Fish population size, and not density, as the determining factor of parasite infection: a case study

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SUMMARY

The diversity and abundance of parasites vary widely among populations of the same host species. These infection parameters are, to some extent, determined by characteristics of the host population or of its habitat. Recent studies have supported predictions derived from epidemiological models regarding the influence of host population density: parasite abundance and parasite species richness are expected to increase with increasing host population density, at least for directly transmitted parasites. Here, we test this prediction using a natural system in which populations of the crucian carp, *Carassius carassius* (L.), occur alone, with no other fish species, in a series of 9 isolated ponds in Finland. The ectoparasite communities in these fish populations consist of only 4 species of monogeneans (*Dactylogyrus formosus, D. wegeneri, D. intermedius* and *Gyrodactylus carassii*); the total and relative abundance of these 4 species varies among ponds, with one or two of the species missing from certain ponds. Across ponds, only one factor, total fish population size, explained a significant portion of the variance in both the mean number of monogenean species per fish and the mean total abundance of monogenean individual per fish. In contrast, fish population density did not influence either monogenean abundance or species richness, and neither did any of the other variables investigated (mean fish length per pond, number of fish examined per pond, distance to the nearest lake, and several water quality measures). In our system, proximity among fish individuals (i.e. host population density) may not be relevant to the proliferation of monogeneans; instead, the overall availability of host individuals in the host population appeared to be the main constraint limiting parasite population growth.

Key words: Monogenea, population size, population density, epidemiology, crucian carp, *Carassius carassius*.

INTRODUCTION

One of the most prominent features of parasite infections in wild host populations is their variability among populations of the same host species. Both the diversity and abundance of parasites differ from one host population to the next. Certain habitat characteristics, either physical or chemical, may facilitate the establishment and proliferation of parasites in particular host populations. In fish hosts, for example, variables such as lake size, water pH or distance from other lakes have been associated with either the number of parasite species per host population, or with the mean abundance of given parasites (e.g. Kennedy, 1978; Marcogliese & Cone, 1991; Hartvigsen & Halvorsen, 1994; Karvonen *et al*. 2003). Features of the host population itself may also be important determinants of how many parasite species and parasite individuals occur in a host population. Epidemiological models predict that the number of hosts in a population influences the transmission success of parasites, by determining

the contact rate between the parasites' infective stages and new hosts (see Hudson *et al*. 2002 for recent reviews). There is therefore a minimum, or threshold, number or density of hosts required for the establishment and spread of a parasite in a host population, and as the number or density of hosts in the population increases, so should the abundance of the parasite. The models use either host density (number of hosts per area or volume) or host population size as the key parameter influencing parasite transmission success. The inclusion of either host density or population size in a model is usually dependent on preliminary information from the study system (see McCallum, Barlow & Hone, 2001). There is empirical support suggesting that host population density is indeed an important predictor of both parasite abundance and parasite species diversity, in comparative studies across related host species (Morand & Poulin, 1998; Arneberg *et al*. 1998; Arneberg, 2001, 2002). To our knowledge, there is currently no empirical evidence that host numbers or density affects macroparasite infections among populations of the same host species in the wild. There is some evidence that host population size or density is important for microparasites, including several human diseases such as measles (Earn *et al*. 2000; Bjornstad, Finkenstadt & Grenfell,

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2002). Studies on macroparasites are complicated by other variables also differing between host populations, in particular the diversity of other host species co-occurring with the host species investigated. Here, we take advantage of a natural system in which populations of the crucian carp, *Carassius carassius* (L.), occur alone, with no other fish species, in a series of isolated ponds. This system represents a natural laboratory in which carp populations of different sizes or densities have established naturally and on which parasites have established and proliferated independently; it provides a great opportunity to test the effects of host population features on parasite infections among populations of the same host species.

The retreat of the ice after the last glaciation left Finland pockmarked with thousands of small ponds (approx. 130 000, size 0·05–1 ha) and lakes (approx. 56 000 > 1 ha) (Raatikainen, 1987). Small ponds are often characterized by brown water, low pH, shallow depth and hypoxia during the long northern winter, making them uninhabitable for most other fish species but suitable habitats for crucian carp, because of its unique tolerance of anoxia (Holopainen, Hyvärinen & Piironen, 1986; Tonn *et al*. 1990). Often crucian carp is the only fish species present under these extreme conditions; in winter, more than 6 months in dark anoxic water near freezing temperatures, and in summer at temperatures up to 30 °C. It is in summer that the carps experience relatively brief periods of vigorous growth and repeated bouts of reproduction in almost continuous daylight (Holopainen, Tonn & Paszkowski, 1997). In all size-classes the food during summer consists mainly of planktonic (cladocerans) or benthic invertebrates, but plant material, phytoplankton and detritus are also commonly found in gut contents (Holopainen, Tonn & Paszkowski, 1992). In winter the metabolic rate is depressed and the fish hibernate just above freezing level. Crucian carps are extremely vulnerable to predation and have therefore adapted to two different kinds of life-styles: aided by its physiological adaptations to extreme conditions, crucian carp can be the sole fish inhabitant in dense monocultures of stunted individuals in the ponds ('pond type'), but in lakes crucian carps grow much larger and display a deeper body shape to avoid predation ('lake type') (Holopainen *et al*. 1997). In the ponds, the fish are gregarious and found in shoals, and they occupy the entire water column.

This study focuses on the ectoparasite communities on 'pond type' crucian carps that live in dense monocultures in very similar extreme conditions, i.e. similar water quality and biotic factors, such as the composition of the flora and fauna in the ponds. They thus represent a perfect natural system of comparable populations. Our central question is: What characteristics of the host population determine the infection (or epidemiological)

parameters of metazoan ectoparasites observed in these ponds?

Specifically, we focused on 5 characteristics of the ponds or of host populations that may influence infection parameters: (1) fish density per m^3, since higher host densities should enhance the transmission success of directly transmitted parasites, such as monogeneans, resulting in higher infection levels; (2) mean fish length, since larger fish provide more attachment space for ectoparasites and can thus sustain more parasite individuals; (3) distance to the nearest lake, since this may determine the rate at which ponds are re-colonized by parasites or fish (note: this may affect the number of ectoparasite species in a pond, but not parasite abundance); (4) fish population size, because this may be actually more important than population density (if the observed densities are all high enough to ensure transmission, then it may be the number of available hosts that limits parasite population growth); and (5) the number of fish examined, a confounding variable that must be included as it may influence our estimates of parasite abundance and diversity. Assessing the effect of these 5 variables was our main objective; as a secondary objective, we also examined the potential influence of various measures of water quality on ectoparasite infections.

MATERIALS AND METHODS

Study areas and estimation of fish populations

The material was collected from 9 ponds in 2 watersheds, one flowing south to the Gulf of Finland (area I) and the other eastward to Lake Ladoga (area II) (Fig. 1). Hereafter we refer to the ponds either as I1 to I6, referring to ponds in the first watershed, or II7–II9, for ponds from the other watershed (see Fig. 1). The quality of water in the ponds was generally poor, which was indicated by a low concentration of oxygen (ponds I1, I5), low pH (pond I1), or high conductivity (ponds I3, I4, I5). Clear signs of eutrophication, indicated by a high concentration of chlorophyll-a, are seen in ponds I3 and I5, and a strong human impact (high density of faecal coliforms) in ponds I4 and I5 (see Table 1).

During the summer of 1998 about 20 (range 12–28) crucian carp of approximately the same size (range 88–120 mm) were studied from each pond (Table 2). The samples were collected with a fish trap during the summer season, mainly between June to mid-August. The surface area, depth and distance of each pond to the nearest lake were determined (see Table 2). The size of crucian carp populations in the ponds was estimated by the capture and recapture method with a fish trap. The water volume of each pond was estimated based on its area and maximum depth, assuming that all ponds have the shape of a cone. The number of

Table 1. *Physical environment of the nine ponds in the two watersheds*

| Parameters	Pond								
	I1	I2	I3	I4	I5	I6	II7	II8	II9
Drainage area	I	I	I	I	I	I	II	II	II
Area, ha	0·02	0·3	0·6	1·5	0·5	1	1	1·5	0·04
Nearest lake, m	940	60	260	580	200	600	500	5000	400
Max. depth, m	2	6	3	2	2	6	1·6	16	2
O_2-concentration, mg/l	3·5	8·7	9·3	10	3·2	5	N.A.*	N.A.	N.A.
pH	5·7	6·9	7·4	6·7	6·6	6·1	N.A.	6·3	N.A.
Chlorophyll-a, mg/l	50	61	118	16	566	33	N.A.	6·9	N.A.
Colour, mg Pt/l	>150	70	80	40	>150	150	N.A.	N.A.	N.A.
Conductivity, mS/m	1·5	5·7	8·6	28	11·3	4·5	N.A.	1·2	N.A.
Density of coliform bacteria, Ecol/ml	72	150	29	1080	272	10	N.A.	N.A.	N.A.

* N.A., Not available.
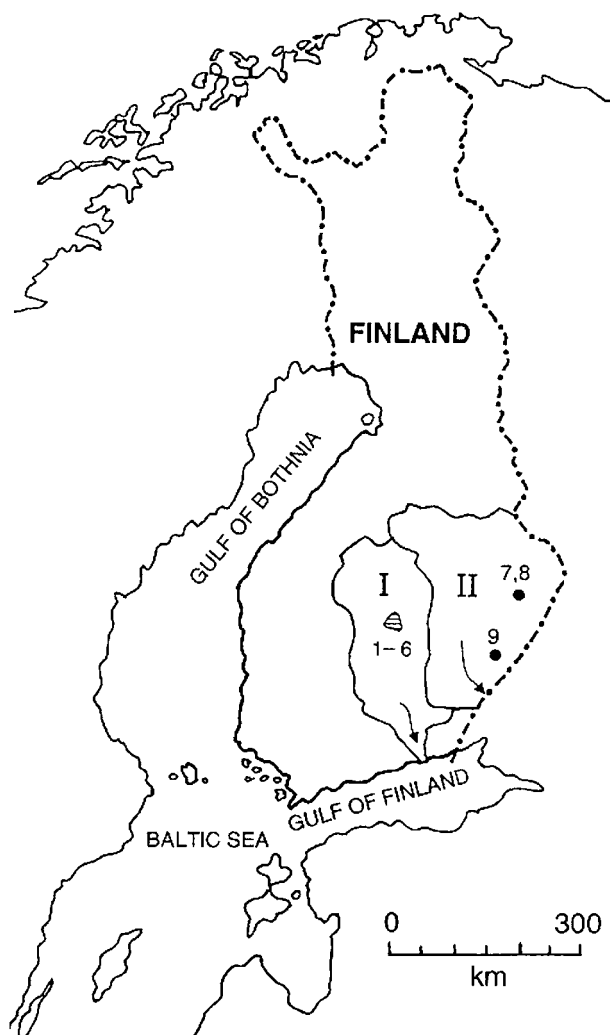
Fig. 1. Study ponds in the two lake and river systems in Finland.

fish/m^3 was then used as a measure of fish population density. The average mean lengths of 100 fish captured by traps in each pond were also measured (range 50–134 mm) (Table 2).

Parasitological analyses

The crucian carp were captured with a trap and killed in the laboratory immediately prior to examination. The length, weight and height of the fish were measured and metazoan parasites studied from the eyes, inner organs and gills. The gill-arches were dissected from the left side of the fish. A separate slide was prepared for each gill-arch, which were numbered 1 to 4 from the outermost to the innermost. All adult monogeneans were identified to the species level with a compound microscope at a magnification of 100–400 × and all post-larvae were counted. Identification was based on the chitinized parts of the parasites (Gusev, 1985) and was performed on fresh slides. Terminology follows the recommendations of Bush *et al.* (1997), where the mean abundance is the total number of individuals of a parasite species in a sample of a host species divided by the total number of hosts studied, and prevalence is the number of hosts infected with a particular parasite species divided by the number of hosts examined. Because of the similar sizes of the monogenean species found in this study, they were pooled for the analyses of variation in total abundance across host populations.

Analysis

The effects of the 5 main predictor variables (fish population density, fish population size, mean fish length, number of fish examined for parasites, and distance to nearest lake) were analysed by stepwise regression analysis with a forward selection procedure and a F-to-enter = 4 criterion (Sokal & Rohlf, 1995). This procedure selects the best subset of predictor variables from the set of 5 above, so that the final regression model includes only the predictor variables that explain a significant proportion of the variance in the dependent variable. This was done for each of the three infection parameters (dependent variables), i.e. the mean number of

Table 2. Parameters examined

Parasite	Area	Pond	N	Prevalence (%)	Abundance	Range	s²/x
Dactylogyrus	I	1	23	91%	10·2	0–30	11·2
formosus		2	18	100%	28·6	8–110	24·2
		3	20	100%	66·3	25–170	27·3
		4	28	100%	116·5	21–280	51·1
		5	18	100%	41·4	1–22	38·0
		6	20	100%	124·3	82–219	12·3
	II	7	20	100%	65·4	21–148	20·8
		8	20	100%	36·8	1–135	24·9
		9	12	100%	25·5	12–37	2·3
Dactylogyrus	I	1	23	0%			
intermidius		2	18	0%			
		3	20	100%	328·4	66–819	144·1
		4	28	100%	539·6	30–1991	479·8
		5	18	72%	12·7	0–26	10·1
		6	20	100%	21·7	5–44	5·3
	II	7	20	95%	12·9	0–35	9·0
		8	20	10%	1·5	0–2	1·6
		9	12	0%			
Dactylogyrus	I	1	23	91%	13·1	0–36	7·1
wegeneri		2	18	100%	14·8	5–29	3·0
		3	20	100%	36·8	8–77	7·6
		4	28	100%	26·5	3–130	23·3
		5	18	67%	14·6	0–29	9·9
		6	20	100%	25·9	14–45	2·6
	II	7	20	100%	32·7	7–100	20·6
		8	20	100%	23·2	1–75	18·6
		9	12	100%	20·2	8–30	2·9
Dactylogyrus	I	1	23	70%	8·0	0–51	28·4
juvenile		2	18	89%	4·7	0–13	1·9
		3	20	95%	56·3	0–179	41·3
		4	28	100%	257·8	47–1153	363·1
		5	18	89%	2·3	0–4	0·7
		6	20	90%	3·3	0–9	1·7
	II	7	20	100%	22·2	28 126	14·8
		8	20	65%	2·1	0–7	2·9
		9	12	67%	2·4	0–9	4·0
Gyrodactylus	I	1	23	0%			
carassii		2	18	39%	1·6	0–3	1·4
		3	20	35%	1·4	0–4	1·8
		4	28	14%	1·5	0–3	1·9
		5	18	0%			
		6	20	0%			
	II	7	20	40%	1·6	0–5	2·2
		8	20	35%	2·0	0–5	2·3
		9	12	0%			

monogenean species per fish, the mean total abundance of parasites per fish, and the-variance-to-mean ratio.

The influence of water quality measures (oxygen concentration, pH, water colour, conductivity, chlorophyl-a concentration, and coliform counts) was also assessed using stepwise regressions for each of the 3 dependent variables above. We had to test the effects of water quality measures separately from those of the 5 main predictor variables above (fish population density, etc.) because combining them would result in more independent variables than we have ponds. In any event, this secondary analysis was only used to detect potential influences of abiotic

factors, believed a priori to be less important than the host population features examined in the above analyses. Variables that did not meet the assumptions of parametric tests were log-transformed prior to analysis.

RESULTS

Except for 4 *Argulus foliaceus* specimens in one pond (I5), all metazoan parasites found were monogeneans. Altogether 4 monogenean species were found. Two of them, *Dactylogyrus formosus* and *D. wegeneri*, occurred in all ponds, *D. intermedius* was found in 6 ponds and *Gyrodactylus carassii* in

Table 3. *Parameters examined in the nine ponds in the two watersheds*

Parameters	I1	I2	I3	I4	I5	I6	II7	II8	II9
Mean length of fish in the pond*	60	112	134	114	95	120	111	127	50
Mean population size of fish	350	4400	20000	33000	5000	30000	26000	38000	1000
No. of fish examined	23	18	20	28	18	20	20	20	12
Mean length of examined fish, mm	95	112	120	109	107	115	88	120	99
Mean age of examined fish	4·1	4·8	3·3	5·3	3·9	4·9	3·0	6·3	4·2
Mean number of species/fish (range)	1·9 (1–2)	2·3 (2–3)	3·4 (3–4)	3·1 (3–4)	2·4 (1–3)	3 (3)	3·4 (3–4)	2·4 (2–3)	2 (2)
Mean number of specimens/fish	27	48	485	941	62	175	133	62	47

* Caught with a cage trap ($N = 100$).

5 ponds, so that 2–4 species occurred in each pond (Table 3, Fig. 2). All monogeneans occurred in both watersheds studied. *D. formosus* dominated in 6 ponds, *D. intermedius* in 2 ponds and *D. wegeneri* in 1 pond (see Fig. 2). A fact worth noting is that *D. formosus* was the dominant species in the ponds of either 4, 3, or 2 species and in both watersheds. The prevalences of all dactylogyrids species were high, approximately 100% in most cases. The prevalence of *G. carassii* varied between 0 and 40% (Table 3).

The mean number of monogenean species per individual fish ranged from 1·9 to 3·4. Abundances were highest in ponds I3 and I4 where *D. intermedius* was very abundant (Tables 2 and 3). In pond I4 the maximum number of parasites in one fish (in the left side of the gills only) was 2802, the mean number being 941. The lowest numbers were observed in a tiny, very isolated pond I1. The highest mean number of species per fish were in ponds I3 and II7 (Table 2).

Results of the main stepwise regression analyses indicate that for each dependent variable there was at best only 1 important predictor variable. For the mean number of monogenean species per fish only log fish population size was included in the regression model ($F_{1,7} = 12·524$, $r^2 = 0·624$, $P = 0·0095$, see Fig. 3A); all 3 other predictor variables were excluded. For the mean total abundance per fish, again only log fish population size was included ($F_{1,7} = 6·9$, $r^2 = 0·496$, $P = 0·0341$, see Fig. 3B). For the variance to mean ratio, only log number of fish examined was included in the regression model ($F_{1,7} = 10·664$, $r^2 = 0·604$, $P = 0·0138$). In all the secondary stepwise regressions using water chemistry measures as predictor variables, only one relationship emerged as almost significant: log water conductivity tended to relate with the mean total abundance of monogeneans per fish ($F_{1,5} = 5·614$, $r^2 = 0·529$, $P = 0·064$).

DISCUSSION

Our study attempted to determine whether key parameters in epidemiological models can indeed explain the patterns of variation in parasite infections observed among populations of the same host species in nature. Overall, our results do provide some support for epidemiological predictions. The larger the fish population (i.e. the more fish there are in the pond), the more monogenean species and individuals occurred on the gills of fish on average; no other feature of the ponds or host populations influenced this pattern significantly. Also, the more fish that are examined, the higher the variance to mean ratio, which is a common result of parasite aggregation when sample sizes are relatively small (because the more fish are in a sample, the more likely it is that a heavily-infected fish will be included, which raises the ratio). The main result, however, remains the effect of host population size on parasite diversity and abundance. The fact that population size is important, and not population density, suggests that density (i.e. proximity among fish hosts) is not a barrier to effective transmission. Instead, the overall availability of hosts might constrain parasite population growth.

Monogeneans are directly transmitted from fish to fish. In such parasites, proximity among hosts might be very important for successful transmission. However, the ponds in our study form closed systems, with no water currents, and with high fish densities (almost 3 fish/m³ on average, see also Holopainen & Pitkänen, 1985 and Paszkowski *et al.* 1990); the densities in all ponds may well all be above the threshold host density necessary for the proliferation of monogenean populations. In this situation, the total number of fish available may become the real determinant of parasite population growth, with small host populations not capable of sustaining relatively high parasite abundances. The
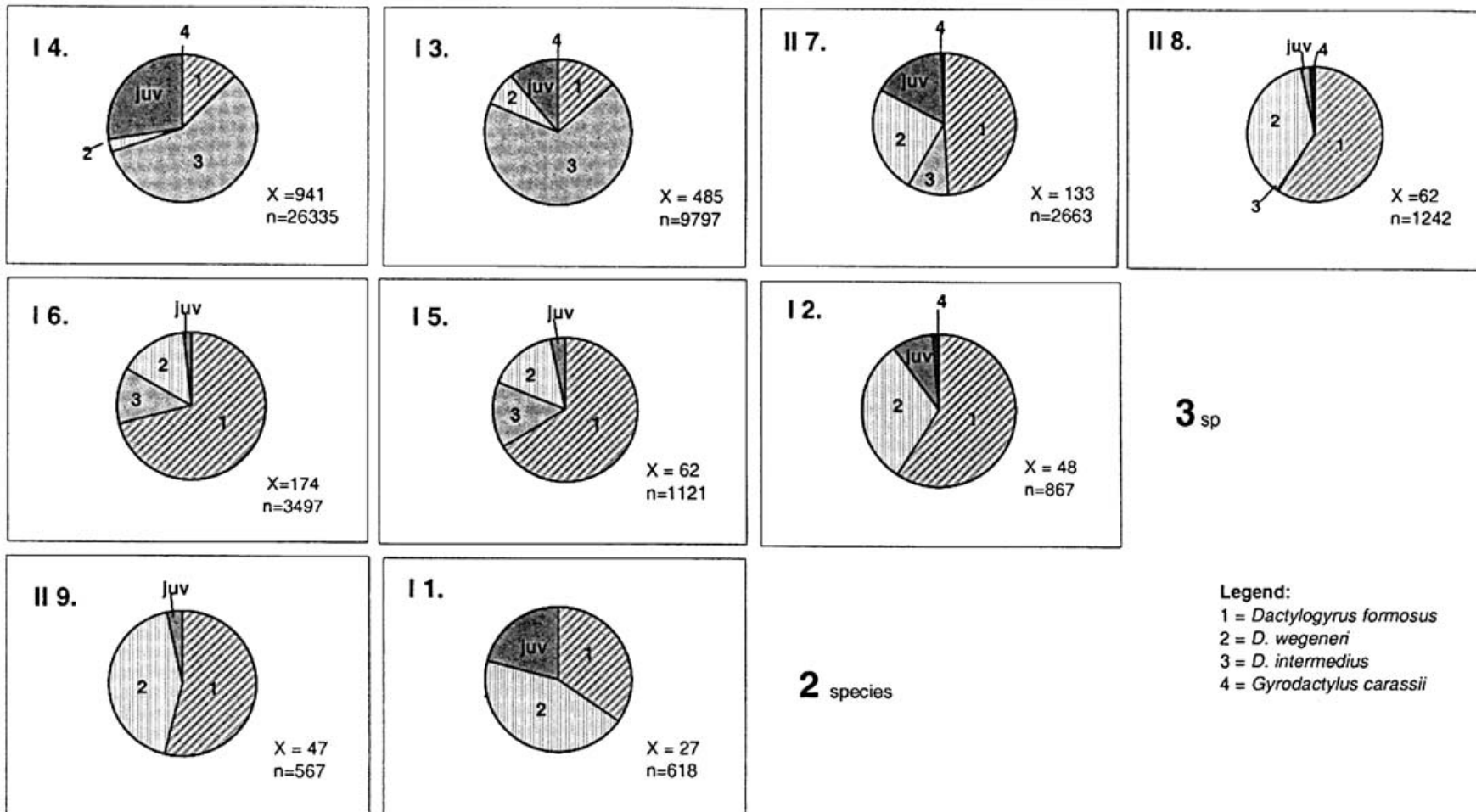
Fig. 2. Percentage of monogenean individuals of each species from the total number of monogeneans in each pond on the gills of crucian carp when 4, 3 or 2 monogenean species were present. Mean number of monogenean specimens (X) per fish in each pond, and total number of worms found in the sample (*n*) are given.
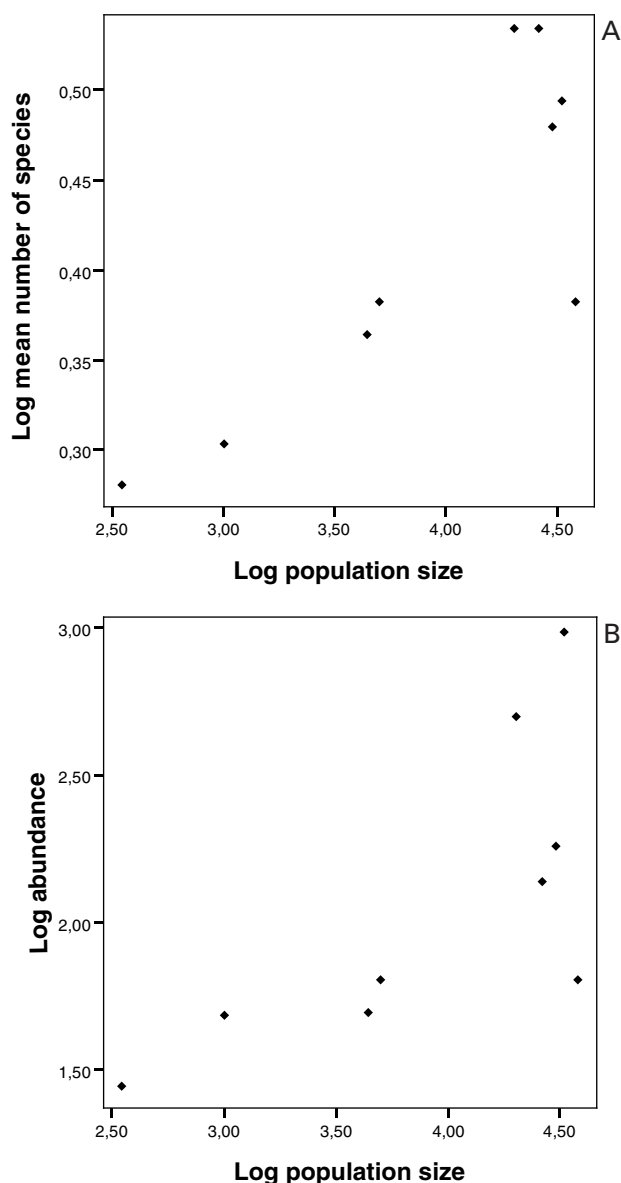
Fig. 3. (A) Relationship between host population size and the mean number of monogenean species per fish in the crucian carp populations from 9 ponds in Finland. (B) Relationship between host population size and the mean abundance of monogeneans per fish in the crucian carp populations from 9 ponds in Finland.

somewhat curvilinear pattern of points in Fig. 3 even suggests that the monogenean populations 'explode' beyond a host population size of 10 000 individuals. In open, marine systems, things may be very different. Indeed, there is evidence that fish density matters: fish species that live in schools, i.e. in patches of high host densities, harbour more monogenean or other ectoparasite species than solitary fish species (Caro, Combes & Euzet, 1997; Sasal & Morand, 1998; Raibaut, Combes & Benoit, 1998). It must be pointed out that in our system, actual fish densities may have been underestimated. Because individual fish can aggregate in space for behavioural or other reasons, dividing fish numbers by pond volume

ignores the possibility that the fish population only occupies a small part of that volume. Thus the potential importance of fish density for monogenean transmission cannot be excluded.

Crucian carp display considerable phenotypic plasticity, i.e. each population adjusting the mean length of fish in relation to the population density; this leads to a situation where the average length of the fishes varies greatly among different ponds (see Holopainen & Pitkänen, 1985 and Paszkowski *et al.* 1990). The larger the fish, the more parasites they generally harbour, as reported in most parasite studies (see e.g. Bagge & Valtonen, 1999 and Koskivaara, Valtonen & Prost, 1991). In the present system, however, it was clearly host population size that mattered, not host body size or density.

Monogenean species are among the most host specific parasites. The specificity of the present 4 species in crucian carp is very strict. *Dactylogyrus formosus*, *D. wegeneri* and *D. intermedius* were never recorded on any other cyprinid species except in *Carassius auratus* gibelio among the 132 reported cyprinid species or subspecies (Gusev, 1985). Similarly *G. carassii* was found in only 3 cyprinid species in additon to crucian carp. Compared to other reports in the literature, the component communities of the crucian carps in the present study is depauperate. Bykhovskaya-Pavlovskaya *et al.* (1962) and Gusev (1985), reported that the total number of species recorded in crucian carp was 69 species, from which 8 were dactylogyrids and 2 were gyrodactylids. Trematodes represent the dominant group with 19 species. This indicates that these earlier records are based on samples consisting of both lake and pond types of crucian carp.

Why were so few parasites found in this study? One of the most important factors influencing the parasite species richness in fish populations is the abiotic environment. In Northern and Eastern Europe, pond-type crucian carps spend one third of their life-time in anoxic conditions close to the freezing point. Here we show that a very small number of parasite species survives in these conditions. As far as we know, only Dzidziul (1973) and Kazubski (1982) have studied the parasites of the pond type crucial carps in Czechoslovakia and Poland, respectively. In our study, in addition to monogeneans, no other metazoan parasites were found except an accidental finding of Argulus foliaceus. The lack of many parasite groups might be also due to the very poor invertebrate fauna of the small lakes as assumed in the work of Petrushevski & Bykhovskaya (1935) and Bykhovskaya (1936), who studied the parasite fauna of fishes from the small, isolated lakes of Karelia (summarized in Dogiel, 1961, pp. 6–7).

It is difficult to explain why the dominant monogenean species varied among the ponds. It may be due to chance colonization events (Kennedy, 1990);

alternatively, the number of monogenean individuals in the infracommunities may be high enough to induce competition between species and depress the population of some species (Hudson *et al.* 2002). In the present data set, *D. intermedius* is missing from 3 ponds and it is extremely rare in one more pond. However, interspecific competition is not thought to be important in ectoparasitic communities of fish (Anderson *et al.* (1993), Bagge & Valtonen (1996, 1999), Geets, Coene & Ollevier (1997), Gutiérrez & Martorelli (1999), Hayward, Lakshmi Perera & Rohde (1998) and Rohde *et al.* (1994), among others). Only signs of competition have been reported to date, observed as a change of niche width by Koskivaara, Valtonen & Vuori (1992) and as negative interactions between 3 species by Gutiérrez (2001). In our system, stochastic events may be responsible for the substantial variation in the relative abundance of species among ponds.

Our ponds have been fragmented and isolated after the Ice Age (9000–8000 years ago) and the only fish that survived the extreme conditions of the ponds was crucian carp. Its ability to survive in these ponds has allowed it to avoid competition with other fish species (Paszkowski *et al.* 1990). These single-fish-species communities are likely to restrict the diversity of parasites in carp, preventing exchanges of parasites with related or non-related fish species (see Valtonen, Pulkkinen & Julkunen, 2003). These features of our system have made it ideal to determine which population parameter is most influential in determining infection levels by directly transmitted ectoparasites. In accordance with some epidemiological predictions, host population size, and not population density, has proved most important. These results suggest that beyond the minimum host density necessary for parasite transmission and maintenance, availability of new hosts may become the limiting factor regulating parasite populations.

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