individually picked off the gills, mounted on microscopic slides, identified and counted. Sometimes gills were fixed in hot formalin and monogeneans were prepared from this preserved material. For some individual hosts, only gills from one side of the body were examined or only a subsample of all monogeneans

Table 1 Summary data for the monogenean communities included in the analysis

Host species	No. of fish examined	No. of monogenean species	No. of monogenean individuals	Source
Epinephelus maculatus	10	12	785	Justine 2007
Epinephelus malabaricus	2	11	327	Justine and Sigura 2007
Epinephelus cyanopodus	12	7	1457	Sigura and Justine 2008
Epinephelus fasciatus	11	2	228	Justine 2005; Hinsinger and Justine 2006
Epinephelus merra	36	2	575	Justine 2005; Hinsinger and Justine 2006
Plectropomus laevis	2	2	106	Justine and Euzet 2006
Plectropomus leopardus	5	3	199	Justine and Euzet 2006
Lethrinus harak	7	3	352	Rascalou and Justine 2007
Lethrinus nebulosus	2	3	299	Rascalou and Justine 2007

were identified and counted; this does not matter in the present analyses because the focus is on relative abundance and not absolute numbers. Justine (2005) has shown that measurements of monogenean dimensions are heavily influenced by the method of preparation; all monogenean body measurements used in the present study were made on slides prepared with the same method (‘carmine’ slides of Justine 2005). Moreover, all species identifications and measurements were made with the same method and by the same person (J-L Justine). Mean body length and maximum body width for each monogenean species were obtained from the sources in Table 1; body surface area, i.e. the product of body length and width, was used as a measure of body size for each monogenean species. Because monogeneans are not rectangular, this product of length and width is only a rough approximation of surface area; however, it remains a better surrogate measure of body size than a linear measure such as length. Because monogeneans are flatworms and because the method used to flatten the worms before measurements was the same for all specimens, body surface area measured this way is a very close equivalent of body volume.

The identity of the monogenean species recovered from each fish species is given in the sources listed in Table 1. Species of the family Diplectanidae were by far the most commonly found with only one or two species of Ancyrocephalidae or Capsalidae also found on some fish species. In all monogenean communities studied, the two most common species were always diplectanids. Members of the genus *Pseudorhabdosynochus* accounted for most species in the communities on the serranid fishes *Epinephelus* spp.; although in terms of abundance, communities on *E. maculatus* and on *E. cyanopodus* were dominated by a species of *Laticola*. Most monogenean species belonged to the genus *Echinoplectanum* on the serranid fishes *Plectropomus* spp. and to the genus *Calydiscoides* on the lethrinid fishes *Lethrinus* spp.

Because of stochastic infection processes, rare species are often absent from some individual hosts although they occur in the host population, and thus a representative picture of abundance patterns can only be obtained from an analysis at the *component community* level, i.e. across all parasites found in all hosts examined. Our focus is on the relative sizes of the different *populations* making up the component community, and not the sizes of the different *infra-populations* co-occurring on a particular host because the latter are often influenced by the individual properties of the host rather than by the local abundance of the different parasite species. In some of the nine monogenean communities studied, there were either few species or rare species were not counted. Using only the three communities with at least seven monogenean species, all on fishes from the genus *Epinephelus*, we constructed species abundance distributions by plotting the relative abundance of each species, expressed as a percentage of the total number of individual monogeneans in the community, against its rank when all species are ranked from most to least abundant.

For each of these three communities, we then computed linear regressions between abundance and body size (body area) across all diplectanid species in the community. Data on the few species of ancyrocephalids and capsalids were not included because precise information of the ancyrocephalids’ body dimensions is unavailable and because capsalids are an order of magnitude larger than diplectanids and their inclusion would bias the analyses. In addition, by restricting the analyses to diplectanids, we exclude groups of different phylogenetic origins with different attachment characteristics. Abundance is taken as the actual numbers of individuals of one species found in the total sample for that community. Data were log-transformed before these analyses; in log–log space, abundance generally decreases as a linear function of body size in most taxa where body size relates to resource use (Gaston and Blackburn 2000).

Finally, to assess whether the difference in abundance between the two most common species in a community is explained by the magnitude of the difference in their body sizes, we computed the ratio between the abundances of those two most common species and also the ratio between their body areas. The two most common species in all communities were always diplectanids. Abundance ratios are always greater than 1 and increase as the difference in abundance between the most and second-most abundant species increases. Because this analysis includes all nine monogenean communities and because for some of them only very few fish individuals have been examined, we checked whether abundance ratios correlated with sample size. No relationship was found ($P>0.1$), suggesting that sampling artefacts are not confounding any observed pattern. Body size ratios are equal to 1 when both species are of the same size, greater than 1 if the most abundant species is the largest and smaller than 1 if the second-most abundant species is the largest. Abundance ratios required log-transformation before both linear and curvilinear functions were fitted to these variables to determine whether body size differences can explain the differences in abundance between common species.

Results

In all, 4,328 monogeneans were individually processed and identified for the analyses presented in this study. The total number of individual monogeneans recovered and examined from each community ranged from 106 to 1,457 (average=481; see Table 1). Such large and mostly random samples of individuals are likely to provide a fair representation of community composition and of the relative abundances of different species.

In each of the three communities consisting of at least seven monogenean species, the most abundant species accounted for between one half and two thirds of all individuals in the community. Even when relative abundance values are shown on a logarithmic scale, the steep drop in abundance between the most abundant and second-most abundant species is still clearly visible for all three communities (Fig. 1). The exclusion of the few ancyrocephalids and capsalids from these species abundance distributions would have no effect on this clear pattern.

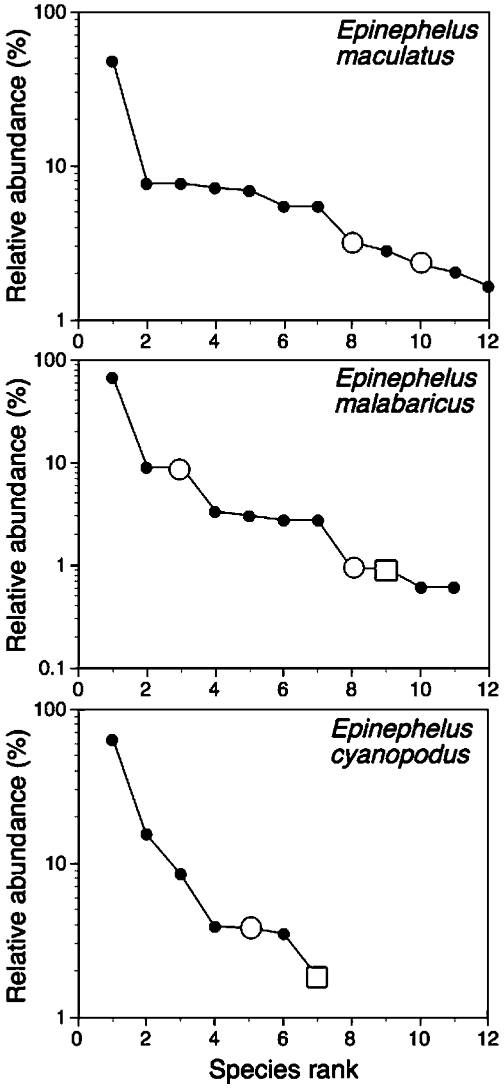

Fig. 1 Species abundance distributions for monogenean communities on three species of serranid fishes. Relative abundance is the percentage of the total number of monogeneans found in one community that belong to a particular species; monogenean species are ranked from most to least abundant on the *x*-axis. All species are diplectanids, except for a few ancyrocephalids (*open circles*) and capsalids (*open squares*)

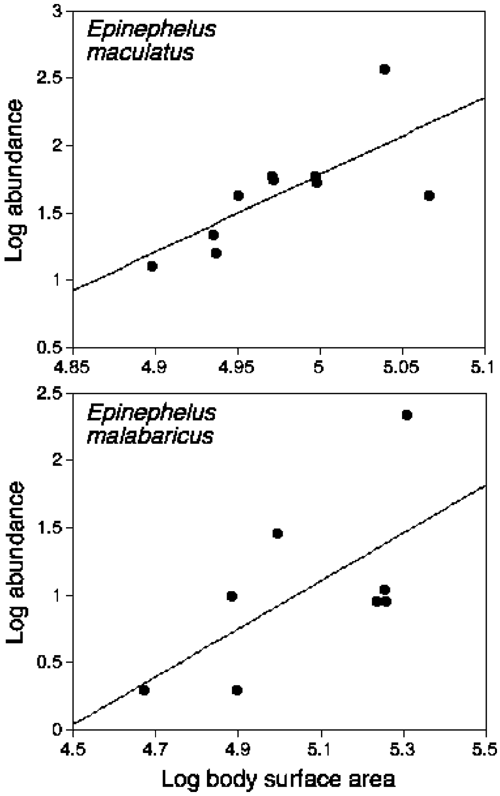

Fig. 2 Relationship between abundance and body size among monogenean species on two species of serranid fishes. Abundance is expressed as the number of individuals belonging to a monogenean species in the total sample, and body size is shown as body surface area (mm^2); all monogenean species included in this study belong to the family Diplectanidae

In two of these three communities, abundance tended to vary as a function of body size among monogenean species, although surprisingly the relationship was positive (Fig. 2). Only diplectanid species were included in these analyses, and interspecific differences in body sizes are therefore not too pronounced. In *Epinephelus maculatus* (r^2=0.51, N=10, P=0.0199), species with larger body surface area occurred at higher abundance; a weak trend in the same direction was also seen in *E. malabaricus* (r^2=0.40, N=8, P=0.0903). The statistical strength of these relationships is limited; most likely because each community includes only relatively few species, but the pattern is clear (Fig. 2). In contrast, in *E. cyanopodus*, there was no association between body surface area and abundance (r^2=0.14, N=5, P=0.5310), although there were very few species in this analysis. Beyond a low number of species, another factor confounds the results obtained for this species. Monogeneans were collected from *E. cyanopodus* mostly during the warm season (see Sigura and Justine 2008), a period during which transmission of monogeneans is likely maximal; therefore, it is possible that the results are biased by the presence of young adult specimens among the individuals used for body measurements.

Among all nine monogenean communities for which we have data, the differences in body sizes between the two most abundant species in a community were never greater than about twofold; this is not surprising because these two species were always from the same family (Diplectanidae) and thus unlikely to display vastly different body dimensions. However, the differences in abundance between the two most abundant species in a community varied widely: the most abundant species had an abundance ranging from 2 times up to more than 100 times greater than that of the second-most abundant species. The ratio of abundance values between these two most abundant species tended to correlate negatively with the ratio in their body sizes (Fig. 3). Neither linear nor curvilinear functions provided a statistically significant fit to the data; however, the best-fitting curve (r^2=0.28, P=0.134) is shown in Fig. 3. One point is mostly responsible for generating the appearance of a weak negative relationship: in the community where the most abundant species is quite small-bodied compared to the second-most abundant species, it also happens to occur at a much higher abundance. This unusual point corresponds to the community from *Epinephelus merra*. It is the only host species for which there is some doubt regarding the strict host specificity of the second-most abundant monogenean species because of discrepancies with the original description (see Hinsinger and Justine 2006): it may represent an accidental colonisation from another sympatric serranid, as yet unidentified. If this single data point is excluded from the analysis, there remains no trace whatsoever of a relationship between body size ratio and abundance ratio.

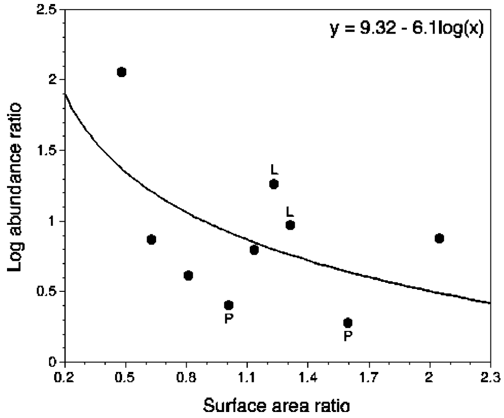

Fig. 3 Relationship between the ratio in abundance between the most and second-most abundant species in a community and the ratio in their body sizes (measured as body surface area, mm^2) across nine monogenean communities. In all cases, the two most abundant monogenean species in a community are diplectanids. The data are from communities in the gills of fishes belonging to the genera *Epinephelus* (*closed circles*), *Plectropomus* (*closed circles* labelled *P*) and *Lethrinus* (*closed circles* labelled *L*)

Discussion

The variation in abundance among species co-existing in the same community is one of the most common ways of providing a description of community structure in ecological studies (Gray et al. 2006; McGill et al. 2007). In parasite communities, patterns of variation in abundance among species can shed light on whether interspecific interactions such as competition are important structuring forces or they can serve to identify species within the community that are at risk of local extinction from stochastic factors. Nevertheless, there have been few attempts to characterise the variation in abundance among species within parasite communities, and more importantly, to elucidate the factors responsible for this variation. Our study tackled this fundamental issue using monogenean assemblages as case studies.

The abundances of different species in the monogenean communities investigated in this study are clearly unequal. The most abundant species in the communities made up of several species typically accounts for at least half of the individual worms in the community. In fact, the abundance of that most common species can be several times, even 100 times, greater than that of the second-most common species. For the 9 communities included in this study, the abundance ratios between the most and second-most common species ranged from about 2 to 114, and their geometric mean (from back-transformed log(x) data) was about 8, i.e. the most common species is on average 8 times more abundant than the second-most abundant species. These figures are not unusual, and they actually match data from a range of other studies of monogenean assemblages on fish hosts (e.g. Geets et al. 1997; Gutiérrez and Martorelli 1999; Gutiérrez 2001; Simkova et al. 2001; Bagge et al. 2004; González and Oliva 2006) and data from communities of gastrointestinal helminths in vertebrate hosts (see Fig. 9.10 in Poulin 2007). So why is there such a gap in abundance between the numerically dominant species in a parasite community and the next most common species?

Based on the well-documented negative relationship between body size and abundance reported from all kinds of animal taxa (Damuth 1981; Marquet et al. 1990; Blackburn and Gaston 1997; Gaston and Blackburn 2000), the most parsimonious explanation seemed a priori to involve differences in body sizes among species exhibiting highly contrasting abundances. However, we found no convincing evidence that the magnitude of the difference in abundance between the two most common species in a community is related to differences in their body sizes. The community in which there was the greatest drop in abundance between the most and second-most common species (about 114-fold) was characterised by the greatest size difference between the two most common species (point in top left corner of Fig. 3), but as specified earlier, the rare species may be an accidental coloniser coming from another fish. After excluding this point, there was no obvious pattern among the remaining communities. Thus, variation in body size is not a simple explanation for variation in abundance among the species in the monogenean communities investigated in this study. It must be pointed out, however, that the body size differences seen between the two most common species in each community were not very large (no greater than twofold); it remains possible that body size variation affects the shape of species abundance distributions but only when size differences occur on larger scales.

Perhaps the most surprising result obtained in this study is the positive relationship between body size and abundance seen in two of the three most species-rich communities investigated. This goes against the general pattern reported for most animal taxa (Damuth 1981; Marquet et al. 1990; Blackburn and Gaston 1997; Gaston and Blackburn 2000). It is interesting to note that it agrees with earlier results for another group of fish ectoparasites, copepods (Poulin 1999). Although the copepod data were assembled from species that do not co-occur whereas the monogenean data treated in this study come from co-existing species, they suggest that larger-bodied species tend to occur at higher abundance than small-bodied species. One possible explanation for this observation is that several life-history traits and epidemiological properties of parasites are related to body size (Poulin 1996, 2007). All else being equal, larger parasites are generally more fecund, producing larger eggs or infective stages which therefore have a slightly higher probability of survival. This could lead to the infective stages of slightly larger species outnumbering those of smaller species, thus leading to higher adult population abundance for the larger species. Of course, in a system where resources are limited, there would be forces acting to reduce the abundance of large species, merely because a given habitat with finite space and resources cannot support as many large individuals as it could with small individuals. Several lines of evidence suggest that assemblages of ectoparasites on fish, and in particular monogeneans, form communities unsaturated in both species and individuals with many vacant niches where intraspecific and interspecific interactions play no significant structuring roles (Rohde 1979, 1991). These are exactly the kind of conditions that could allow slightly larger species benefiting from somewhat greater reproductive output to exceed smaller species in terms of abundance without the normal constraints imposed on larger-bodied species. All the species included in our abundance-versus-size analyses were diplectanids that do not vary hugely in body dimensions (all within the same order of magnitude), and it may be that, on this size scale, reproductive advantages are manifested whereas constraints are not.

Yet, despite these relationships between size and abundance, differences in body sizes among species do not appear to underpin the shape of species abundance distributions. So if body size variation is not the answer, what other mechanism can explain these abundance distributions? Why are these monogenean communities characterised by a dominant and several rare species? Of the many mechanistic and statistical models that have been proposed to describe and/or explain species abundance distributions (see McGill et al. 2007), most are inadequate for monogenean communities in particular or parasite communities in general. For example, neutral models based on dispersal processes and equivalence between different species (e.g. Hubbell 2001) make assumptions that are clearly invalid in the context of parasite communities (Poulin 2004). Given that species abundance distributions seem to have a common shape for a wide range of parasite communities with a sharp drop in relative abundance from the most to the second-most abundant species, it is tempting to expect that a common process is responsible for the general pattern. A concerted effort will be needed from parasite ecologists to, first, provide more detailed empirical information on the shape of species abundance distributions and, second, to test hypotheses regarding their causes.

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