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Variation in infection parameters among populations within parasite species: Intrinsic properties versus local factors

Robert Poulin *

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

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Abstract

Within any parasite species, variation among populations in standard infection parameters (prevalence, intensity and abundance) is an accepted fact. The proportion of hosts infected and the mean number of parasites per host are not fixed values across the entire geographic range of any parasite species. The question is whether this inter-population variation occurs within a narrow, species-specific range and is thus driven mainly by the biological features of the parasite, or whether it is substantial and unpredictable, leaving population parameters at the mercy of local conditions. Here, the repeatability of estimates of prevalence, intensity and abundance of infection was assessed across populations of the same parasite species, for 77 metazoan parasite species of Canadian freshwater fishes. Overall, parameter values from different populations of the same parasite species were more similar to each other and more different from those of other species, than expected by chance alone. Much of the variation in parameter values in the dataset was associated with differences between parasite species, rather than with differences among populations within species. This was particularly true for intensity and abundance of infection; in contrast, prevalence values, while somewhat repeatable among populations of the same species, still showed considerable variation. Among the higher taxa investigated (monogeneans, trematodes, cestodes, nematodes, acanthocephalans, copepods), there was no evidence that species of one taxon display intrinsically greater variation in population parameters than species of other taxa. Overall, the results suggest that intensity and abundance of infection are real species characters, though somewhat variable. This conclusion supports the view that the biological features of parasite species can potentially override local environmental conditions in driving parasite population dynamics.

Keywords: Abundance; Freshwater fish; Helminths; Intensity; Prevalence; Repeatability analysis; Species character

1. Introduction

Understanding why certain organisms are common and abundant while others are rare has been one of the central aims of ecology. Several physiological and ecological traits of animal species are known to correlate strongly with their abundance or their population density, providing the framework for hypotheses about the processes maintaining differences in abundance among species in an ecosystem (Gaston, 1994; Brown, 1995; Gaston and Blackburn, 2000). The underlying assumption here is that population abundance or density, e.g. the number of individuals per unit of habitat, is a species character. In other words, it is assumed that population density does not vary substantially among the different populations making up a species. In fact, inter-population variation in density or other population parameters is common and although long neglected, it can shed light on many aspects of the interaction between local environmental factors and a species' life history traits (see Frederiksen et al., 2005).

The parameters (prevalence, intensity and abundance) traditionally used to quantify parasite populations or the severity of parasitic infection, are also subject to variation. The proportion of hosts infected and the mean number of parasites per host are not fixed values across the entire geographic range of any given parasite species. Is this inter-population variation limited to a narrow, species-specific range of values, such that prevalence and intensity of infection remain 'true' species characters? Or is the variation substantial and unpredictable, leaving population parameters at the mercy of local conditions? On the one hand, several biological features of parasites will tend to produce similar population characteristics wherever the parasite becomes established. For instance, life history traits such as body size, lifespan and reproductive output, although

* Tel.: +64 3 479 7983; fax: +64 3 479 7584.
E-mail address: robert.poulin@stonebow.otago.ac.nz.

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variable among individuals of the same species, are constrained within species-specific limits and thus remain species traits. Therefore, the potential for a parasite species to spread to many host individuals and accumulate in these hosts is to some extent determined by its life history strategy. On the other hand, local factors can have such an impact on parasite populations that the link between life history traits and population parameters can be broken. For example, local abiotic conditions can regulate the survival and transmission success of infective stages (Pietrock and Marcogliese, 2003) and consequently cause inter-population variation in prevalence, intensity or abundance within a given parasite species. Similarly, the local availability of alternative prey can impact the structure of local food webs and predator–prey interactions with consequences for the population ecology of trophically transmitted parasites. In the end, are intrinsic life history characteristics of parasites sufficient to override the heterogeneity created by local environmental factors? Are parameters such as prevalence or intensity, used to describe parasite populations, true parasite species traits or merely the reflection of extrinsic factors?

Surprisingly, despite the importance of these questions, only one previous study has attempted to address them empirically. Focusing on nematode species parasitic in mammals, Arneberg et al. (1997) used repeatability analyses to show that both intensity of infection and, to a lesser extent abundance, are less variable within parasite species than among species and can therefore be considered species characters. This was not the case for prevalence, which varied too widely among populations of the same nematode species (Arneberg et al., 1997). These results need to be validated with analyses on other taxa, because the issue of inter-population variation in population parameters has several important implications. For instance, numerous comparative analyses have treated either prevalence, intensity or abundance as species characters (e.g. Arneberg et al., 1998; Poulin, 1999; Arneberg, 2001); it is crucial to determine whether this assumption is valid. Furthermore, the main output of most epidemiological models is some estimate of parasite population parameters (McCallum, 2000). If these predicted values are not characteristics of the species being modelled, then the models would lose much of their generality. It is, therefore, essential to determine whether population parameters of parasite species are species characters or not.

Here, I address this issue for metazoan parasite species of Canadian freshwater fishes. Specifically, I evaluate the repeatability of estimates of prevalence, intensity and abundance of infection across populations of the same parasite species, to determine whether these values are more consistent among populations of the same parasite species than among different parasite species. All estimates of prevalence, intensity and abundance used here were obtained during the same season, thus eliminating seasonal factors as a source of variability. As a secondary question, I also determine whether prevalence, intensity and abundance of infection vary more among populations of the same species in certain taxa of parasites than in others, by comparing inter-population variation among species of monogeneans, trematodes, cestodes, nematodes, acanthocephalans and copepods.

2. Methods

Data were obtained from published surveys on the metazoan parasites of fish from seven freshwater bodies, located across an area spanning most of Canada. They are: the Parsnip River and the McGregor River in British Columbia (Arai and Mudry, 1983), Aishihik Lake in the Yukon Territory (Arthur et al., 1976), Cold Lake in Alberta (Leong and Holmes, 1981), Lake of the Woods in Ontario (Dechtiar, 1972), Lake Huron in Ontario (Bangham, 1955) and the Smallwood Reservoir in Labrador (Chinniah and Threlfall, 1978). All these lakes and rivers were sampled during summer. These surveys were chosen not only because the various lakes and rivers have many species of fish and parasites in common but also because in each location all fish species were sampled for parasites. Thus, for each parasite species it is possible to identify the main host species, i.e. the one on which the parasite is most abundant, for each lake or river.

Data were recorded for monogenean, trematode, cestode, nematode, acanthocephalan and copepod species. However, only parasite species occurring in fish as adults were considered; therefore, the many helminth species using fish as intermediate hosts are excluded. For each lake or river, records of the various parasite species on fish species were compiled; in other words, all host–parasite species combinations observed were listed. Prevalence of infection (the proportion of fish infected by a given parasite species) was available for all records, whereas intensity of infection (the mean number of parasites of a given species per infected fish) was only available for five of the seven lakes and rivers. Where possible, abundance of infection (the product of prevalence and intensity) was calculated from the survey data. Records based on the examination of fewer than 15 individual fish were excluded from the analysis; this arbitrary cut-off value was chosen to balance the level of reliability of estimates of prevalence, intensity or abundance of infection with the number of records for which data would be available. Within and among lakes and rivers, the same parasite species was often recorded from several different fish species. In order to focus on a single host species per parasite species, in all such cases the parasite's main host was identified as the fish species in which the parasite achieved its highest average prevalence across all populations sampled and only records of the parasite on this host were used in the analyses. The final dataset included only parasite species for which there were at least two records, i.e. parasite species occurring on the same host species in at least two of the seven lakes and rivers surveyed.

Two approaches were used to determine whether prevalence, intensity and abundance of infection by metazoan parasites on fish hosts are true parasite species characters, i.e. features that vary less among populations of the same species than among species. Firstly, interspecific correlations were performed across all parasite species, separately for each of the three measures, in which the lowest value recorded for a given

parasite species was plotted against all other values recorded in other lakes or rivers for that species. Significant and strong positive correlations, characterised by data points falling along a narrow band, are expected if prevalence, intensity and abundance values for the same parasite species are consistent with each other across the various populations surveyed. For these and subsequent analyses, intensity and abundance data were $\log_{10}$-transformed to meet the assumptions of parametric tests.

Second, a repeatability analysis following that of Arneberg et al. (1997) was also used. Variation in prevalence, intensity and abundance of infection was analysed in separate Model II ANOVAs (one for each of the three measures), in which parasite species identity was the only factor. A significant effect of parasite species would indicate that the measures are repeatable within species, i.e. that they are more similar to each other than to measures from other parasite species. The proportion of the variance that occurs among species, as opposed to within species, was estimated using the coefficient of intraclass correlation as explained in Sokal and Rohlf (1995, p. 214).

Finally, to determine whether intraspecific variation in either prevalence, intensity or abundance of infection is greater in one of the six higher taxa of parasites considered here than in the others, the coefficient of variation (standard deviation expressed as a percentage of the mean) in each of the three measures was calculated for each parasite species. Coefficient values were then compared among the six parasite taxa using separate ANOVAs, one for each of the three measures.

3. Results

A total of 185 host–parasite records were used in the analyses of prevalence (Table 1). These represent 77 parasite species from 42 genera, which infect a total of 24 different fish species (including only the parasites' main host species). Of the 77 parasite species, 42 (55%) occurred in only one or two host species; the remaining species, although generalists, typically occurred at low abundance in host species other than the main host. In Table 1, fish species names follow the latest nomenclature, whereas parasite species names are given as in the original publications, even when they have changed, to make it easier to link the present study with the original sources. The only taxonomic revision that may affect the present analysis concerns the cestode genus *Proteocephalus*, as it has recently been suggested that three of the species in the present dataset (*Proteocephalus exiguus*, *Proteocephalus laruei* and *Proteocephalus salmonidicola*) may in fact be synonymous (Hanzelova and Scholz, 1999). They are here kept as separate species, though treating them as a single species or removing them from the analysis had no influence on the results presented below.

The majority of parasite species, i.e. 57 out of 77, were recorded on the same host species from only two of the lakes or rivers, the rest occurring in up to six of the seven localities surveyed (Table 1). Fewer records included data on intensity, and therefore abundance, in addition to data on prevalence; thus, only 93 records were used in the analyses of intensity and abundance of infection. Data on intensity and abundance were available for 49 parasite species but records of intensity and prevalence from more than one lake or river were only available for 37 of those parasite species. Prevalence and intensity of infection were positively correlated, whether across all available records ($r=0.536$, $N=93$, $P=0.0001$), or across mean species values ($r=0.606$, $N=49$, $P=0.0001$). Still, in some cases low prevalence values were associated with relatively high intensity values, and there was much scatter in the data (Fig. 1). The relationship also becomes non-significant in some parasite taxa (i.e. trematodes and nematodes) when they are treated separately but this may be due to the small number of species. To some extent the overall positive relationship may also be a product of pooling together heterogeneous data from the different taxa.

In an interspecific correlation of prevalence values, where the lowest value recorded for each parasite species was plotted against all its other values recorded in other lakes or rivers, a strong positive relationship emerged ($r=0.607$, $N=77$ species, $P=0.0001$). However, the triangular scatter of points (see Fig. 2) suggests that although some parasite species are characterised by high prevalence wherever they occur, others display a wide range of prevalence values, from very low to very high. For intensity and abundance of infection, the correlation between the lowest value and other values recorded is also strong and positive (intensity: $r=0.818$, $N=37$ species, $P=0.0001$; abundance: $r=0.741$, $N=37$ species, $P=0.0001$). However, for these parameters the pattern is clearer (Fig. 2): the roughly linear arrangement of data points suggests that the various parasite species are characterised by a narrow range of intensity or abundance values, observed wherever they occur.

The results of the repeatability analyses support the above findings to a large extent. Prevalence values from different populations of the same parasite species are more similar to each other and more different from those of other species than expected by chance alone ($F_{76,108}=2.649$, $P=0.0001$). Approximately 41% of the variation in prevalence among records is associated with differences between parasite species, rather than with differences among populations within species. Nevertheless, whereas some parasite species seem to always occur at roughly the same prevalence, many others display considerable inter-population variability in prevalence (Fig. 3). Repeatability is stronger for both intensity and abundance of infection, for which values from different populations of the same parasite species are also statistically more similar to each other, than expected by chance (intensity: $F_{36,44}=4.908$, $P=0.0001$; abundance: $F_{36,44}=3.335$, $P=0.0001$). Approximately, 64 and 52% of the variation in intensity and abundance, respectively, among all records is associated with differences between parasite species, rather than with differences within species. The intensity and abundance values for any given parasite species fall within a relatively narrow range (Fig. 3) and these two population parameters are thus repeatable within the same parasite species.

Table 1
Parasite species used in the analyses, with ranges of prevalence and intensity values

Parasite species	Host species	Range in prevalence (%)	Range in intensity (rounded)	Localities[a]
Monogeneans				
Acolpenteron catostomi	*Catostomus catostomus*	4.1–5.9	4–17	1,2
Anonchohaptor anomalum	*Catostomus commersonii*	7.8–13.6	1	1,5
Discocotyle sagittata	*Coregonus clupeaformis*	18.0–79.4	2–7	3–5,7
Octomacrum lanceatum	*Catostomus commersonii*	2.6–11.8	–	5,6
Pseudomurraytrema copulata	*Catostomus macrocheilus*	25.6–57.1	13–15	1,2
Tetraonchus borealis	*Thymallus arcticus*	34.0–88.6	6–9	1,3
Tetraonchus monenteron	*Esox lucius*	69.6–100	232–880	3,5,7
Tetraonchus variabilis	*Prosopium williamsoni*	19.6–20.7	3–4	1,2
Trematodes				
Azygia angusticauda	*Ambloplites rupestris*	4.3–30.0	–	5,6
Azygia longa	*Esox lucius*	3.0–8.7	–	5,6
Bunodera luciopercae	*Oncorhynchus mykiss*	3.1–8.0	19–86	1,2
Bunodera sacculata	*Perca flavescens*	4.5–21.9	–	5,6
Bunoderina eucaliae	*Culaea inconstans*	29.4–73.5	–	5,6
Crepidostomum cooperi	*Lepomis gibbosus*	1.8–37.5	–	5,6
Crepidostomum cornutum	*Ambloplites rupestris*	35.0–58.6	–	5,6
Crepidostomum farionis	*Salvelinus namaycush*	9.0–90.2	62–63	3,7
Cryptogonimus chilli	*Ambloplites rupestris*	40.0–63.8	–	5,6
Microphallus opacus	*Micropterus dolomieu*	7.7–16.2	–	5,6
Phyllodistomum coregoni	*Coregonus clupeaformis*	1.9–60.0	3	4,5,7
Plagioporus sinitsini	*Catostomus commersonii*	0.7–5.9	–	5,6
Cestodes				
Bothriocephalus claviceps	*Ambloplites rupestris*	0.9–30.0	–	5,6
Bothriocephalus cuspidatus	*Sander vitreus*	51.2–100	10	4–6
Bothriocephalus formosus	*Percopsis omiscomaycus*	15.8–23.1	–	5,6
Bothriocephalus opsariichthydis	*Ptychocheilus oregonensis*	35.0–48.5	3–8	1,2
Corallobothrium fimbriatum	*Ictalurus nebulosus*	65.0–71.4	–	5,6
Cyathocephalus truncatus	*Coregonus clupeaformis*	34.9–100	7–28	3–6
Eubothrium rugosum	*Lota lota*	79.3–82.3	13	4,5
Eubothrium salvelini	*Salvelinus namaycush*	37.5–100	4–36	1–4,6,7
Glaridacris catostomi	*Catostomus commersonii*	4.5–34.2	1	1,5,6
Hunterella nodulosa	*Catostomus commersonii*	5.6–31.8	3–9	1,4,5
Proteocephalus ambloplitis	*Micropterus dolomieu*	64.8–64.9	–	5,6
Proteocephalus exiguus	*Coregonus clupeaformis*	13.3–64.6	13	4–6
Proteocephalus laruei	*Coregonus artedi*	5.8–89.9	–	5,6
Proteocephalus pearsei	*Perca flavescens*	17.9–33.3	–	5,6
Proteocephalus pinguis	*Esox lucius*	1.6–90.9	21–37	4–7
Proteocephalus ptychocheilus	*Ptychocheilus oregonensis*	50.0–60.6	4–6	1,2
Proteocephalus salmonidicola	*Salvelinus malma*	5.9–12.9	26–32	1,2
Proteocephalus stizostethi	*Sander vitreus*	24.4–27.6	–	5,6
Proteocephalus tumidocollus	*Salvelinus namaycush*	25.0–100	13–326	3,7
Triaenophorus crassus	*Esox lucius*	3.2–69.6	2–25	3–7
Triaenophorus nodulosus	*Esox lucius*	47.8–90.3	35	4,5
Triaenophorus stizostedionis	*Sander vitreus*	4.9–20.7	–	5,6
Nematodes				
Camallanus oxycephalus	*Micropterus dolomieu*	0.5–21.6	–	5,6
Capillaria salvelini	*Salvelinus namaycush*	21.3–59.0	4–74	3,7
Cystidicola farionis	*Coregonus clupeaformis*	13.1–76.2	13–69	3–6
Cystidicoloides tenuissima	*Oncorhynchus mykiss*	5.0–40.0	21–36	1,2,6
Dichelyne cotylophora	*Perca flavescens*	13.4–54.7	–	5,6
Haplonema hamulatum	*Lota lota*	5.2–38.1	6	4,6
Hysterothylacium brachyurum	*Esox lucius*	53.0–95.7	–	5,6
Philometra cylindracea	*Perca flavescens*	1.0–7.5	–	5,6
Philometroides huronensis	*Catostomus catostomus*	2.0–10.2	3	1,2
Philonema agubernaculum	*Prosopium williamsoni*	1.4–2.6	2–6	1,2
Raphidascaris acus	*Esox lucius*	3.2–57.1	2–7	3,4,7
Rhabdochona canadensis	*Salvelinus malma*	1.0–1.2	2–3	1,2
Rhabdochona cascadilla	*Notropis hudsonius*	8.0–19.0	–	5,6
Rhabdochona cotti	*Cottus cognatus*	10.3–26.1	2	1,2
Rhabdochona kisutchi	*Salvelinus malma*	5.9–18.8	9–26	1,2
Rhabdochona zacconis	*Catostomus macrocheilus*	9.3–16.3	1–5	1,2

(*continued on next page*)

Table 1 (*continued*)

Parasite species	Host species	Range in prevalence (%)	Range in intensity (rounded)	Localities[a]
Spinitectus carolini	*Ambloplites rupestris*	15.0–81.0	–	5,6
Spinitectus gracilis	*Lota lota*	4.8–11.8	–	5,6
Acanthocephalans				
Echinorhynchus salmonis	*Lota lota*	70.6–100	174	4–6
Leptorhynchoides thecatus	*Micropterus dolomieu*	81.1–81.4	–	5,6
Neoechinorhynchus crassus	*Catostomus catostomus*	38.5–57.0	15	6,7
Neoechinorhynchus cristatus	*Catostomus macrocheilus*	20.9–67.3	10–13	1,2
Neoechinorhynchus cylindratus	*Micropterus dolomieu*	62.9–86.5	–	5,6
Neoechinorhynchus rutili	*Salvelinus malma*	9.4–47.5	4	1,2
Neoechinorhynchus strigosus	*Catostomus commersonii*	3.9–13.8	2	4–6
Neoechinorhynchus tumidus	*Prosopium cylindraceum*	9.1–86.0	5	3,6
Octospinifer macilentus	*Catostomus commersonii*	3.9–4.5	2	1,5,6
Pomphorhynchus bulbocolli	*Catostomus commersonii*	27.3–100	38–103	1,4–6
Copepods				
Ergasilus caeruleus	*Sander vitreus*	24.4–100	–	5,6
Ergasilus nerkae	*Coregonus clupeaformis*	5.1–11.6	9–14	1,4
Salmincola californiensis	*Oncorhynchus mykiss*	11.2–12.0	1–3	1,2
Salmincola corpulentus	*Coregonus clupeaformis*	2.0–26.3	1–2	4–7
Salmincola edwardsii	*Salvelinus namaycush*	37.5–53.8	2–5	1–3
Salmincola extensus	*Coregonus clupeaformis*	4.8–30.9	1–2	3,4
Salmincola thymalli	*Thymallus arcticus*	34.1–45.0	2–6	1,3

[a] 1, Parsnip river; 2, McGregor river; 3, Aishihik lake; 4, Cold lake; 5, Lake of the Woods; 6, lake Huron; 7, Smallwood reservoir.

Although the points in Fig. 3 do not show any clumping of the sort that would result in one higher taxon being solely responsible for the observed pattern, the repeatability analyses were also performed separately for each of the six parasite taxa considered in this study. The results are generally consistent with the previous analyses, although significant differences among parasite species were not always found (Table 2). Because of the low number of species included in some analyses (see Table 2), some of these tests lack statistical power and thus non-significant results are not necessarily an indication that population parameters are not repeatable across species within any given taxon.

The possibility that variability in prevalence, intensity or abundance might be greater within certain taxa than within others was addressed by comparing the coefficient of inter-population variation among species of the six higher taxa. No evidence was found that species of one taxon display intrinsically greater variation in population parameters than species of other taxa (prevalence: $F_{5,71}=2.096$, $P=0.0758$; intensity: $F_{5,31}=1.021$, $P=0.4221$; abundance: $F_{5,31}=1.519$, $P=0.2125$). The average values of the coefficient of variation sometimes differ greatly between different taxa of parasites; for instance, variation in intensity of infection within acanthocephalan species is much less pronounced than what is observed in species of cestodes or nematodes (Fig. 4). Once again, the small number of species in certain taxa may have prevented the detection of real differences.

4. Discussion

Variation in abundance or density among populations of the same animal species has long been ignored by ecologists but when considered it can provide new insights into the interaction between life history traits and local processes (Frederiksen et al., 2005). Similarly, heterogeneity in infection levels among host or parasite populations is often reported by parasitologists but rarely analysed. The results of the present study indicate that both intensity and abundance of infection, although showing some variation among parasite populations of the same species, are nonetheless repeatable enough to be considered as parasite species characters. In contrast, prevalence of infection was not as clearly consistent and repeatable among populations of the same parasite species and cannot as readily be seen as a species character. These findings apply to all major taxa parasitic on fish included in this analysis, since no difference in intraspecific variation was found among these taxa. There are therefore parasite species that consistently exist at high local abundance wherever they occur and others that are consistently found at low infection levels. If local rarity or commonness are indeed species traits, then their relationship with host specificity could shed light on the specialist–generalist debate and how it may relate to large-scale patterns of parasite occurrence (see Poulin, 1998).

In a typical fish parasite species, intensity and abundance of infection show little inter-population variation, whereas prevalence varies more widely. This is exactly what Arneberg et al. (1997) found among nematodes parasitic in mammals, leading them to conclude that intensity and abundance, but not prevalence, are species characters of parasites. Why is it that prevalence varies more widely than intensity among populations of the same parasite species? Prevalence is a function of the number of hosts that are parasitised and therefore it is determined by encounter rates

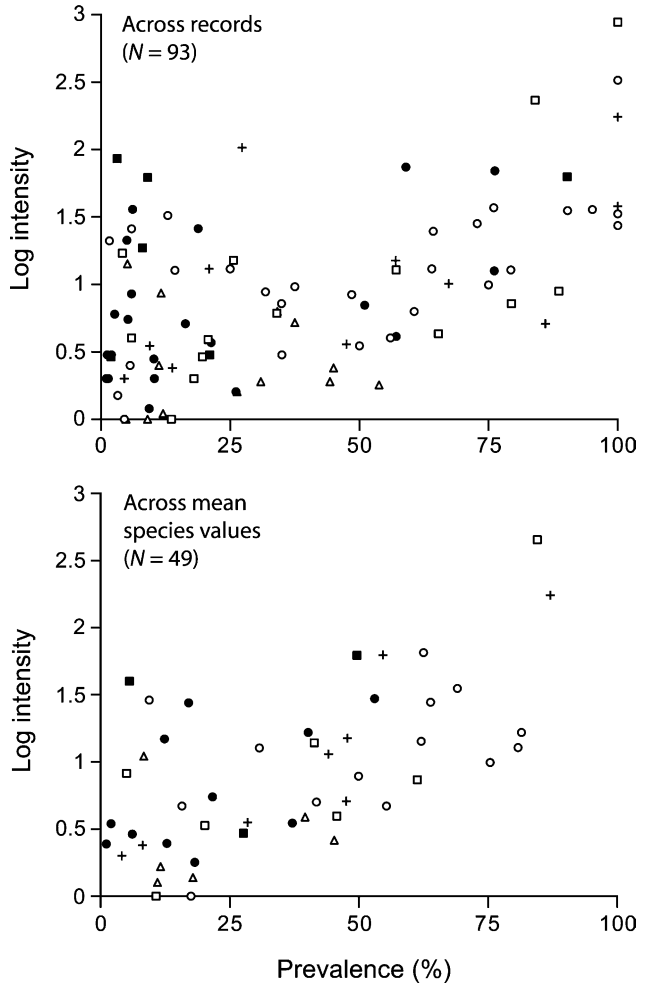

Fig. 1. Relationship between intensity and prevalence of infection among metazoan parasites of freshwater fish. The relationship is shown using data from all records in the dataset (top) as well as using mean species values (bottom) for all species for which data on both prevalence and intensity were available. Different symbols are used to distinguish between monogeneans (open squares), trematodes (filled squares), cestodes (open circles), nematodes (filled circles), acanthocephalans (crosses) and copepods (open triangles).

between parasites and hosts. Encounters between the infective stages of parasites and their fish hosts are influenced by processes outside the fish. These include the survival of free-living parasite stages and the diversity of prey items available to fish that determines the predation rates on the particular prey species that harbour larval parasites. Such processes are likely to be determined strongly by local factors, making prevalence of infection in one locality unpredictable based solely on data from other localities.

In contrast, intensity of infection is determined to a large extent by processes acting within the fish. The relative size difference between the parasite and its site of infection (e.g. the intestine) places an upper limit on how many individual parasites can 'fit' inside a host. Density-dependent interactions among conspecific parasites can also regulate the number of parasites per host (Keymer, 1982; Shostak and

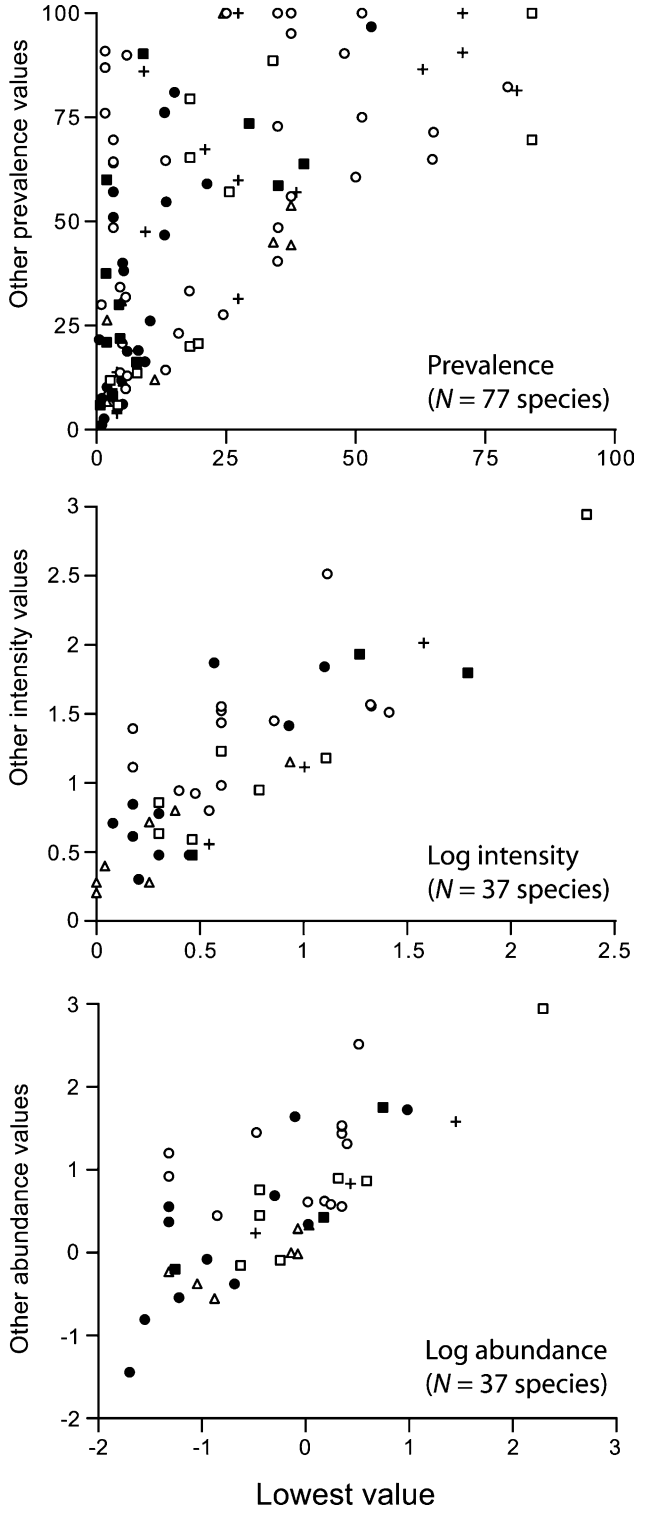

Fig. 2. Relationship between the lowest value (on the *x*-axis) and all other values of either prevalence (top), intensity (middle) or abundance (bottom), for all metazoan parasite species of freshwater fish for which two or more values were available. The symbols are as in Fig. 1.

Scott, 1993). For instance, in many acanthocephalans parasitic in fish, the initial establishment success and subsequent survival of worms drops dramatically beyond a certain number of individuals per host (Uznanski and Nickol,

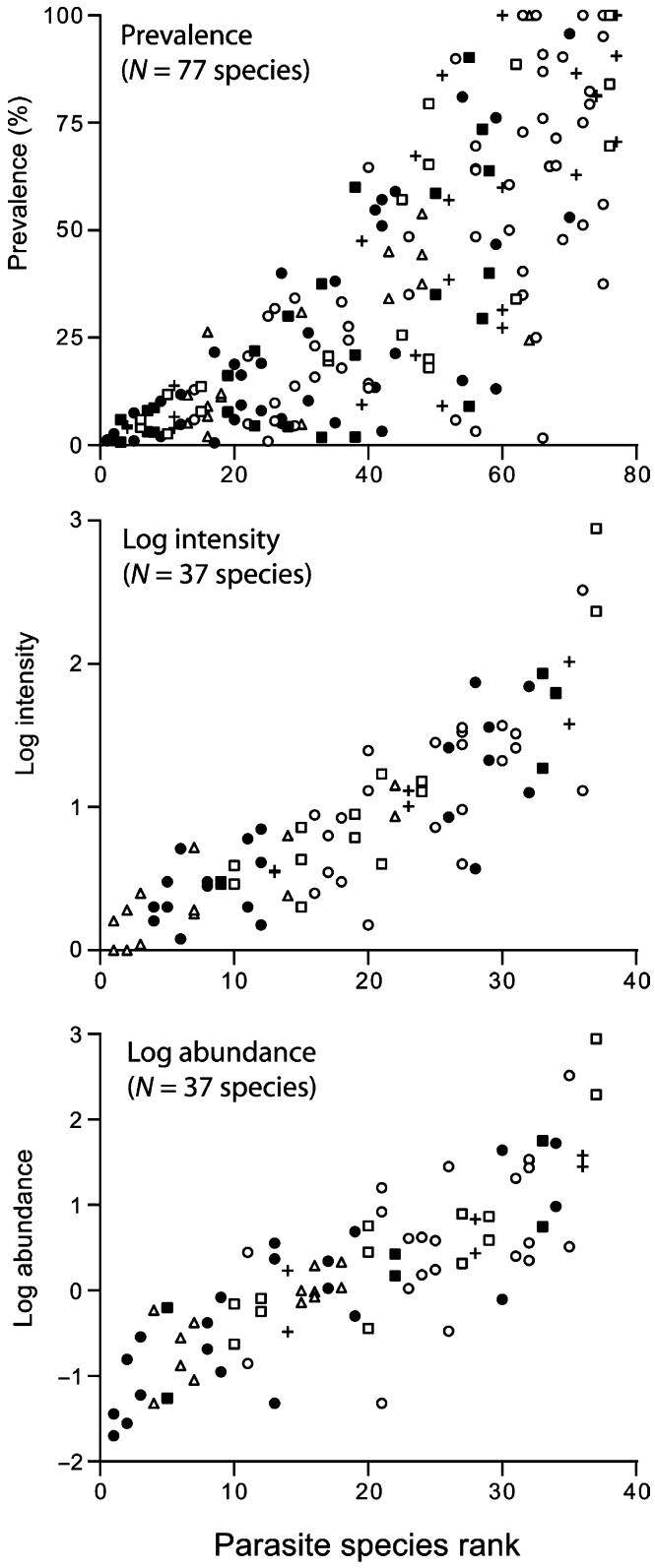

Fig. 3. Rank plots of prevalence (top), intensity (middle) and abundance (bottom). Parasite species are ranked according to their mean values of either prevalence, $\log_{10}$ intensity or $\log_{10}$ abundance, with rank 1 given to the species with the lowest mean value. All population estimates are plotted for each species. If variation is small within compared with between parasite species, we expect to see a narrow band of points extending from the lower left corner to the upper right corner of the plot, with few or no points in the upper left or lower right corner. The symbols are as in Fig. 1.

1982; Brown, 1986). This density-dependence imposes a ceiling on intensity of infection, one that is specific to a particular parasite species. Importantly, this should apply equally to all populations of the same parasite species in the same host species. Local external conditions may have an effect on intensity but it should be much smaller than their effect on prevalence. Abundance, being the product of prevalence and intensity of infection, shows an intermediate level of inter-population variation but is still repeatable enough to be taken as a species character.

It is perhaps surprising that there were no differences among higher taxa of parasites with respect to intraspecific variability in population parameters. Among the taxa studied here, there is a clear ecological dichotomy between the ectoparasites (monogeneans, copepods) and the endoparasites (trematodes, cestodes, nematodes, acanthocephalans) on at least three levels. Firstly, the ectoparasites infect their fish host via contact with the host's external surfaces, whereas all endoparasites included in this study infect their host trophically, when the fish host ingests an infected intermediate host. Second, the ectoparasites remain exposed to external conditions throughout their lives, whereas the endoparasites live within the fish's body. Third, there is a single transmission event in the life cycle of the ectoparasites, whereas in the endoparasites there may be two or three, depending on the number of intermediate hosts required for the life cycle to be completed. This last difference in particular may be important: a greater number of transmission events could generate greater variability in population parameters, since the vagaries of transmission are multiplied. A much larger number of species than the ones available here would be necessary for definitive comparisons among higher taxa; still, the evidence from the present analysis suggests that these differences may be small.

The present study has considered infection parameters, i.e. prevalence, intensity and abundance, as potential species characters of parasites. There is a second partner in the association, however. Could prevalence, intensity and abundance of infection by parasites be seen instead as properties of the host species? It seems logical to suppose that certain host species are characterised by higher infection levels, by any parasite species, than other host species. Indeed, Arneberg et al. (1997) have found that the intensity and abundance of nematode infections are repeatable within the same mammalian host species. Some mammal species have consistently many nematodes per host individual whereas other mammals have consistently few nematodes per individual host, independently of which nematode species are considered. The repeatability among host species was much weaker than that observed among parasite species, however (Arneberg et al., 1997). Along the same lines, Poulin and Mouritsen (2003) have observed that the prevalence of larval trematodes in snails is repeatable among populations of the same snail species, although the repeatability was not particularly pronounced.

Table 2
Repeatability analyses (ANOVAs) of infection measures within species of different parasite taxa, with the percent of variance occurring among species shown in parentheses

Parasite taxon	Prevalence	Intensity	Abundance
Monogeneans	$F_{7,11}=4.04$ (57%)[a]	$F_{5,7}=16.47$ (88%)[b]	$F_{5,7}=12.38$ (84%)[b]
Trematodes	$F_{11,13}=1.25$ (11%)	$F_{2,3}=13.97$ (87%)[a]	$F_{2,3}=5.36$ (69%)
Cestodes	$F_{21,37}=2.23$ (32%)[a]	$F_{8,13}=1.51$ (18%)	$F_{8,13}=0.75$ (12%)
Nematodes	$F_{17,22}=1.88$ (29%)[c]	$F_{9,11}=2.79$ (46%)[c]	$F_{9,11}=3.23$ (52%)[a]
Acanthocephalans	$F_{9,15}=3.61$ (51%)[a]	$F_{2,3}=23.45$ (92%)[a]	$F_{2,3}=11.74$ (84%)[a]
Copepods	$F_{6,10}=2.73$ (42%)[c]	$F_{5,7}=4.83$ (64%)[a]	$F_{5,7}=2.96$ (48%)[c]

[a] $P<0.05$.
[b] $P<0.01$.
[c] $P<0.10$.

Is a similar phenomenon present among parasites of fish? The host fish species considered here ranged in body mass over several orders of magnitude, from sticklebacks and minnows to lake trout and pike and also varied considerably in general behaviour and ecology; it is therefore conceivable that they were also characterised by different levels of exposure to infective stages and different rates of parasite accumulation. When the repeatability analyses were performed using host species instead of parasite species as the single factor, significant repeatability among host species was only observed for prevalence and not for intensity or abundance. The proportion of the variance that occurred among host species, as opposed to within, was rather low, however: 19, 6 and 13% for prevalence, intensity and abundance, respectively. Compared with the values obtained when parasite species are used as the source of repeatability (41, 64 and 52%, respectively; see results), it is clear that although the identity of the host species can have a certain effect, the three infection parameters are mainly properties of parasite species and not host species. Ideally, infection levels by the same parasite species but in different host species would be used to test this and to determine whether infection parameters are also properties of the parasite–host interaction; however, there were insufficient records of one parasite species from different host species in the database to allow such a test.

Together with the results of Arneberg et al. (1997), the findings of the present study demonstrate that values of both intensity and abundance of infection by metazoans tend to vary across different populations of the same species within narrow species-specific limits. In addition, Krasnov et al. (2006) have recently shown that aggregation levels of fleas on their small mammalian hosts are also repeatable within species. These observations mean that intensity, abundance and aggregation of metazoan infection are real species characters, though they are somewhat variable. This conclusion validates the use of these population parameters in comparative analyses and in modelling studies. It also supports the view that the biological features of parasite species can potentially override local environmental conditions in driving parasite population dynamics.

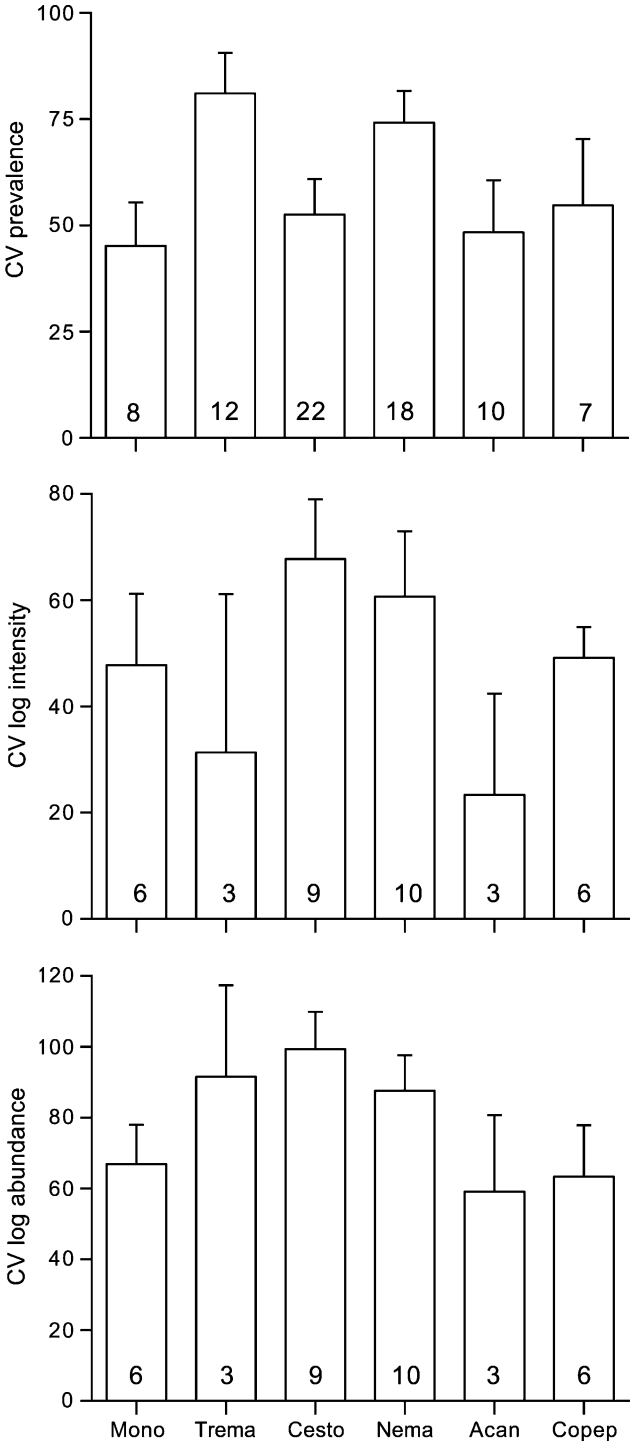

Fig. 4. Mean (±SE) inter-population coefficient of variation (CV) in prevalence (top), intensity (middle) and abundance (bottom) among metazoan parasites of freshwater fish. Data are shown separately for monogeneans (Mono), trematodes (Trema), cestodes (Cesto), nematodes (Nema), acanthocephalans (Acan), and copepods (Copep); the number of species for which the coefficient of variation could be computed is indicated at the base of each bar.

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