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# THE COMPARATIVE BIOLOGY OF PARASITE SPECIES DIVERSITY: INTERNAL HELMINTHS OF FRESHWATER FISH

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## SUMMARY

(1) This paper describes and analyses the mean number of parasitic helminth species per host individual among Canadian freshwater fish.

(2) Helminth diversity varies among host species.

(3) The diversities of different taxa of helminths are correlated both within and among host species.

(4) Helminth diversity is positively correlated with host size, longevity, diet and geographical range. Size (or longevity) produces the strongest correlations; when the effect of size is removed, only diet remains correlated with helminth diversity. Size and diet together explain about 40% of variance in helminth diversity among host species; the model is most successful for cestodes, where about 60% of the variance is explained.

(5) Most of the ecological covariance of helminth diversity is displayed at rather high taxonomic levels, perhaps because of lag between host evolution and parasite adaptation.

## INTRODUCTION

The diversity of organisms living in the same place has always been of great interest to ecologists. Physically discrete areas, in particular, such as islands, have attracted a great deal of theoretical and empirical investigation (see Williamson 1981). This paper is concerned with a situation of this sort: the diversity of parasite communities within host individuals. The particular communities we have chosen to survey are the helminth endoparasites of Canadian freshwater fish. The helminth taxa included are Digenea, Cestoda, Nematoda and Acanthocephala. These comprise relatively large, easily seen and well-studied organisms, so that we are reasonably sure that a large proportion of the species actually present has been identified. These parasites are found in the alimentary tract, in the body cavity and internal organs, or encysted in muscle. We have excluded all ectoparasites, such as ectoparasitic copepods; we have also excluded the gill flukes (Monogenea), although eye flukes are included. The hosts surveyed are restricted to host species whose geographical range extends into Canada. Anadromous and introduced fish are excluded. We chose Canadian freshwater fish in order to define a set of hosts all of which could be surveyed, minimizing artefacts caused by the exclusion of lightly parasitized and little-studied hosts.

Published accounts of the occurrence of parasites mostly fall into one of two categories: the distribution of a single species or higher taxon of parasites within a

single species or a few species of hosts, or the occurrence of all species of parasite from a broad range of taxa within one or more species of host. We have used only publications in the latter category, in which we are satisfied that all helminths have been sought, and would have been recorded if present, which typically list the helminths from all species of host collected from a given locality. We have accepted surveys from any part of northern North America, provided that the geographical range of the host species extends into Canada. The main source of our data is the detailed surveys published by Bangham and his colleagues (Bangham & Hunter 1939; Bangham 1940, 1941, 1946, 1951, 1955; Bangham & Venard 1946; Bangham & Adams 1954), together with a few studies by other authors made in Canada or in the adjacent United States (Woods 1971; Dechtiar 1972; Muzzall 1982, 1984). We have used these surveys as a representative sample, not a complete list. Defining a 'survey' as the listing of parasite species found in a single sample of a host species, the database comprises 697 surveys from twelve publications.

All statistical analyses were performed using Release 6.3 of SAS (SAS Institute 1985). A summary of host-species means for parasite diversity and ecological covariates is given in the Appendix.

#### *Mean parasite species per host individual*

Our parameter of parasite diversity is the mean number of parasite species per host individual. We chose this parameter partly in order to avoid the problems associated with using the total number of parasite species ever recorded for a given host species, and partly because an individual measure may be relevant to assessing the effect of parasites on the variation and variability of their hosts.

In conducting a survey, a parasitologist will often notice the occurrence or absence of each of a number of parasite species in each of the  $H$  host individuals in the sample. The occurrence of the  $j$ th parasite species in the  $i$ th host individual can be represented as  $\lambda_{ij}$ , which takes the value of either 0 (if that species was not found in that host individual) or 1 (if it was). The mean number of parasite species per host individual is then

$$S = (1/H) \sum_i \left( \sum_j \lambda_{ij} \right).$$

In very many cases, we have found that the published data comprise a list of all the parasite species found, together with the total number of host individuals from which each species was recorded. Let  $H_j$  be the number of host individuals from which the  $j$ th parasite species was recorded. Then it is easy to see that we can estimate the mean number of parasite species per host individual as

$$S = (1/H) \sum_j H_j.$$

To investigate the relationship between  $S$  and the sample size of host individuals, we define  $S_{kl}$  as the mean number of parasite species per individual of the  $k$ th host species in the  $l$ th sample, and  $H_{kl}$  as the number of individuals of the  $k$ th host scored in the  $l$ th sample. We can then regress  $\log S_{kl}$  on  $\log H_{kl}$  for a subset of the data, comprising the thirty species of hosts for which we have data from six or more samples, different samples being taken from different localities. The unweighted mean of regression coefficients was  $-0.057$  (S.E. 0.026), only 3/30 coefficients being

individually significant at  $P < 0.05$ . Estimates of  $S$  are therefore nearly or wholly independent of the sample size of host individuals.

We found that estimates of  $S$  are positively skewed, but the skew is removed by square-root transformation; species means of  $\sqrt{S}$  and the deviations of sample values from species means are approximately normally distributed both for total helminth species and for each of the four major taxa considered separately, except that it was impossible to transform satisfactorily the data for acanthocephalans, the least frequent group of helminths.

*Variance of parasite diversity among species of host*

Having obtained a measure of parasite diversity,  $\sqrt{S}$ , we can ask two fundamental questions about its behaviour: first, whether overall diversity varies among species of host; and secondly, whether different elements of the parasite fauna vary independently. Our data enable us to show unequivocally that parasite diversity does vary among host species, and that the different helminth groups are positively correlated.

Table 1 summarizes the mean and variance of parasite diversity within and among host species. Overall parasite diversity varies significantly, and substantially, among host species. Moreover, the among-host variance is significant for all four helminth taxa. These results validate out subsequent attempts to identify ecological factors which are correlated with the parasite diversity of host species. There remains, however, substantial variance among surveys within host species. This variance could arise from any or all of three sources. First, there is true error variance arising from failure to detect or to identify correctly species of helminths. We believe this to be a minor contribution to the within-host-species variance because of the relative ease with which large helminths can be scored. Secondly, stochastic variance will inevitably arise as a consequence of the small sample size of host individuals in many of the surveys. However, the greater part of this variance is probably attributable to a third source of variation, the variation among sites. We estimated environmental components of variance for extensive surveys of British Columbia (seventy-one localities: Bangham 1946) and northern Wisconsin (forty-three localities: Bangham &

TABLE 1. Mean and variance of parasite diversity among hosts. The variable analysed is  $\sqrt{S}$ , which is approximately normally distributed among and within species. The first two data columns give the mean and standard deviation of  $\sqrt{S}$  for different helminth taxa over host species. The second pair of data columns give the among-host-species and within-host-species variance components calculated from the one-way analysis of variance by equating observed with expected mean squares. The among-host-species variance is highly significant ( $P < 0.0001$ ) in all cases. The final data column is the intra-class correlation coefficient  $t = s^2_{\text{among}} / (s^2_{\text{among}} + s^2_{\text{within}})$ , corresponding to the correlation between two random samples of the same host species

Taxon	Mean	S.D.	$s^2_{\text{among}}$	$s^2_{\text{within}}$	$t$
Trematodes	0.651	0.314	0.0802	0.2329	0.256
Cestodes	0.379	0.325	0.0824	0.1226	0.402
Nematodes	0.310	0.212	0.0206	0.1323	0.135
Acanthocephalans	0.258	0.250	0.0390	0.1423	0.215
Total helminths	1.055	0.402	0.1269	0.2359	0.350

Adams 1954). Each lake–host combination is represented by a single value (or none), so the samples constitute an unbalanced, unreplicated two-way design in which the lake–host interaction is confounded with error. The among-lake variance components were  $\sigma_E^2 = 0.0778$  in British Columbia ( $P < 0.0001$ ) and  $\sigma_E^2 = 0.0453$  in Wisconsin ( $P = 0.004$ ). The estimate from British Columbia was large relative to the among-host variance (73% of attributable variance), whereas in Wisconsin it was small (14% of attributable variance). We conclude that parasite diversity generally varies both among lakes and among host species, that either component may be substantial, and that the balance between the two will depend on the particular species and area sampled. In the remainder of this paper we shall be concerned exclusively with variance among host species, but here we emphasize that species means should not be thought of as fixed or unique characters of species as, in the present case, the variance among species means may comprise on average only about half the total variance in diversity.

Table 2 gives the correlations between different elements of the helminth fauna. All four parasite taxa are positively correlated with one another; i.e. fish which are infested with more species of trematode than average will tend also to be infested with more species of nematode, and so forth. This overall correlation can be decomposed into two components, one representing the correlation between the mean diversities of two parasite taxa over host species, and the other the correlation between surveys within host species. Both are significant and positive, but the correlation among species is in all cases greater than the correlation within species. Thus, lakes which support more species of one parasite taxon tend also to support more species of other taxa; the same tendency for diversity to covary between

TABLE 2. Correlations among helminth taxa. The three correlation coefficients cited in each cell are as follows: (i) uppermost value—Spearman rank correlation of observed host species means; (ii) middle value—intrinsic correlation ('variance component correlation') of species means, from nested analysis of covariance; (iii) lowermost value—correlation of sample estimates within species, from nested analysis of covariance; this is equivalent to the Pearson correlation of deviations from species means

	Cestodes	Nematodes	Acanthocephalans	Total helminths
Trematodes	+ 0.234*	+ 0.401***	+ 0.150	+ 0.716***
	+ 0.320	+ 0.942	+ 0.228	+ 0.831
	+ 0.141***	+ 0.102**	+ 0.174***	+ 0.775***
Cestodes		+ 0.359***	+ 0.610***	+ 0.693***
		+ 0.476	+ 0.512	+ 0.732
		+ 0.091*	+ 0.173***	+ 0.475***
Nematodes			+ 0.381***	+ 0.641***
			+ 0.337	+ 0.913
			+ 0.117**	+ 0.404***
Acanthocephalans				+ 0.653***
				+ 0.628
				+ 0.480***

The analysis variable is  $\sqrt{S}$ . For (i) and (iii), the probability that the estimate of a parameter differs from zero by chance alone is indicated as follows: no asterisk  $1 > P > 0.1$ ; \*  $0.1 > P > 0.01$ ; \*\*  $0.01 > P > 0.001$ ; \*\*\*  $0.001 > P > 0$ .

parasite taxa is displayed more strongly by species of host. The four parasite taxa do not therefore supply independent measures of parasite diversity in fish, although each may be interesting in its own right.

### *Ecological correlates of parasite diversity*

#### *Development of predictive hypotheses*

A great many relationships between parasite diversity and host characteristics might be postulated. We chose to examine six hypotheses, partly on the basis of their generality, and partly because they can be expressed in precisely quantifiable form.

*H1:* In larger hosts, labour can be more finely divided and thus a more diverse parasite community sustained. This idea recalls the relationship between species diversity and island area, hosts being interpreted as islands which parasites colonize. Hence, parasite diversity is positively correlated with host body size.

*H2:* Longer-lived hosts are vulnerable to infestation for longer periods of time, and will thus accumulate a more diverse parasite fauna. Hence, parasite diversity is positively correlated with host longevity.

*H3:* Hosts are likely to become infested by certain taxa of parasites as the result of eating infested prey. Such parasites might be accumulated along food chains in the same way as some toxins and metals. Hence, parasite diversity is positively correlated with the proportion of other fish in the diet.

*H4:* More widely distributed hosts will encounter more species of parasite, perhaps through encountering more species of intermediate hosts. Hence, parasite diversity will be positively correlated with geographical range. This is an argument which applies more naturally to populations than to individuals. However, a parasite originally encountered at one edge of a host's range may in time spread through the whole of the range. Thus, the parasites acquired by an individual fish may reflect properties of the host population as a whole.

*H5:* Hosts which occur in a greater proportion of sites within their geographical range will more readily sustain populations of parasites. The number of sites occupied by a given species of host within a defined area will be referred to as the local prevalence of the host. Hence, parasite diversity will be positively correlated with host local prevalence. Again, this is a population process which may produce effects at the level of the individual.

*H6:* Hosts which are numerically more abundant at those sites where they do occur will more readily sustain populations of parasites. Hence, parasite diversity will be positively correlated with host local abundance.

#### *Exploratory correlation analysis*

The ecological covariates suggested by these hypotheses are too numerous to permit an exhaustive investigation of all possibilities. We therefore carried out a preliminary survey by collating data from the secondary literature. The purpose of this approach was to identify especially promising covariates, which could then be investigated in more detail; at the same time, a complete lack of correlation can be used to reject especially unpromising hypotheses. The relationship between variables such as body size, abundance and geographical range is of course the subject of many studies in the wider ecological literature (e.g. Gaston & Lawton 1988, 1990).

The result of this analysis is shown in Fig. 1. Body size was expressed in two ways, as length at age I and as maximum recorded length. Neither is in itself a satisfactory interpretation of H1; fish may usually become infested after age I, and maximum recorded length may be a function of abundance or sporting value. However, if both variables show the same patten of correlation, with helminth diversity and with other ecological covariates, it seems reasonable to argue that both reflect the properties of some more fundamental measure of body size; a more satisfactory measure of size can then be sought later. Similarly, longevity was expressed both as average age at first reproduction and as greatest recorded age. The proportion of fish and of plants in the diet was expressed on an eight-point scale. Data for size, age and diet was obtained from Scott & Crossman (1973) and Becker (1983). Geographical range was estimated from the distribution maps published by these two authors; local prevalence was taken from Becker's very detailed survey of Wisconsin. We could find no acceptable data on the abundance of species in natural communities. We then calculated the rank correlations among species means, which were used to draw Fig. 1. The alternative measures of size, age and diet are strongly correlated with one another. These are moderately large and highly significant positive correlations between size, age and diet, and between all three variables and helminth diversity. We tentatively concluded that large fish tend to be long-lived and piscivorous, and

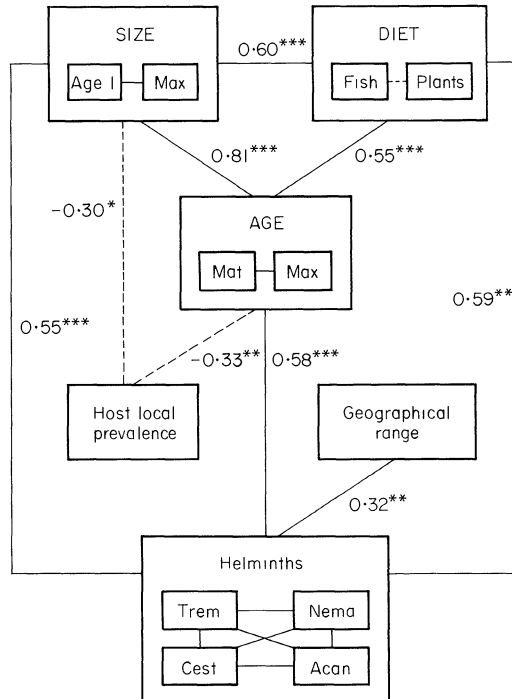


FIG. 1. Ecological correlates of parasite diversity. Lines drawn within and between boxes represent correlations, solid lines being positive and broken lines negative correlations; only those correlations significant at  $P < 0.05$  are shown. The values by each line are the Spearman rank correlations; the parametric Pearson correlations are very similar, and generally somewhat greater.

that such species tended to harbour highly diverse helminth communities. Local prevalence was weakly negatively correlated with size and age, but was uncorrelated with helminth diversity. Geographical range was weakly positively correlated with helminth diversity but uncorrelated with any of the other ecological variables, including local prevalence.

On the basis of these results, we rejected H5. We could not reject H6, since we had no direct measure of abundance. However, if H6 were true the positive correlation of body size with parasite diversity is unexpected. Body size is generally negatively related with abundance across taxa (Peters 1983); although this relationship is often weak or absent within taxa (Lawton 1989) we have no reason to expect it to be reversed. The analysis most strongly supports H1, H2 and H3. We chose to investigate H1 in more detail, by seeking more precise measures of body size. Our reasons were that size can be measured more easily and more precisely than age or diet, and that more information is available on size than on any other variable. We acknowledge that size and age are so highly colinear that their effects cannot easily be distinguished, and our concentration on H1 cannot be held to constitute a rejection of H2.

#### *Body size and helminth diversity*

Most fish grow throughout their lives, so we defined a consistent measure of body size as the mean size of individuals at the mean age of first reproduction. Data were obtained from Becker (1983) and Scott & Crossman (1973), and in addition from Carlander (1969, 1977). We used total length rather than mass as a measure of size because information on length is more readily available; however, the two measures are highly correlated. Species means and deviations from means of  $\log_{10}$  length were normally distributed, so all data were log-transformed before any analysis. Analysis of variance of 333 estimates from eighty-seven species showed that length varies significantly among species ( $F_{86,246} = 57.7$ ,  $P < 0.0001$ ), the estimates of the variance components being  $s^2$  (among species) = 0.1264 and  $s^2$  (within species) = 0.0085.

The regression of helminth diversity on host size is shown in Fig. 2, together with a summary of the regression analysis for the helminth taxa separately. The regression is highly significant, with a slope of about 1/2. The regression of  $\log S$  on  $\log$  body length has about the same slope ( $b = 0.447 \pm \text{S.E. } 0.054$ ), so helminth diversity increases roughly with the square root of body length. However, host size explains only about 23% of variance in helminth diversity among host species. The failure of the model to explain a greater proportion of the variance can be attributed to five causes. First, the relationship may be non-linear; analysis of residuals showed that this was not the case. Secondly, uncertainty in the estimates of species means for the independent variate (body size) implies that some departure from a perfect fit is inevitable; the fact that the variance among species is much greater than that within species shows that this will be a minor effect. Thirdly, different helminth taxa may respond to body size in different ways. This appears to be the case. The diversity of digenean trematodes is uncorrelated with host body size, whereas the other three helminth taxa show highly significant correlations (Fig. 2, legend). Cestode diversity, in particular, increases steeply and consistently with host size, and the overall response of helminth diversity is in large part attributable to this element of the helminth fauna. Fourthly, the functional relationship of parasite diversity to host size within any given taxon may be to some extent obscured by constraints of descent, if



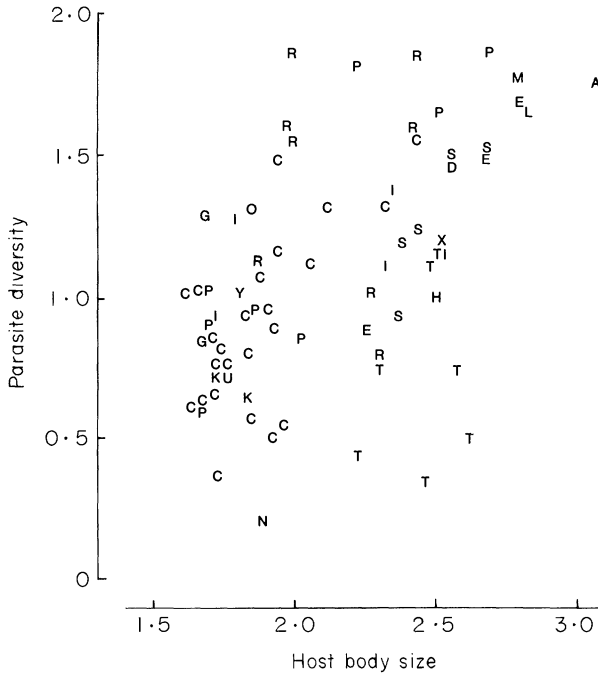


FIG. 2. Relationship between helminth species diversity and fish host body size. Letters indicate family as follows: A, Acipenseridae; C, Cyprinidae; D, Gadidae; E, Esocidae; G, Gasterosteidae; H, Hiodontidae; I, Ictaluridae; K, Cottidae; L, Lepisosteidae; M, Amiidae; N, Atherinidae; P, Percidae; R, Centrarchidae; S, Salmonidae; T, Catastomidae; U, Umbridae; X, Sciaenidae. The dependent variable is helminth diversity as  $\sqrt{S}$ ; the independent variable is host body size as  $\log_{10}$  total length (mm) at age of first reproduction. Regression statistics for total helminths and for each helminth taxon separately are as follows:

Taxon	Zero-intercept	Slope $\pm$ S.E.	$r^2$
Trematodes	0.494	0.074 $\pm$ 0.101	0.01
Cestodes	-0.763	0.544 $\pm$ 0.081	0.39
Nematodes	-0.245	0.258 $\pm$ 0.058	0.22
Acanthocephalans	-0.283	0.254 $\pm$ 0.067	0.17
Total helminths	-0.033	0.517 $\pm$ 0.112	0.23

taxa inherit characteristic suites of parasites from their ancestors; a comparative analysis of the data is given above. Finally, ecological factors uncorrelated with body size may influence the susceptibility of hosts to infection; this is the topic of the next section.

#### *Diet and helminth diversity*

Residual values of helminth diversity and of ecological covariates, from which the linear effect of host body size had been removed, were obtained by regression. Repeating the correlation analysis reported above on these residual values yields partial correlation coefficients. These were significant only for diet, with largely piscivorous fish seeming to harbour more species of helminths than non-piscivorous fish of the same body size. This led us to reject H4, and to concentrate our efforts on

further testing H3. We therefore sought more precise measures of diet. These cannot be obtained from the secondary literature. Instead, we attempted to identify one or more original studies of diet for each host species from the extensive lists given by Carlander (1969, 1977) and Becker (1983). In this way we collected about 100 primary sources, on which our analysis of diet is based; only accounts of adult fish were included. These sources generally quantified diet either as percentage composition by volume, or as frequency of occurrence among individuals. The two measures turned out to be well-correlated; we shall discuss only volumetric composition, for which more extensive data are available. Although we recorded several different categories of diet items (detritus, plants, benthic and planktonic crustaceans, molluscs, insects and fish), these are inevitably inter-correlated, and our analysis will emphasize fish. Our measure is the volume of fish remains as a proportion of the total volume of stomach contents, transformed by arcsin square-root, which we refer to for convenience as 'diet'. We obtained 284 estimates of diet from seventy-one species. Diet is approximately normally distributed within species, but the many species which seldom or never eat other fish preclude normalization of species means. Bearing this in mind, there was significant variance of diet among species ( $F_{70,213} = 12.8, P < 0.0001$ ), the estimates of the variance components being  $s^2$  (among species) = 0.1685 and  $s^2$  (within species) = 0.0523. The relationship between our two covariates, size and diet, is shown in Fig. 3; large size and piscivory are clearly related, although there are several large fish which are not piscivorous, sturgeons being an extreme example.

The relationship between helminth diversity and diet is shown in Fig. 4a. Non-piscivorous fish vary enormously in helminth diversity, but all piscivores support diverse helminth communities. As in the case of size, this relationship is most

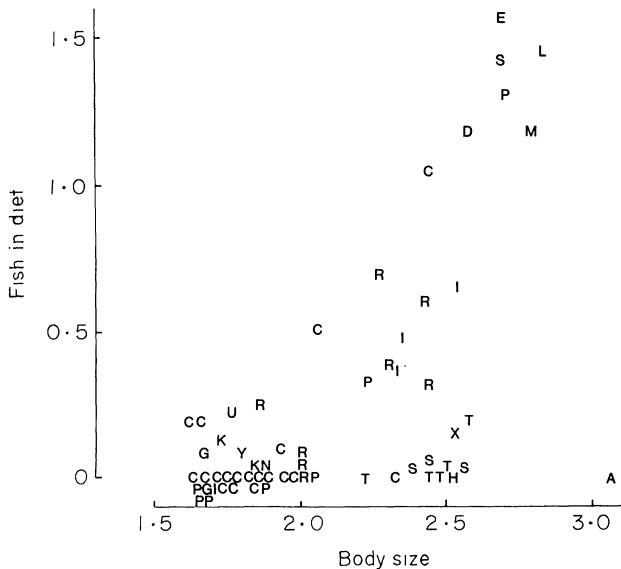


FIG. 3. Size and diet among fish. Conventions as in Fig. 3. The diet variable is the percentage of fish remains in stomach by volume, transformed by arcsin square-root. The linear regression equation for species means has zero-intercept  $-1.136$  and slope  $+0.658$  (S.E.  $0.116$ ), correlation  $+0.595$ .

convincing for cestodes, which are plotted separately in Fig. 4b. The outcome of multiple regression of helminth diversity on size and diet is summarized in Table 3. Overall, both size and diet contribute independently to variance in helminth diversity, and jointly explain about 39% of this variance. However, the success of the approach is again very uneven. Trematode diversity is uncorrelated with either size or diet, so the analysis has no predictive power for this group. Nematodes and acanthocephalans respond to host size but not to diet, so that the inclusion of diet in the model gives no significant increase in predictive power. Cestodes respond to both size and diet, the two variables jointly explaining 59% of variance in cestode diversity.

The analysis of diet can be extended by inspecting the correlations between each component of diet and each component of the helminth fauna, as shown in Fig. 5. These correlations are consistent, in the sense that, where any significant correlation exists between the frequency of a diet category and the diversity of helminth taxa, it has the same sign for all taxa. Thus, benthic crustaceans and fish seem to be

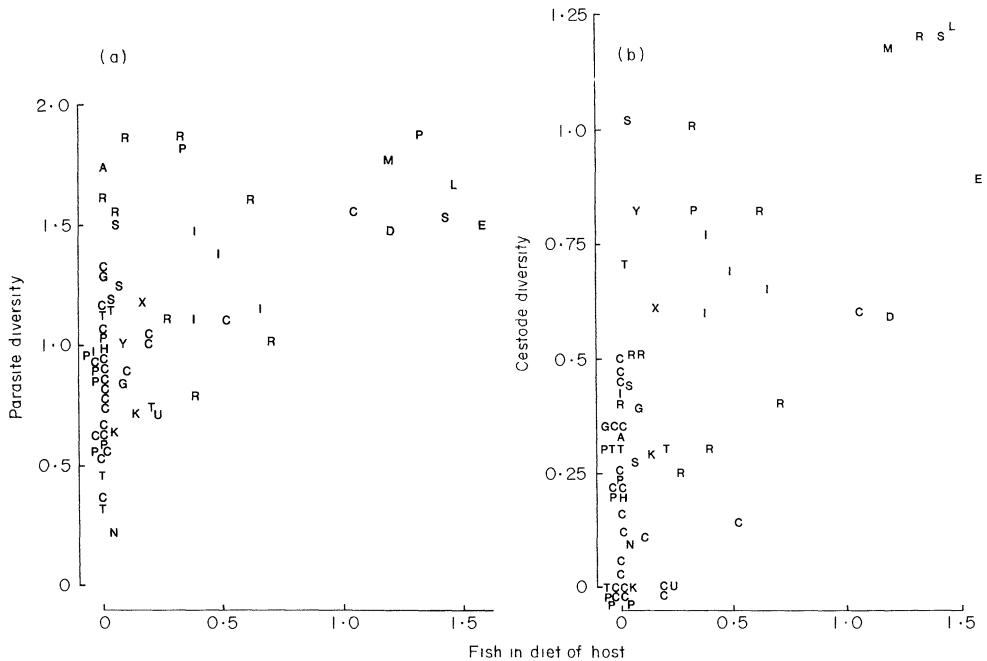


FIG. 4. Helminth diversity and diet. Conventions as in Fig. 3. Regression statistics are as follows:

Taxon	Zero-intercept	Slope $\pm$ S.E.	$r^2$
Trematodes	+ 0.618	+ 0.167 $\pm$ 0.092	0.05
Cestodes	+ 0.245	+ 0.574 $\pm$ 0.073	0.49
Nematodes	+ 0.258	+ 0.139 $\pm$ 0.063	0.07
Acanthocephalans	+ 0.204	+ 0.210 $\pm$ 0.068	0.13
Total helminths	+ 0.937	+ 0.532 $\pm$ 0.106	0.29

Total helminths and cestodes are shown in Fig. 4a and b, respectively.

TABLE 3. Multiple linear regression analysis for the effect of host size and diet on helminth species diversity

Taxon	Regression coefficients			$r^2$
	Intercept	Size	Diet	
Trematodes	+ 0.370	+ 0.124	+ 0.110	0.07
Cestodes	- 0.445	+ 0.352***	+ 0.370***	0.59***
Nematodes	- 0.375	+ 0.333***	+ 0.049	0.30***
Acanthocephalans	- 0.136	+ 0.173*	+ 0.100	0.18*
Total helminths	+ 0.060	+ 0.446**	+ 0.278*	0.39***

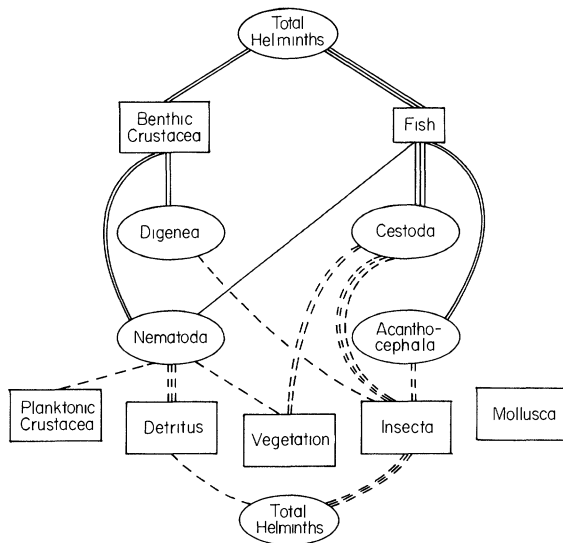


FIG. 5. Relationship between components of diet and components of the helminth fauna. Solid lines represent positive and broken lines negative correlation; single line  $0.1 > P > 0.01$ , double line  $0.01 > P > 0.001$ , triple line  $P < 0.001$ .

hazardous things to eat, in that they are consistently associated with a greater diversity of helminths, while detritus, vegetation, insects and perhaps planktonic crustaceans are relatively innocuous. These results seem to be consistent with the modes of transmission of the various helminth taxa.

*Comparative analysis of the ecological correlates*

It has become widely recognized in evolutionary biology that correlations between characters may arise either through ancestry or through convergent evolution. A number of ways in which the effect of ancestry can be eliminated or estimated have been proposed (Clutton-Brock & Harvey 1979; Ridley 1983; Felsenstein 1985; Bell 1989; Burt 1989). One way of expressing the problem is to argue that species means (in diagrams such as Figs 2, 3 and 4) do not represent independent sampling points if the means of related species are correlated because they share a recent common

ancestor. Thus, functional hypotheses should be tested only within taxa, whose members share the same ancestry, and not among the means of different taxa. These considerations arise in all comparative studies, whether in evolutionary biology as usually defined, or in more conventionally ecological work, or in more distant fields such as economics and sociology. Comparative analysis is still relatively uncommon in ecology, but its use will increase as methods become more clearly worked out (Wanntorp *et al.* 1990).

As no phylogenetic classification or cladogram is available for Canadian freshwater fish, we use the Linnaean classification as a phylogenetic hypothesis, assuming the monophyly of nominate taxa. We then analyse helminth diversity, host size and host diet by partitioning their variances and covariances among taxonomic levels, as described by Bell (1989). The analysis is based on species means, as data for helminths, size and diet can be related only at the species level, and no within-species covariances can be calculated; the within-species variances have already been given. In order to retain at each level a reasonable number of degrees of freedom, the taxonomic levels chosen for analysis were order, family, genus and species.

The comparative analysis is summarized in Fig. 6, which illustrates the variance of helminth diversity as a whole, and cestode diversity in particular, in relation to size and diet. Parasite diversity varies at all taxonomic levels, except that families (within orders) tend to have about the same number of helminths in total. Size and diet are more complex, but neither varies much among species (within genera). Patterns of covariance tend to show rather similar patterns. The overall positive correlation of helminth diversity with size is generally maintained, at about the same magnitude, over all taxonomic levels. The correlation of helminth diversity with diet, on the other hand, tends to be strongest at rather high taxonomic levels, and diminishes or disappears among species (within genera). The effect of removing the effect of body size is to shift the distribution of variances for helminth diversity and diet to the right, towards lower taxonomic levels. This is a consequence of the variance of size among higher taxa; one interpretation is that size acts as a constraint, slow to change in evolution, which masks the expression of variation in parasite diversity and diet within taxa. At the same time, the correlation of helminth diversity with diet is essentially eliminated at lower taxonomic levels, being retained only among orders or families. Thus, among fish of the same size, a switch to piscivory will not immediately procure an increase in the number of species of parasitic helminths. One interpretation of this result is that parasites can evolve the capacity to infect a new species of host only rather slowly, so that there is a substantial time-lag between when a host becomes exposed, through a diet shift, to new species of parasite and when those parasites acquire the ability to maintain themselves within the new species of host.

#### *General conclusions*

The diversity of parasite communities may vary among localities or among host species: some authorities have emphasized the environmental variance (e.g. Wisniewski 1958; Chubb 1970) and others the taxonomic variance (e.g. Halvorsen 1971; Wootten 1973). Both sources of variance are present in the surveys of freshwater

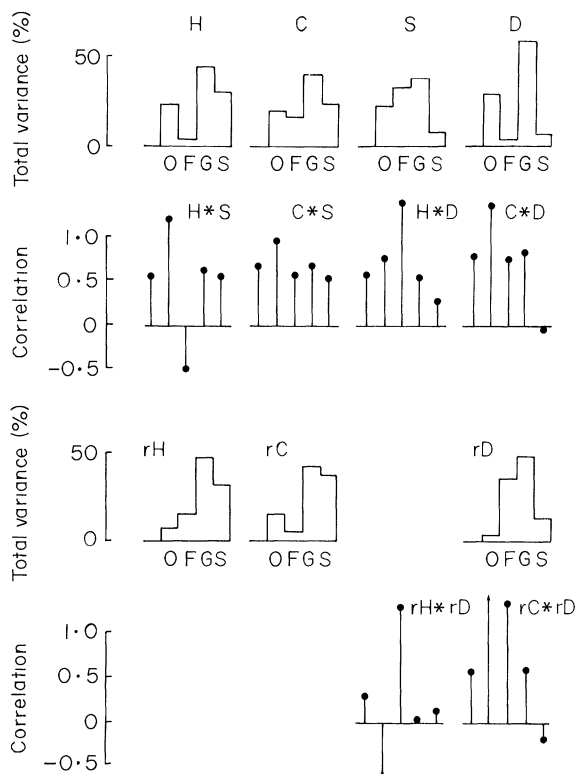


FIG. 6. A summary of the comparative analysis of parasitism, size and diet. The first two rows concern helminth diversity (H), cestode diversity (C), host size (S) and host diet (D). The first row shows estimates of variances (as proportions of the total variance) and the second row estimates of covariances (as correlation coefficients) at the levels of order O, family F, genus G and species S. The second two rows give similar diagrams, for H, C and D when the linear effect of S has been removed from each. The first value in the correlation diagram is the overall correlation.

fish that we have analysed, both are substantial and significant, and either may be the larger. The ecological factors which cause the parasite communities of hosts to differ have often been discussed. Polyanski (1961) suggested that host diet, range, abundance, size and longevity affect the parasite diversity of marine fishes, but there do not seem to be any quantitative analyses of these patterns in the literature (Holmes 1990).

We have found that helminth species diversity per host individual is correlated with host body size, or perhaps with longevity, and to a lesser extent with host diet. This suggests that the diversity of the internal fauna supported by a host is determined primarily by its ability to maintain a parasite population, and secondarily by its liability to acquire it. This is contrary to the conclusion reached by Kennedy (1990), who argues that transmission is more important than maintenance, on the grounds that the parasite community of individual eels (*Anguilla anguilla* L.) is usually far less diverse than it might be.

Metabolic rate commonly scales as about the 3/4-power of body mass. Our results suggest that helminth diversity scales roughly with the 1/2-power of body length, or

equivalently that diversity scales with about the  $1/6$ -power of body mass. It follows that individuals of larger species of fish either bear fewer parasites per unit metabolism, or that the total number of parasite individuals rises with host metabolism more steeply than does the number of different species of parasite. We have no data that would enable us to distinguish between these two hypotheses.

We have already mentioned the analogy between host individuals and islands, which suggests a parallel between our conclusion that helminth diversity varies primarily with body size and the well-known tendency for the species diversity of taxa to increase with island size. As the exponent relating diversity to body length is 0.45, the corresponding exponent for an area will be about 0.22. Connor & McCoy (1979) reviewed ninety island studies and found that the average value of the exponent relating species diversity to island area was 0.31, with standard deviation 0.23. These results seem mutually consistent, though it must be borne in mind that 'island size' refers to a particular island of fixed size, whereas 'body size' refers to an average value for a category of host.

The prediction of taxon-specific species diversity from island area is much more successful than the attempt to relate helminth diversity to host body size: about 53% of the variance in species diversity is explained by regression on island size (42% if only studies of islands varying over one order of magnitude are included), whereas only about 23% of helminth species diversity is explained by regression on host body size. Indeed, even when diet is included, we can account for only about 40% of the variance in helminth diversity among hosts, although this rises to about 60% for the particular case of cestodes. A possible explanation for this lack of success is our concentration on ecological factors. Hosts and their internal parasites are often highly coevolved, so historical and evolutionary factors may contribute largely to the unexplained variance. Brooks (1980) has discussed parasite communities from the point of view of host-parasite coevolution and stressed the importance of phylogeny, though other authors (e.g. Price 1980) have taken the opposite stand.

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#### REFERENCES

- Bangham, R.V. (1940).** Parasites of fish of Algonquin Park lakes. *Transactions of the American Fisheries Society*, **70**, 161–171.
- Bangham, R.V. (1941).** Parasites from fish of Buckeye Lake, Ohio. *Ohio Journal of Science*, **41**, 441–448.
- Bangham, R.V. (1946).** Parasites of Northern Wisconsin fish. *Transactions of the Wisconsin Academy of Science, Arts and Letters*, **36**, 291–325.
- Bangham, R.V. (1951).** Parasites of fish in the Upper Snake River drainage and in Yellowstone Lake, Wyoming. *Zoologica*, **36**, 213–217.
- Bangham, R.V. (1955).** Studies on fish parasites of Lake Huron and Manitoulin Island. *American Midland Naturalist*, **53**, 184–194.
- Bangham, R.V. & Adams, J.R. (1954).** A survey of the parasites of freshwater fishes from the mainland of British Columbia. *Journal of the Fisheries Research Board of Canada*, **11**, 673–708.

- Bangham, R.V. & Hunter, G.W. (1939). Studies on fish parasites of Lake Erie. Distribution studies. *Zoologica*, **24**, 385–448.
- Bangham, R.V. & Venard, C.E. (1946). *Parasites of fish of Algonquin Park lakes. II. Distribution studies*. Ontario Fisheries Research Laboratory Publication 65.
- Becker, G.C. (1983). *Fishes of Wisconsin*. University of Wisconsin Press, Madison.
- Bell, G. (1989). A comparative method. *American Naturalist*, **133**, 553–571.
- Brooks, D.R. (1980). Allopatric speciation and non-interactive parasite community structure. *Systematic Zoology*, **29**, 192–203.
- Burt, A. (1989). Comparative methods using phylogenetically independent contrasts. *Oxford Surveys in Evolutionary Biology*, **6**, 33–53.
- Carlander, K.D. (1969). *Handbook of Freshwater Fishery Biology, Vol. 1*. Iowa State University Press, Ames.
- Carlander, K.D. (1977). *Handbook of Freshwater Fishery Biology, Vol. 2*. Iowa State University Press, Ames.
- Chubb, J.C. (1970). The parasite fauna of British freshwater fish. *Symposia of the British Society of Parasitology*, **8**, 119–144.
- Clutton-Brock, T.H. & Harvey, P.H. (1979). Comparison and adaptation. *Proceedings of the Royal Society of London B*, **205**, 547–565.
- Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Dechtiar, A.O. (1972). Parasites of fish from Lake of the Woods, Ontario. *Journal of the Fisheries Research Board of Canada*, **29**, 275–283.
- Felsenstein, J. (1985). Phylogenetics and the comparative method. *American Naturalist*, **125**, 1–15.
- Gaston, K.J. & Lawton, J.H. (1988). Patterns in body size, population dynamics and regional distribution of bracken herbivores. *American Naturalist*, **132**, 662–680.
- Gaston, K.J. & Lawton, J.H. (1988). Patterns in the distribution and abundance of insect populations. *Nature*, **331**, 709–712.
- Halvorsen, O. (1971). Studies on the helminth fauna of Norway. XVIII. On the composition of the parasite fauna of coarse fish in the River Glomma, southeastern Norway. *Norwegian Journal of Zoology*, **19**, 181–192.
- Holmes, J.C. (1990). Helminth communities in marine fishes. *Parasite Communities: Patterns and Processes* (Ed. by G.W. Esch, A.O. Bush & J.M. Aho), pp. 101–130. Chapman and Hall, London.
- Kennedy, C.R. (1990). Helminth communities in freshwater fish: structured communities or stochastic assemblages? *Parasite Communities: Patterns and Processes* (Ed. by G.W. Esch, A.O. Bush & J.M. Aho), pp. 131–156. Chapman and Hall, London.
- Lawton, J.H. (1989). What is the relationship between population density and body size in animals? *Oikos*, **55**, 429–434.
- Margolis, L. & Arthur, J.R. (1979). *Synopsis of the Parasites of Fishes of Canada*. Bulletin of the Fisheries Research Board of Canada 199. Ottawa, Canada.
- Muzzall, P.M. (1982). Metazoan parasites of fish from the Red Cedar River, Ingham County, Michigan. *Proceedings of the Helminthological Society of Washington*, **49**, 93–98.
- Muzzall, P.M. (1984). Helminths of fishes from the St. Mary's River, Michigan. *Canadian Journal of Zoology*, **62**, 516–519.
- Peters, R.H. (1983). *The Ecological Correlates of Body Size*. Cambridge University Press.
- Polyanski, Y.I. (1961). Ecology of parasites of marine fishes. *Parasitology of Fishes* (Ed. by V.A. Dogiel, G.K. Petrushevski & Y.I. Polyanski), pp. 48–83. Oliver and Boyd, Edinburgh.
- Price, P.W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, New Jersey.
- Ridley, M. (1983). *The Explanation of Organic Diversity*. Oxford University Press, Oxford.
- SAS Institute Inc. (1985). *SAS/STAT Guide for Personal Computers, Version 6 Edition*. SAS Institute, Cary, North Carolina.
- Scott, W.B. & Crossman, E.J. (1973). *Freshwater Fishes of Canada*. Fisheries Research Board of Canada Bulletin 184.
- Wanntorp, H.E., Brooks, D.R., Nilsson, T., Nylén, S., Ronquist, F., Stearns, S.C. & Wedell, N. (1990). Phylogenetic approaches to ecology. *Oikos*, **57**, 119–132.
- Williamson, M.H. (1981). *Island Populations*. Oxford University Press, Oxford.
- Wisniewski, W.L. (1958). Characterization of the parasitofauna of an eutrophic lake. *Acta Parasitologica Polska*, **6**, 1–64.
- Woods, C.E. (1971). Helminth parasites of fishes from the Forest River, North Dakota. *American Midland Naturalist*, **86**, 212–215.
- Wootten, R. (1973). The metazoan parasite fauna of fish from Hanningfield Reservoir, Essex, in relation to features of the habitat and host populations. *Journal of Zoology (London)*, **171**, 323–331.





## APPENDIX (cont.)

## Summary of species means

ord	fam	gen	sp		P	N host	N loc	Size	Age	Prev	Range	Diet	Helminths
5	8	21	45	<i>Ptylocheilus oregonensis</i> (Richardson 1836)	14	487	32	2-445	0-812	.	.	1-054	1-55703
5	8	22	46	<i>Rhinichthys atratulus</i> (Hermann 1804)	2	79	6	1-844	0-301	229	4-67	0	0-92702
5	8	22	47	<i>Rhinichthys cataractae</i> (Cuvier and Valenciennes 1842)	11	142	10	1-915	0-301	127	5-04	.	0-95796
5	8	23	48	<i>Richardsonius balteatus</i> (Richardson 1836)	15	2011	51	1-944	0-477	.	4-37	.	1-47589
5	8	24	49	<i>Semotilus atromaculatus</i> (Mitchill 1818)	16	207	7	2-062	0-360	236	4-90	0-515	1-11125
5	8	24	50	<i>Semotilus corporalis</i> (Mitchill 1817)	9	67	1	.	.	.	4-39	.	1-03664
5	8	24	51	<i>Semotilus margarita</i> (Cope 1869)	4	52	3	1-933	0-301	126	4-91	.	0-50106
5	8	25	52	<i>Carpiodes cyprinus</i> (LeSueur 1817)	10	24	4	2-631	0-778	44	4-66	.	0-50525
5	9	26	53	<i>Catastomus catastomus</i> (Forster 1773)	34	278	27	2-493	0-839	10	5-19	0	1-11693
5	9	26	54	<i>Catastomus commersoni</i> (Lacépède 1803)	51	491	23	2-515	0-648	554	5-15	0-025	1-15234
5	9	26	55	<i>Catastomus macrocheilus</i> Girard 1857	17	303	27	.	.	.	4-39	.	1-27414
5	9	27	57	<i>Erimyzon sucetta</i> (Lacépède 1803)	0	9	1	2-303	0-477	8	4-29	.	0-74536
5	9	28	58	<i>Hypentelium nigricans</i> (LeSueur 1817)	0	42	5	2-230	0-477	164	4-43	0	0-44663
5	9	31	61	<i>Moxostoma anisurum</i> (Rafinesque 1820)	2	19	3	2-585	0-699	84	4-56	0-201	0-74488
5	9	31	62	<i>Moxostoma erythrurum</i> (Rafinesque 1818)	5	10	5	2-469	0-602	125	4-45	0	0-34142
5	9	32	64	<i>Ictalurus melas</i> (Rafinesque 1820)	10	54	6	2-329	0-477	207	4-94	0-375	1-12274
5	10	32	65	<i>Ictalurus nebulosus</i> (LeSueur 1819)	40	215	14	2-349	0-477	15	4-76	0-484	1-37971
5	10	32	66	<i>Ictalurus punctatus</i> (Rafinesque 1818)	21	55	5	2-535	0-709	47	4-98	0-649	1-14566
5	10	33	67	<i>Noturus flavus</i> Rafinesque 1818	8	5	1	.	.	50	4-53	0-383	1-48324
5	10	33	68	<i>Noturus gyrinus</i> (Mitchill 1817)	4	30	4	1-723	0	98	4-68	0	0-93181
5	10	33	69	<i>Noturus miurus</i> Jordan 1877	4	3	1	1-785	.	.	.	.	1-29099
6	10	34	70	<i>Fundulus diaphanus</i> (LeSueur 1817)	20	35	4	1-810	0-301	35	4-46	0-079	1-00484
7	11	35	71	<i>Lota lota</i> Linnaeus 1758	28	92	13	2-569	0-499	52	5-18	1-186	1-48079
8	12	36	72	<i>Labidesthes sicculus</i> (Cope 1865)	5	51	3	1-875	0	73	4-56	0-041	0-21082
9	13	37	73	<i>Culea inconstans</i> (Kirtland 1841)	12	132	10	1-672	0	184	4-90	0-080	0-83621
9	14	38	74	<i>Pungitius pungitius</i> (Linnaeus 1758)	10	5	2	1-693	0-176	9	.	0	1-29057
10	14	39	75	<i>Percopsis omiscomaycus</i> (Walbaum 1792)	26	94	5	1-850	0-075	36	4-93	.	1-31031
11	15	40	76	<i>Ambloplites rupestris</i> (Rafinesque 1817)	41	350	19	1-998	0-438	197	4-61	0-087	1-86850
11	16	41	77	<i>Lepomis gibbosus</i> (Linnaeus 1758)	35	310	24	1-973	0-382	245	4-62	0	1-61421
11	16	41	78	<i>Lepomis macrochirus</i> Rafinesque 1819	11	288	27	1-991	0-299	177	5-00	0-055	1-55618
11	16	41	79	<i>Lepomis megalotis</i> (Rafinesque 1820)	1	5	2	1-858	0-301	5	4-68	0-256	1-11237
11	16	42	80	<i>Micropterus dolomieu</i> Lacépède 1802	44	483	17	2-436	0-665	179	4-75	0-317	1-86745
11	16	42	81	<i>Micropterus salmoides</i> (Lacépède 1802)	25	159	21	2-422	0-515	209	5-03	0-613	1-60198
11	16	43	82	<i>Pomoxis annularis</i> Rafinesque 1818	5	49	4	2-305	0-461	48	4-75	0-381	0-79048

APPENDIX (cont.)  
 Summary of species means

ord	fam	gen	sp	P	N host	N loc	Size	Age	Prev	Range	Diet	Helminths
11	16	43	<i>Pomoxis nigromaculatus</i> (LeSueur 1829)	7	117	15	2-273	0-477	220	4-94	0-698	1-01128
11	16	44	<i>Perca flavescens</i> (Mitchill 1814)	66	743	34	2-219	0-521	298	5-04	0-330	1-81506
11	17	45	<i>Stizostedion canadense</i> (Smith in Cuvier 1834)	15	63	5	2-516	0-551	20	4-72	.	1-65929
11	17	45	<i>Stizostedion vitreum</i> (Mitchill 1818)	38	241	21	2-698	0-768	75	5-15	1-307	1-87387
11	17	46	<i>Etheostoma blennioides</i> Rafinesque 1819	3	10	1	.	.	.	4-40	0	0-54772
11	17	46	<i>Etheostoma exile</i> (Girard 1860)	16	42	6	1-658	0	95	4-67	0	1-01595
11	17	46	<i>Etheostoma flabellare</i> Rafinesque 1819	4	23	2	1-672	0-301	107	.	0	0-59628
11	17	46	<i>Etheostoma nigrum</i> Rafinesque 1820	17	145	9	1-695	0	513	4-81	0	0-88748
11	17	47	<i>Percina caprodes</i> (Rafinesque 1818)	12	98	7	2-025	0-301	180	4-72	0	0-84505
11	17	47	<i>Percina copelandi</i> (Jordan 1877)	4	34	1	.	.	.	.	.	0-56880
11	17	47	<i>Percina maculata</i> (Girard 1860)	1	19	3	1-851	0-301	183	.	0	0-95203
11	18	48	<i>Aplodinotus grunniens</i> Rafinesque 1819	17	48	2	2-526	0-628	40	4-79	0-162	1-18288
11	19	49	<i>Cottus bairdi</i> Girard 1850	3	35	6	1-724	0-301	194	4-88	0-127	0-71919
11	19	49	<i>Cottus cognatus</i> Richardson 1836	11	49	3	1-833	0-398	12	5-19	0-045	0-63776

ord, fam, gen, sp are numeric codes for taxonomic order, family, genus and species of host.

P, total number of helminth species recorded (in Margolis & Arthur 1979).

N host, total number of host individuals examined (by original authors).

N loc, total number of localities examined (by original authors).

Size, log<sub>10</sub> body length at average age at first reproduction (mm).

Age, log<sub>10</sub> average age at first reproduction (years).

Prev local prevalence: number of localities in Wisconsin.

Range, log<sub>10</sub> total geographical range in North America (km<sup>2</sup>).

Diet, arcsin square root proportion of fish remains in stomach by volume.

Helminths, square root of mean number of helminth species per host individual.

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