

INFRACOMMUNITIES: STRUCTURE AND COMPOSITION

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Parasite communities from single host individuals have one undoubted feature: the overwhelming majority of parasite infrapopulations cannot maintain their numbers by self-reproduction. These communities are rigorously defined spatially. The existence of an infracommunity is restricted to its individual host's lifetime. However, at this level parasites only interact or do not interact, compete or do not compete with each other, and either form or do not form guilds. As a result of these interactions isolationist or interactive communities are formed.

Holmes & Price (1986) suggested that the host organism is analogous to an "island" which is inhabited by parasites. A number of studies of communities of intestinal helminths have clearly shown that even component communities consist of few helminth species (5-10). But taking into account host numbers one can assume a great number of empty or partly populated "islands" (Simberloff, 1990). Frequency distributions of numbers of parasite species in 899 infracommunities revealed the fact that most of them consist

of 1-2 parasite species. Frequency distributions of parasite species are overdispersed ($\lambda^2/M = 2.23$) and can be fitted by Gamma or Poisson distributions. The same distribution type was found when infracommunities were grouped according to fish ecology or systematic position. This distribution is typical for the frequency distribution of numbers of a single parasite species in one host population. Parasite species frequency distributions vary in different component communities: from typically overdispersed to asymmetrical. This reflects different life conditions for different host populations. Thus, one of the important parameters of infracommunity - species number is stochastic.

For all host individuals a low probability of events occurring and approximately equal probabilities of a parasite being acquired (but not establishing) are the basis of overdispersed or aggregated distributions. Research into free-living communities often focuses on spatial segregation

(overdispersion) and on changing patterns of spatial use as evidence for interspecific interactions, particularly competition (Simberloff, 1990). Overdispersed species distribution seems not to be a feature at the infracommunity level or even to have no sense because of the impossibility of studying the same host individual several times. Nevertheless it is difficult to fit another type of distribution for an association each member of which is overdispersed. This phenomenon is based on a very low probability for parasites to complete their life cycle. If prevalence is the probabilistic estimation for the event (to complete life cycle), the next probabilistic estimation could be done for a cestode: $P = 0,0005 * 0,05 * 0,8 = 0,00002$, where the first number is prevalence of infection of a planktonic copepod, the second - prevalence of infection of the second intermediate host (fish) and the third number - prevalence of infection of the final host (predatory fish). Perhaps the probability of infecting a host increases from first intermediate to final host. Hence the probability of occurring in the same host individual comes to zero as we have to add another multiplier $1/N$ where N is the number of host specimens in the population. This very low probability is compensated for by high fecundity, reservoir parasitism etc. Such a property is typical of parasites with complicated life cycles that are less dependent on the external environment. It could be supposed that parasites with direct life cycles which have a greater probability of infecting the host will be found more often and in higher numbers than parasites with complex life cycles, which means that they will be dominant species in infracommunities. However, these species were dominant in only 25% of infracommunities

despite the fact that both parasite groups are nearly equally represented in the region (44% and 56%). Thus, parasites with direct life cycles which are more dependent on the external environment but with a greater probability of infecting the host are less often dominant in infracommunities than parasites with complex life cycles. This is one evidence of the interactive nature of infracommunities. On the other hand spatial segregation (overdispersion) is the result of interaction (ghost of competition in the past) when all problems within the community have been solved, whereas any disturbance of overdispersion is the sign of serious infracommunity reorganization when competition plays an important role. These periods can be short, for example during fish spawning, migration etc.

Simberloff (1990) stated that "host individuals may more closely approximate replicates of one other, than islands do". It could be supposed that a real island has a greater variety of biotopes than a host individual, but host population genotype variety, diversity and the extent of host reaction to "parasite-colonists" are more diverse or at least the same as on a real island. The main difference is that species colonizing a real island compete with each other while the parasite habitat (host organism) reacts actively to such a colonist's occurrence. The other difference is that the number of "hosts-islands" is much higher than the number of islands in any archipelago. It is well known that the number of species inhabiting an island depends on the size of the island. In parasitology the analo-

gous parameter could be host size. We use fish length as the measure of host size. No great correlation was found between fish length and species number or fish length and number of parasite individuals (Fig. 1). None of the infracommunity parameters (dominance index, evenness, Brillouin index) correlated with host size either when all infracommunities were included into analyses or when infracommunities without multicellular parasites ($S=0$) were excluded. This means that the host organism is not completely analogous to an island. The same fact was found when infracommunities were grouped according to fish ecology. When the systematic position of the host was included in the analysis the situation changed. Salmonidae s.l. show a weak significant correlation between S and $\ln N$ with fish length which became less when infracommunities with $S=0$ were excluded.

Cyprinidae show weak a significant correlation of S and N with fish length which increases slightly when infracommunities with $S=0$ are excluded. Among Salmonidae S was correlated with fish length in the case of graylings ($r=0,33$; $p=0,01$) when infracommunities with $S=0$ were included. A negative significant correlation was found between S , N and fish length in the case of round whitefish (*Prosopium cylindraceum*) ($r=-0,4678$, $p=0,003$; $r=-0,3488$, $p=0,032$). Such a correlation was not found among other salmonid species (*Salvelinus malma*, *Brachymystax lenok*, *Coregonus sardinella*). The picture is much more diverse among Cyprinidae. Species of the genus *Phoxinus* in a combined sample did not demonstrate significant correlations between S , N and fish length, while in the case of species of the related genus

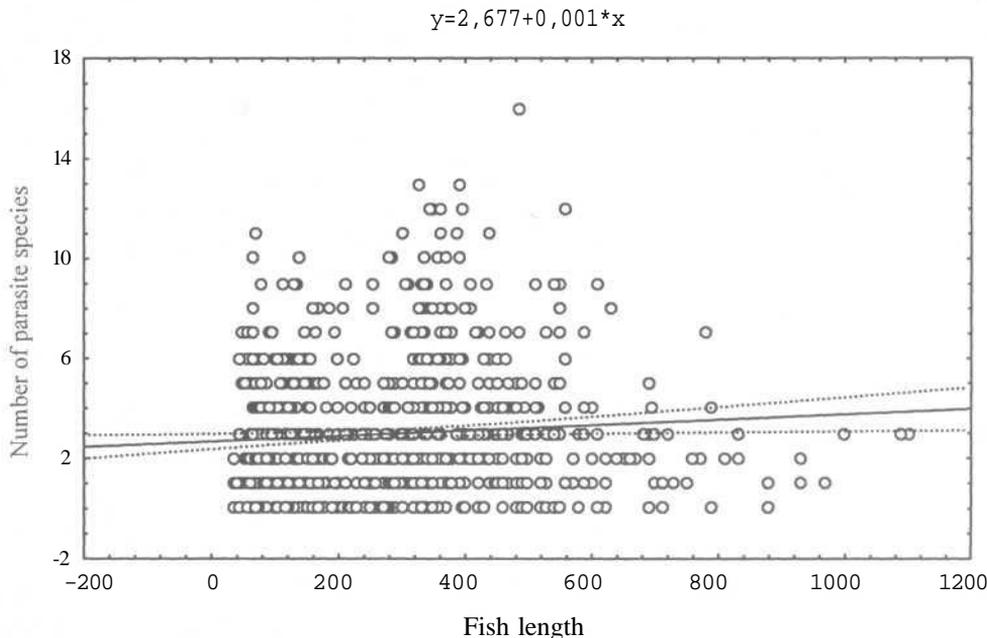


Fig. 1. Relationship between fish length and number of parasite species ($r=0,077$).

Oreoleuciscus such correlations were observed ($r=0,5058$, $p=0,0001$; $r=0,3534$, $p=0,0001$). Lake minnow (*Phoxinus phoxinus*) demonstrated a weak negative correlation between S and fish length only if infracommunities with $S=0$ were excluded ($r=-0,2512$, $p=0,045$). River minnow (*Ph. phoxinus*) demonstrated a weak positive correlation between N and fish length only if infracommunities with $S=0$ were excluded ($r=0,282$, $p=0,16$, $r=0,24$, $p=0,02$). The lacustrine form of the two species of west-mongolian minnows (*Oreoleuciscus potanini* and *O. pewzowi*) from Big Lake Valley demonstrated significant correlations between S, N and fish length. The third species of the genus *Oreoleuciscus* (*O. humilis*), which has lacustrine and riverine forms, demonstrated a significant negative correlation only between S and fish length ($r=-0,3591$, $p=0,015$). No significant correlations between these parameters were found among lacustrine forms of this species while its riverine form demonstrated a significant correlation between N and fish length only ($r=0,4529$, $p=0,012$).

Thus, two main parameters - number of species and number of parasite individuals - of the infracommunity show very diverse correlations with host size only when we take into account host phylogenetic relationships. The diversity of these correlations demonstrates the impossibility of making a direct analogy with free-living animal ecology. If we would like to make such an analogy in the case of "host-island" theory then every host species would consist of "populations-archipelagos which are situated in the same geographical zone". Only among "islands" of one and the same "archipel-

ago" could correlations be revealed. Host species of different sizes can harbour many parasite species, for example minnow and pike (Pugachev, 1997).

The numbers of parasites (N) in infracommunities varied greatly. 95% of infracommunities had less than 1000 parasites; 86% - less than 500; 76% - less than 200. Frequency distributions of parasite numbers were overdispersed as were numbers of parasite species. Numbers of species and numbers of parasite individuals are connected by a significant positive correlation, the value of which increased considerably when infracommunities with more than 500 parasite individuals (14% of infracommunities) or more than 200 (24% of infracommunities) were excluded from the sample. This correlation between S and N was revealed in the case of fish ecological groups, systematic groups (Salmonidae and Cyprinidae) and all fish species except burbot (*Lota lota*). The value of the significant correlation varied from 0.38 to 0.45 in the case of fish ecological groups and from 0.31 to 0.66 in the case of different fish species and was 0.35 for Salmonidae and 0.45 for Cyprinidae. The numbers of parasite individuals in infracommunities reached "saturation level" on the average when infracommunities consisted of 150 parasite individuals and 9-10 species (Fig. 2). This "saturation level" was revealed in all fish ecological and systematic groups. Thus, the number of parasite individuals in the infracommunity being a stochastic and overdispersely distributed value shows the tendency to achieve saturation on the

$$\text{Median} = -68,589 + 184,731 * \log_{10}(x)$$

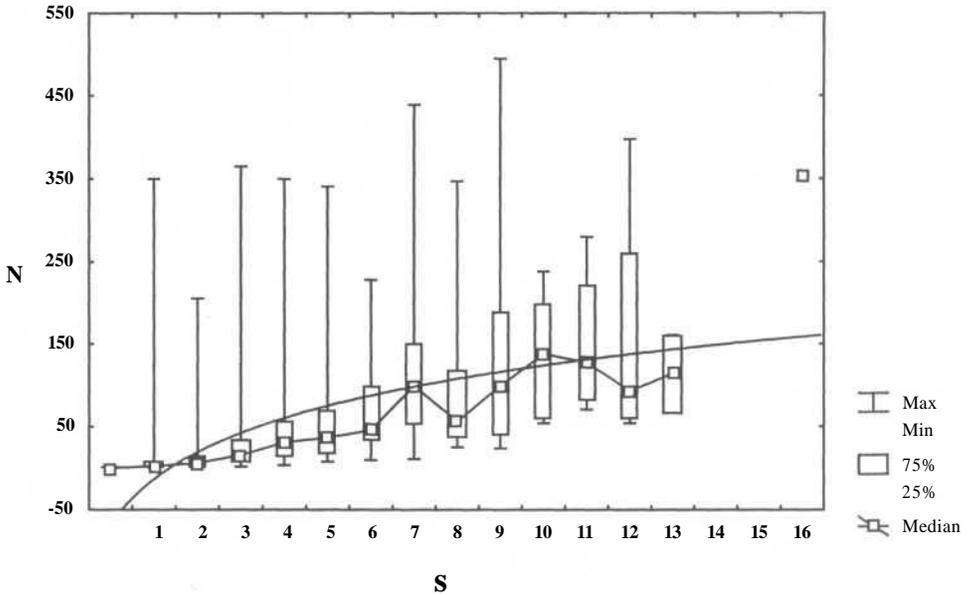


Fig. 2. Relationship between number of species (S) and numbers of parasites (N) within infracommunities (regression line by average values, $N < 500$)

average. This is possible evidence for recognizing an infracommunity as interactive, nonisolationist and saturated, which is the result of interactions between host organism and parasites as well as between parasites. Only if we suggest that a host organism is an indifferent habitat can we come to the conclusion that there are "empty niches" and unlimited food resources. Absence of parasites is not evidence of the existence of empty niches. Niches can be "closed" by host reactions or even be non-existent.

There are infracommunities which consist of a large number of parasite individuals and which could be defined as "oversaturated" (Fig.2). These oversaturated infracommunities mask the saturation. Infracommunities consist of parasite species with different life strategies. Some parasites cannot complete their life cycle

in a fish and are "interested in" the host's death and its availability to a predator. The others are not. 55% of oversaturated infracommunities had dominant parasites of the first group. Thus, such parasite species exert an important influence on the fate of an infracommunity. A rapid increase in parasite numbers corresponds to their life strategy. These oversaturated infracommunities have to have short life spans. In these cases parasites from the second group have little chance of completing their life cycles.

An analysis of relationships between the main three parameters of infracommunities was carried out. As Brillouin index and evenness are connected by formula their correlation is not discussed. Dominance index was significantly negatively correlated with

number of parasite species (S), evenness and Brillouin indices but not with number of parasite individuals. These correlations were found for fish ecological groups, and for most species of Salmonidae and Cyprinidae. Evenness index was positively correlated with S but not with N . The same relationship is characteristic for Brillouin index also. Thus, three main parameters of infracommunities demonstrate the usual relationships. When the number of species in the infracommunity increases, evenness and Brillouin index increases but dominance decreases. This is further evidence of the interactive nature of parasite infracommunities. The character of such interaction, presence or absence of competition between or within species, presence or absence of competition between or within guilds, needs further investigations.

Fundamental infracommunity features are: existence is restricted to the lifetime of an individual host; spatial distinctness; high rates of emigration and immigration; co-existence of species with different life strategies; habitat (host organism) reacts actively to the parasite; parasite intrapopulations cannot maintain their numbers by self-reproduction. These features clearly distinguish parasite infracommunities from communities of free-living animals. In this respect a parasite infracommunity is a "subcommunity" or "hemicommunity".

Summary

1. Analysis of infracommunity structure for separate fish species did not reveal any clear tendencies for main infracommunity parameters. The infracommunity looks stochastic and unpredictable.

2. The reasons for stochasticity are large numbers of hosts and diversity of interactions within different host-parasite systems.

3. Analysis of all infracommunities has demonstrated saturation and even oversaturation for parasite numbers; functional dependence between parasite species number and number of individuals; dependence of S and N on host size when host phylogenetic relationships were considered; clear correlations between main infracommunity parameters.

4. Being stochastic by nature infracommunities are sufficiently predictable and interactive.

References

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