





ABSTRACT

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Factors affecting the development and structure of monogenean communities on cyprinid fish

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The central aim of community ecology is to understand how the numbers and relative abundances of species in an assemblage are determined. Parasite communities in freshwater fish are often described as unpredictable, depauperate communities. However, monogenean species on the gills of cyprinid fish often form multispecies communities with even thousands of specimens on one gill-arch. The factors affecting parasite communities were studied at infra- and component community level in two cyprinid fish species; roach (*Rutilus rutilus*) and crucian carp (*Carassius carassius*). First, I discuss the environmental factors determining the numbers and species of parasites in the community. I focus on host population structure, but environmental diversity, host immunity and physiology are also discussed. Recruitment of the parasite species onto the gills is another important theme not previously studied. Second, I concentrate on the factors affecting the site-preference of the parasite specimen on the gills. Competition between species is one possible factor determining site preference. However, no competition between species was detected in any of the communities studied, in spite of unusually high abundances. Aggregation of parasites on certain host specimens is one of the most peculiar phenomena of parasite communities. Here I show that it is one of the most prominent features also at the infracommunity level. Individuals are more aggregated at lower abundances, in order better to find a mate. Other possible factors determining the occurrence on the gill-arch are the size of the gill-arch and the direction of the water current through the gills. Finally, the level of the study and its usefulness in other freshwater fish parasite communities are discussed.

Key words: Community structure; crucian carp; *Dactylogyrus* spp.; Monogenea; parasite aggregation; population density recruitment, roach.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which will be referred to in the text by their Roman numerals. I have carried out all the data collection, except that in paper II some data were collected by Mari Koskivaara, and in paper V the exposure experiment was done by Anssi Karvonen. I also analyzed and wrote papers I and II. Papers III-V were written and analyzed together with the co-authors.

- I Bagge, A. M. & Valtonen, E. T. 1996. Experimental study on the influence of paper and pulp mill effluent on the gill parasite communities of roach (*Rutilus rutilus*). *Parasitology* 112: 499-508.
- II Bagge, A. M. & Valtonen, E. T. 1999. Development of monogenean communities on the gills of roach fry (*Rutilus rutilus*). *Parasitology* 118: 479-487.
- III Bagge, A. M., Poulin R. & Valtonen, E. T. 2004. Fish population size, and not density, as the determining factor of parasite infection: a case study. *Parasitology* 128: 305-313.
- IV Bagge, A. M., Sasal, P., Valtonen, E. T. & Karvonen, A. 2004. Infracommunity level aggregation in the monogenean communities of crucian carp (*Carassius carassius*). Manuscript, submitted.
- V Karvonen, A., Bagge, A. M. & Valtonen, E. T. 2004. Parasite assemblages of crucian carp (*Carassius carassius*) – is depauperate composition explained by lack of parasite exchange, extreme environmental conditions or host unsuitability? Manuscript, submitted.

1 INTRODUCTION

1.1 What is ecological parasitology?

More than half of the known species on earth have selected a parasitic lifestyle, i.e. taking advantage of another species' resources for the existence of their own (May 1988, Windsor 1998). Thus parasitism is a much more common phenomenon than has generally been imagined. Parasites harm their hosts in several ways (Esch et al. 1990, Smyth 1994). They can affect their host's health, reproduction, mortality and even behaviour. Parasites have an important impact on survival, immunology and evolution of other species. For example *Gyrodactylus salaris* (Malmberg), a monogenean gill-parasite of salmon (*Salmo salar*), colonized many of Norway's rivers at the end of the 20th century and wiped out many of the local salmon populations (Bakke et al. 1990). However, many species co-occur in their hosts having no or minor effects on their hosts.

Few species on earth live alone, but they live in communities having positive or negative interactions with other species. Parasites are no exception. Because of the remarkable numbers of parasite species, each host often carries several parasite species providing a resource for an entire parasite community. It is thus surprising that the first community studies of parasite species were done only as late as the early 1970's. Two of the pioneers have been Canadian Professor John Holmes, who has been studying the structure of helminth communities, and English Professor Clive Kennedy, the main study object of whom has been fish parasites. They have both extended several terms from ecology to parasitology and created the base for ecological parasitology (Esch et al. 1990). Later Albert Bush, Robert May, Klaus Rohde, Robert Poulin and E. Tellervo Valtonen, to mention a few, have been involved in ecological parasite studies.

1.2 Why study monogenean communities?

From an ecological viewpoint, a community includes all of the organisms living in a prescribed area. Although the current literature is rich in community studies, there exist no thorough studies of communities (Bush et al. 2001). One reason for this is that it is difficult or impossible to outline where a community begins and where it ends. However, as the biodiversity of most ecosystems is decreasing at an alarming rate, it is crucially important to study the interactions and factors influencing communities of living organisms. Because many parasites can affect the survival of their host communities, they can have a substantial impact on the biodiversity of an area. Moreover, studies on communities of parasites can often tell us much about the ecology of the hosts in which they are found.

Monogeneans are common, host-specific ectoparasites usually living in multispecies communities on the skin, fins or gills of teleost fishes. They are hermaphrodites with a direct life-cycle and thus the infracommunity, i.e. the parasites within one fish specimen, of monogeneans are easy to define compared with communities of free-living organisms, and moreover replicates are often easily available. Monogenean communities are thus considered as a good tool for studying interactions and factors operating in community ecology (Rohde 1991).

The central aim of community ecology has been and remains, the understanding of factors determining the number of species in an assemblage, and their relative abundance (e.g. May 1975, Pielou 1975, Tokeshi 1999, Weither & Keddy 1999). A number of hypotheses and models have been formulated to explain observed patterns of parasite communities (see e.g. Bush et al. 2001). It is probably true that each of the hypotheses and models is explaining some of the observed patterns, in some of the hosts, at some time. However, a small but increasing number of monogenean community studies suggest that monogenean communities are generally not structured by competition nor by cospeciation with their hosts (Rohde 1991, Sasal & Morand 1998). Monogeneans seem to specialise on large hosts, which might be considered predictable resources or easy target (Morand et al. 2002).

1.3 The level of the study

In community ecology studies, the level considered in the study is crucial. Factors operating at the infracommunity level differ essentially from factors important at the component community level, i.e. the ensemble of populations of all parasite species exploiting the host population at one point of time (Bush et al. 1997). At the level of infracommunities important factors affecting community structure in general niche size, saturation, isolationism, recruitment

and loss of parasites, number of congenics, competition (in terms of changes in abundances), other positive or negative intra- or interspecific associations, aggregation, and mating 'rendezvous', i.e. parasites aggregate to ensure mating. In addition, the vulnerability and immune system of the host determines if the parasite is able to attach to the host. The richness and composition of one parasite infracommunity is, however, often the product of stochastic events and several infracommunities have to be studied for understanding any patterns (Kennedy 1990, Poulin 1998).

At the component community level, important factors affecting community richness include parasite exchange between populations, richness and population dynamics of intermediate and main host populations, the size of the habitat, colonizing ability, aggregation, distance between populations, stochastic events and historical contingencies i.e. the time-scale (Kennedy 1990, Poulin, 1998). Moreover, many external factors such as water quality, temperature, salinity and local habitat characteristics are important.

1.4 The aim of the study

This study continues the substantial work done by Dr. Mari Koskivaara from the late 1980s to the beginning of the 1990s in describing the basics of monogenean communities of fish species, mainly roach (*Rutilus rutilus*), in central Finland. She determined the species and their composition in the Rautalampi river and lake system and observed seasonal changes and interactions between the species (see Koskivaara & Valtonen 1991, 1992, Koskivaara et al. 1991, 1992). This laid good foundations for this work.

The first paper of this thesis tested experimentally two findings of Koskivaara & Valtonen (1992): first the lack of interaction between gill parasite species in summer, and second the fact that the abundance and prevalence of monogenean species on roach were increased in a lake polluted with paper and pulp mill effluents. Paper I presents an infracommunity level study concerning both the interaction between species and how water quality affect the composition of monogenean communities. Paper II is an infracommunity level study following the recruitment and composition of gill parasite communities. I followed the development and composition of monogenean community on the gills of roach fry during their first summer. Recruitment of parasite species on to the gills has not been previously reported in the literature. I also followed the recruitment of different species both in the laboratory and in nature. A further aim was to evaluate the dissemination capacity and the colonization ability of monogeneans.

The following three papers deal with monogenean communities of crucian carp (*Carassius carassius*). Crucian carp can be found in small ponds under extreme conditions; such ponds are often characterised by brown water, low pH, shallow depth and hypoxia during the long northern winter, making them

uninhabitable for most other fish species but suitable for crucian carp, because of their unique tolerance of anoxia (Holopainen et al. 1986, Tonn et al. 1990). Crucian carp was chosen because it was rather easy to outline the factors influencing the 9 isolated ponds studied in Central and Eastern Finland, and thus it was possible to detect and weight most factors influencing the monogenean communities. Paper III presents a component community level study, as does paper V, where I compared the parasite communities of the pond-type crucian carp to the fauna of crucian carp living in a typical lake environment in coexistence with other fish species. I thus had an ideal natural experiment of populations living in isolated, extreme conditions compared with more diverse and less isolated environments. Additionally crucian carp were exposed to hundreds of *Diplostomum spathaceum* cercariae to test whether the fish resisted infection. Paper IV is an infracommunity level study where I pooled the parasite communities from 9 ponds in order to study aggregation at different abundance levels. Despite the distinctive feature of aggregation in most parasite-host relationships, aggregation at the infracommunity level had not previously been studied.

2 MATERIAL AND METHODS

2.1 Fish material and exposure experiments

The fish material consists of roach (*Rutilus rutilus*) and crucian carp (*Carassius carassius*). The 581 roach were collected in 1992 from Lake Peurunka in the Rautalampi river and lake system and the River Rutajoki (in Central Finland, flowing via Lake Päijänne to the Gulf of Finland). Crucian carp were sampled during 1998-2000 and in 2003, yielding 540 fish from 9 ponds and 7 lakes in Central and Eastern Finland. The fish were collected with fish traps or by angling and killed in the laboratory immediately prior to examination and determination of length and weight.

For the experiment in Paper I, 81 roach (mean length 164 mm) were caught on 23 May 1992 from the unpolluted lake Peurunka and kept in a cage for two weeks in order to establish homogenous parasite populations. Prior to the transfer (4.6.), 9 roach were examined, 38 fish were left in the unpolluted lake and 34 were transferred to a polluted lake Saravesi (connected to lake Peurunka) to a similar cage. Fish were handled identically in both cages and fed daily with pelleted dry food. Five fish were examined weekly from each lake from the beginning of July until 17 August.

The material for Paper II was collected in the summer of 1992 from the small, humic River Rutajoki, flowing via Lake Päijänne to the Gulf of Finland, and from a fish farm connected to the river. Approximately 20 roach fry were captured weekly from the river between 25 June and 6 October (totalling 291 fish). Additionally, roach fry were raised in the fish farm from naturally fertilized eggs collected from a pond connected to the river and moved to two 500 l flow-through tanks in the fish farm. Unfiltered river water was pumped to the fish farm separately to each tank. The distance between the river and the tanks was 120 m. Fish were fed daily with commercial fish food. The number of fry and thus the density was higher in Tank 1. The first fish were studied from Tank 1 10 days after hatching, and later 8-21 fry were studied at 2-7 days intervals so that all of the fry had been examined by the end of July.

Crucian carp were sampled from nine ponds (area 0.02-1.5 ha) and seven lakes (area 23-250 ha) using fish traps (Paper III, V). The surface area, depth and distance from each pond to the nearest lake were determined. The size of the crucian carp population was estimated using the mark 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 are conical. The number of fish/m³ was then used as a measure of fish population density.

For the exposure experiment in Paper V, the crucian carp were collected from one of the ponds (P3) and exposed to *Diplostomum spathaceum* cercariae in the laboratory. Parasite cercariae were obtained from several naturally infected *Lymnaea stagnalis* by allowing the snails to release cercariae in a small amount of water for three hours. The cercarial suspensions from each snail were pooled and cercarial density in the combined suspension was estimated from ten 1 ml sub-samples. Prior to exposure, the eyes of the fish were studied with a slit-lamp microscope under anaesthesia (MS-222 as anaesthetic) to ensure that fish were free from *D. spathaceum* infection (see Karvonen et al. 2004a,b for methodological details). Individual, randomly selected fish (mean length \pm SE: 102.6 \pm 1.6 mm) were then exposed to 50, 100, 150, 300, 500 and 1000 cercariae in 1 l of aerated water for 30 min providing five replicate fish for each treatment. In addition, to determine the tolerance limit for the fish, single fish were also exposed to five extreme cercarial doses, which ranged from 2900 to 10300 cercariae per fish. After the exposure, fish were maintained in larger tanks for a minimum of 24 h to allow parasite establishment and subsequently studied for parasites by dissecting the eye lenses. Cercariae used here were also used in concurrent exposure experiments with rainbow trout (*Oncorhynchus mykiss*). These exposures resulted as heavy infection in the lenses of these fish (Karvonen et al. 2005), which confirms that the cercariae were infectious and of the right species.

2.2 Parasitological analyses

Ectoparasites, including monogeneans, were studied from freshly killed fish. Gill-arches from the left side of the fish were dissected. In papers I-IV each arch was divided into four sectors (numbered 1-4 from the outermost to the innermost) and a separate slide was prepared for each, totalling 16 sectors and slides per fish. All adult monogeneans were identified to the species level with a compound microscope at a magnification of 100 - 400x and all post-larval forms were counted. Identification was based on the morphometrics of the chitinized parts (haptor, male copulatory organ, vagina) of the monogenean species (Gusev 1985) and was performed on fresh slides, which is the most precise and less time-consuming method.

In Paper V, all metazoan parasites were examined from the first gill-arch, skin, fins, eyes and internal organs (heart, liver, kidney, spleen, gall bladder,

swim bladder and intestine), and identified under a microscope. Prevalence (the number of infected fish compared with all fish sampled) and mean abundance (the mean total number of parasites per studied fish) were then counted for each parasite species (Bush et al. 1997).

3 RESULTS AND DISCUSSION

3.1 External factors affecting monogenean communities

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 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 and Halvorsen 1994, Karvonen & Valtonen 2004). Pojmanska and Dzika (1987) studied parasites of bream (*Abramis brama*) affected by long-term thermal pollution and found changes in the structure of the parasite community and population dynamics. Recruitment of the monogenean *Paradiplozoon homoion* started earlier in populations of roach caught in a thermally elevated artificial lake located outside a nuclear power station (Höglund & Thulin 1989). Simkova et al. (2001) have also found water temperature to influence dactylogyrid species communities in roach in the Czech Republic. In paper I we tested experimentally the findings of Koskivaara et al. (1992) that the abundance and prevalence of monogenean species were increased in a lake polluted with pulp and paper mill effluents compared with an unpolluted lake. As predicted, in less than two months the prevalence of one species and abundance of three *Dactylogyrus* species increased significantly in the roach brought from the unpolluted lake to the polluted lake when compared to the roach treated in the same way in the unpolluted lake. Paper I thus confirms that water quality affects monogenean community and population dynamics. The reason for higher abundances and prevalences in the polluted lake is probably that roach become more susceptible to parasite infection due to an impaired immunological response of the fish (Jokinen et al. 1995, Siddall et al. 1996).

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 parasite's infective stages and new hosts (see Hudson et al. 2002 for a recent review). 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. 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). There is also some evidence that host population size or density is important for macroparasites, including several human diseases such as measles (Earn et al. 2000, Bjørnstad et al. 2002). However, 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.

Paper III took advantage of a natural system in which populations of crucian carp occur alone, with no other fish species, in a series of isolated ponds. Across the ponds, only one factor, total fish population size, explained a significant proportion of the variance in both the mean number of monogenean species per fish and the mean total abundance of monogenean individuals 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). This is probably due to the rather similar characteristics of the ponds. Distance from other lakes does not matter, at a recent time scale, however, if the ponds are isolated, there is no change or possibility for recruitment of new parasites. The result that fish population size and not density predicts infection levels, suggests that, beyond the minimum host density necessary for parasite transmission and maintenance, availability of new hosts may become the limiting factor regulating parasite populations. To my knowledge there is currently no other empirical evidence that host numbers or density affects macroparasite infections among populations of the same host species in the wild, but some empirical suggesting that host population density is indeed an important predictor of both parasite abundance and parasite species diversity has been found in comparative studies across related host species (Morand & Poulin 1998, Arneberg et al. 1998, Arneberg 2001, 2002). In Paper II the same phenomenon was seen when I compared the numbers of species or abundances; in the tank A, where the number of roach fry was highest, the number of parasite species and specimens were also highest. This is explained by the possibility of the recruitment of the parasites, which is highest in the most dense (and numerous) population.

In paper V, I compared the parasite assemblages of pond-type crucian carp with lake populations coexisting with other fish species. As predicted, crucian carp had more diverse species composition in lakes, which supports the hypothesis of increased opportunities for parasite exchange with other fish species and better environmental conditions for the parasites. Also the food composition of crucian carp in lakes consists mainly of invertebrates and plant material, whereas in the ponds the food consists mainly of phytoplankton, planktonic crustaceans and detritus (Holopainen et al. 1997). The lack of intermediate hosts explains the absence of some parasite species, but nevertheless, for instance diplostomids were found in only a few fish individuals and in very low numbers. In the laboratory, experimental exposure trials with the eye fluke *Diplostomum spathaceum* indicated that crucian carp were totally resistant to infection, which suggests that the low number of these parasites in crucian carp was due to physiological unsuitability of the host. To obtain better understanding of the mechanism underlying the formation of parasite assemblages in these fish, further studies on the relationships between the unique physiology of crucian carp and infection success by other parasites are needed.

3.2 Internal factors affecting monogenean communities

The co-occurrence of species with similar ecological demands is often inhibited by interspecific competition (see Brown 1975, Schoener 1986 and Werner 1986). Koskivaara & Valtonen (1992) and Koskivaara et al. (1992) found species-specific differences between dactylogyrids in the site preferences on the gill-arches of roach during spring when the species diversity and the abundance of infection were highest. In Paper I, I tested the prediction of Koskivaara et al. (1992) and found no interaction between the species on the gills of roach during the summer period. This suggests that there is plenty of room and resources on the gills of roach, and what parasite species are able to occupy suitable specific microhabitats, at least outside the spring period. This may be related to the very small size of the dactylogyrids (less than 1.0 mm). The present monogenean species appear to be well adapted to the roach host since Valtonen et al. (1997) and Haaparanta et al. (1998) found no evidence of a cellular response by the host when studying the gills histologically.

An important factor determining the location of parasites on the gills is considered to be differences in the water currents over the gills (Syudam 1971, Hanek & Fernando 1978). Wootten (1974) studied the location of *Dactylogyrus amphibothrium* on the gills of ruffe (*Gymnocephalus cernuus*), and found that this parasite prefers the middle gill-arches where the water current is strongest. He suggested, however, that the site of *D. amphibothrium* on the gills does not depend on the stronger water current but on the greater area available on the middle gill-arches which enables the attachment of more parasites. The gill-arches most preferred by dactylogyrids of roach are also the middle gill-arches

which are largest (Koskivaara et al. 1992). Also in Paper I, considering adult roach gill parasite composition, the most preferred gill-arches were the middle gill-arches. Conversely, for the monogeneans of crucian carp, the first gill-arch was the most preferred for most species (see Paper IV). This is explained by the largest area of the first gill-arch in crucian carp and apparently also the water current. On the gills of whiting (*Merlangus merlangus*), Arme & Halton (1972) noticed that the monogenean *Diclidophora merlangi* prefers the first gill-arches, but in multiple infections specimens were also found on other gill-arches. They stated that water current may be an important factor in determining the distribution of infections with one parasite, but when intensity is higher, other factors such as mucus secretion by the gills, may be important. We also found a significant increase in niche size when intensity of infection was high (Paper IV). The reason for expanding the niche is possibly that the monogenean species need not be aggregated when intensity of infection is high, in order to find mates (Rohde 1991). The possibility of niche expansion also indicates that there is plenty of room on the gills for these tiny parasites.

In Paper II we studied the recruitment of monogenean species to roach fry during the first summer of their lives, in order to analyse the construction and development of infracommunities. Poulin (1998) suggested that studying species interactions and recruitment of the parasites would be the only way to analyse the construction of infracommunities. In Paper II the first parasite appeared on the gills of 12 mm long fish fry, when the ultrastructure of the gill lamellae was developed (the fry being about 3 weeks old). According to Izjumova (1956), the main factors influencing the invasion of the gills by monogeneans are morphology and especially the degree of differentiation of the branchial apparatus and the fine-scaled histological structure of the gills. I found that the most preferred gill-arches on the gills of fingerlings were the middle gill-arches for *D. nanus* and *D. micracanthus* and the first gill-arch for *Dactylogyrus* juveniles. I stated that this is because of the greater likelihood of the free-swimming juvenile stages to attach the outermost parts of the gills when locating on the fish host. A new monogenean generation appeared to be recruited at approximately 3-4 weeks intervals. The first species appearing on the gills was *D. nanus* and *D. crucifer*, the other species, appeared later on in summer. Surprising was also high numbers of *Gyrodactylus* specimens on gills, which may be connected with the undeveloped immune system of young fish (Ellis 1988). The oncomiracidia stages of monogeneans were able to disseminate and colonize over 120 m from the river to the farm. The recruitment and composition of species was also affected by the temperature (seasonality), water quality and coincidence. No interactions between the monogenean species were detected and the numbers of dactylogyrids remained low compared with adult roach monogenean communities. A lack of competition was suggested; for example, *D. crucifer* appeared on the gills at that time when abundance of *D. nanus* was at its' highest.

A lack of competition was also found in monogenean communities of crucian carp (Paper IV); no negative interactions between the three *Dactylogyrus* species were detected. Our results thus strengthen the hypothesis that

monogenean communities are a subset of species occurring at the same place. They also indicate that there is plenty of room on the gills. We studied the hypothesis of Rohde (1991), that monogenean species are aggregated to ensure cross-fertilisation, expecting that when abundances are high they would be less aggregated (i.e. more widely dispersed on the gills) since the distance to a neighbouring mate is shorter. This happened to be the case, although all *Dactylogyirus* species seemed to prefer the outermost gill-sections. The niche expansion leads to avoidance of competition, since there is a lot of room on the gills, and a possibility for several species to use the same resources. Is the guild on the gills a cause or a consequence of shared past, or just a coincidence. This question remains open. Since aggregation at the infracommunity level has not been studied before, it would be interesting to establish how common a phenomenon this is. One of the main features of ecological parasitology is the aggregation of parasites in a few specimens within the host population (see e.g. Morand et al. 1999).

Niche diversification has repeatedly been reported in most monogenean studies (Rohde et al. 1994, Geets et al 1997, Gutiérrez 2001, Gutiérrez & Martorelli 1999, Hayward et al. 1998). However, selective site segregation, in which the parasite species occupies a restricted microhabitat, independent of the presence or absence of other parasite species, is far more common than interactive site segregation, which has mainly been detected from endoparasites (Holmes 1973, Bush & Holmes 1986, Stock & Holmes 1988, Bush et al. 1990). Indeed, the findings of interspecific or intraspecific interactions are highly sensitive to study scale. Dactylogyrids are very small in relation to the size of their habitat and interactions between individuals are likely to take place even at the scale of individual gill lamellae. I have studied monogeneans at several scales: from the scale of one fish to the scale of 1/16 part of the gills. I consider that dividing each gill-arch to four sections is a reasonable method for studying these rather sessile species. It is probable that juveniles tend to move closer to conspecific individuals as they mature, but not very likely that they move very far, because of the risk of being driven away from the lamellae with the water effluent. When the abundance of monogeneans decreases, the number of empty niches increases and parasites occupy much narrower sites (Rohde 1979, 1991). The site preference of the microhabitat does not usually change when the abundance changes (see references above). Since it was possible to detect aggregation and microhabitat preference in the infracommunity studies, this indicates that the level of the study was appropriate. The observations that microhabitats become narrower (aggregation increases) when the abundance decreases and adults are more aggregated than juveniles give support to the conclusion that the major problem for most ectoparasites is not to avoid competition but to find suitable sites for feeding and mating, which strongly supports the theory of reinforcement of reproductive barriers as an important function of niche segregation (Rohde 1991). Selective site segregation and the lack of competition are important factors leading to a rich and multispecies community with the possibility of several species living together (see e.g. Euzet & Combes 1998, Sasal & Morand 1998, Morand et al. 2002).

4 CONCLUSIONS

This thesis consists of five papers concerning monogenean communities on freshwater cyprinid fish. The purpose of the thesis was to detect the main factors determining the structure and development of these communities. Understanding the factors underlying the development of parasite communities may help in detecting complicated interactions between species in ecosystems and to restrict serious parasite invasions, such as *Gyrodactylus salaris*. Gill-parasites of cyprinid fish form multispecies and rich infracommunities. Despite the high numbers of specimens, there were no negative interactions between the species, nor competition in terms of abundance changes. Instead, aggregation to ensure cross-fertilisation was found to be an important factor determining the distribution on the gills of infrapopulations of each species. This was supported by the evidence that when the abundances are high, individuals tended to be less aggregated and niche size increased, because the distance to a neighbouring mate is shortened.

The main factors at component community level are those affecting the invasion and transmission rate of these direct life-cycle parasites. The most important is the size of the host population. Comparing pond-type crucian carp parasite populations with those in lakes, we found, as expected, that parasite populations in lakes were more diverse. This is likely to be because a more diverse environment maintains a more diverse parasite fauna. Also the diet of the fish is more diverse in lakes, than in ponds, where the food consists mainly of planktonic crustaceans. However, in lakes 99 % of the parasites found were also monogeneans. It seems that the unique physiology of crucian carp can restrict the number of parasite species, as we found in an exposure experiment with the eye-fluke (*Diplostomum spathaceum*).

Finally, many environmental factors, such as the quality of water and seasonality, affect monogenean communities. We showed experimentally that the abundances of monogenean species increased in a polluted lake compared to an unpolluted lake. The reason for this may be chemical effects on the immunological capacity of fish, for example by impairing the development of antibodies against parasites.

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YHTEENVETO (Summary in Finnish)

Kidusloisyhteisöjen rakenteeseen ja kehitykseen vaikuttavat tekijät sisävesikalvilla

Yhteisöekologian yksi keskeinen tavoite on ymmärtää, kuinka erilaiset eliöyhteisöt muodostuvat ja mitkä tekijät vaikuttavat yhteisöjen koostumukseen ja runsauteen. Eliöyhteisöjen monimuotoisuuden väheneminen on tällä hetkellä yksi huolestuttavimmista piirteistä maapallon ekosysteemeissä. Loiset muodostavat maapallon eliöistä merkittävän osan ja kuuluvat lähes jokaisen eliön elämään ja aivan jokaiseen eliöyhteisöön. Koska loiset vaikuttavat myös isäntäeliöihin monin tavoin, on tärkeää tietää, mitkä tekijät vaikuttavat loisyhteisöjen syntymiseen ja rakenteeseen. Sisävesikalvojen loisyhteisöjä on usein kuvattu sattumanvaraiseksi eri loisyksilöiden kokoonpanoksi. Kuitenkin monien särkikalvojen kidusloiset muodostavat monilajisen ja runsaan yhteisön. Tämä väitöskirja koostuu viidestä artikkelista, jotka käsittelevät särjen (*Rutilus rutilus*) ja ruutanan (*Carassius carassius*) kidusloisyhteisöjä ja niihin vaikuttavia tekijöitä eri yhteisötasoilla. Tarkoituksena oli selvittää sekä kokeellisin että kuvailevin keinoin niitä tekijöitä, jotka vaikuttavat näiden loisyhteisöjen muodostumiseen ja kehittymiseen.

Infrayhteisötasolla (yhden kalan kaikki loiset) merkittävimäksi tekijäksi osoittautui aggregoituminen eli yksilöiden sijoittuminen toistensa läheisyyteen; mitä vähemmän loisyksilöitä, sen aggregoituneemmin ne sijaitsevat kiduksella. Tämä siksi, että niiden ristisiitos ja näin ollen lisääntyminen varmistuisi. Sijainti kiduksilla määräytyy mahdollisesti myös vedenvirtauksen ja muiden kiduskaaren ominaisuuksiin liittyvillä tekijöillä. Sen sijaan loisten välisillä interaktioilla ja kilpailulla ei näytä olevan merkitystä loisyhteisön muodostumiseen tai rakenteeseen. Populaatiotasolla tärkeimmiksi osoittautuivat tekijät, jotka vaikuttavat näiden suoran elinkierron omaavien loisten siirtymiseen isännästä toiseen. Näistä merkittävin on isäntälajin tiheys, mutta myös muiden tekijöiden kuten esimerkiksi isäntäpopulaation koon, eristyneisyyden, sattuman, järven koon ja elinympäristön monimuotoisuuden merkitystä pohditaan. Näiden lisäksi loisyhteisöjen rakentumiseen vaikuttavat isäntälajin immunitettivaste, johon vaikuttavat muun muassa veden laatu ja lämpötila, sekä isännän fysiologiset tekijät.

REFERENCES

- Arme, C. & Halton, D. W. 1972. Observations on the occurrence of *Dicliophora merlangi* (Trematoda; Monogenea) on the gills of whiting, *Gadus merlangus*. *J. Fish. Biol.* 4: 27-32.
- Arneberg, P. 2001. An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* 24: 352-358.
- Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematods of mammals. *Ecography* 25: 88-94.
- Arneberg, P., Scorpington, A., Grenfell, B. T. & Read, A. F. 1998. Host densities as determinants of abundance in parasite communities. *Proc. R. Soc. Lond. B* 265: 1283-1289.
- Bakke, T. A., Jansen, P. A. & Hansen, L. P. 1990. Differences in the host resistance of Atlantic salmon (*Salmo salar*) stocks to the monogenean *Gyrodactylus salaris* Malmberg, 1957. *J. Fish Biol.* 37: 577-587.
- Bjørnstad, O. N., Finkenstadt, B. F. & Grenfell, B. T. 2002. Dynamics of measles epidemics: estimating scaling of transmission rates using a time series SIR model. *Ecol. Monographs* 72: 169-184.
- Brown, J. H. 1975. Geographical ecology of desert rodents. In: Cody, M. L. & Diamond, J. M. (eds.), *Ecology and evolution of communities*: 315-341. Cambridge, Belknap Press.
- Bush, A. O. & Holmes, J. C. 1986. Intestinal helminths of lesser scaup ducks: an interactive community. *Can. J. Zool.* 64:142-152.
- Bush, A. O., Aho, J. M. & Kennedy, G. R. 1990. Ecological versus phylogenetic determinants of helminth parasite community richness. *Evol. Ecol.* 4: 1-20.
- Bush, A. O., Fernandez, J. C., Esch G. W. & Seed, J. R. 2001. *Parasitism. The diversity and ecology of animal parasites*. Cambridge University Press, Cambridge. 566 p.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. & Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83, 575-583.
- Earn, D. J. D., Rohani, P., Bolker, B. M. & Grenfell, B. T. 2000. A simple model for complex dynamical transitions in epidemics. *Science* 287: 667-670.
- Esch, G. W., Bush, A. O. & Aho, J. M. 1990. *Parasite communities: patterns and processes*. Chapman & Hall, London. 335 p.
- Ellis, A. E. 1988. *Fish vaccination*. Academic Press, London.
- Euzet, L. & Combes, C. 1998. The selection of habitats among the monogenea. *Int. J. Parasitol.* 28: 1645-1652.
- Geets, A., Coene, H. & Ollevier, F. 1997. Ectoparasites of the whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835) of the Kenyan Coast: Distribution within the host population and site selection on the gills. *Parasitology* 115: 69-79.

- Gusev, A. V. 1985. Keys to Parasites of Freshwater Fish of the USSR Vol 2. Parasitic Metazoa, Leningrad, Nauka. (In Russian.)
- Gutiérrez, P. A. 2001. Monogenean community structure on the gills of *Pimelodus albicans* from Río de la Plata (Argentina): a comparative approach. *Parasitology* 122, 465-470.
- Gutiérrez, P. A. & Martorelli, S. R. 1999. The structure of the monogenean community on the gills of *Pimelodus maculatus* in Río de la Plata (Argentina). *Parasitology* 119, 177-82.
- Haaparanta, A., Valtonen, E. T. & Hoffmann, R. 1998. Gill anomalies of perch and roach from four lakes in Central Finland. *J. Fish. Biol.* 50: 575-595.
- Hartvigsen, R. & Halvorsen, O. 1994. Spatial patterns in the abundance and distribution of parasites of freshwater fish. *Parasitol. today* 10: 28-31.
- Hanek, G. & Fernando, C. H. 1978. Spatial distribution of gill parasites of *Lepomis gibbosus* (L.) and *Ambloplites rupestris* (Raf.). *Can. J. Zool.* 56: 1235-40.
- Hayward, G. J., Lahksmi Perera, K. M. & Rohde, K. 1998. Assemblages of ectoparasites of a pelagic fish, slimy mackerel (*Scomber australasicus*), from south-eastern Australia. *Int. J. Parasitol.* 28: 263-273.
- Höglund, J. & Thulin, J. 1989. Thermal effects on the seasonal dynamics *Paradiplozoon homoion* (Bychowsky & Nagibina, 1959) parasiting roach *Rutilus rutilus* (L.). *J. Helminthol.* 63: 93-101.
- Holmes, J. C. 1973. Site selection by parasitic helminths: Interspecific interactions, site segregation, and their importance to the development of helminth communities. *Can. J. Zool.* 51: 333-347.
- Holopainen, I. J., Hyvärinen, H. & Piironen, A. K. 1986. Anaerobic wintering of Crucian carp (*Carassius carassius*, L.). II Metabolic products. *Comp. Bioch. Physiol.* 83A: 397-406.
- Holopainen, I. J., Tonn, W. M. & Paszkowski, C. A. 1997. Tales of two fish: the dichotomous biology of (*Carassius carassius* (L.)) in Northern Europe. *Ann. Zool. Fennici* 34: 1-22.
- Hudson, P.J., Rizzolli, A., Grenfell, B.T., Heesterbreek, H. & Dobson, A.P. 2002. The ecology of wildlife diseases. Oxford University Press, Oxford.
- Izjumova, N. A. 1956. Materialy po biologii *Dactylogyrus vastator* Nybelin. *Parazitologitseskij Sbornik otdel Parazitologii i Zoologitseskogo Instituta an USSR* 16. (In Russian.)
- Jokinen, E. I., Aaltonen, T. M. & Valtonen, E. T. 1995. Subchronic effects of pulp and paper mill effluents on the immunoglobulin synthesis of roach *Rutilus rutilus*. *Aq. Tox. Env. Safe.* 32: 219-263.
- Karvonen, A. & Valtonen, E. T. 2004. Helminth assemblages of whitefish (*Coregonus lavaretus*) in interconnected lakes: similarity as a function of species specific parasites and geographical separation. *J. Parasitol.* 90: 471-76.
- Karvonen, A., Seppälä, O. & Valtonen, E. T. 2004a. Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. *Parasitology* 129: 159-164.

- Karvonen, A., Seppälä, O. & Valtonen, E. T. 2004b. Eye fluke - induced cataract formation in fish: quantitative analysis using an ophthalmological microscope. *Parasitology* 129: 473-478.
- Karvonen, A., Paukku, S., Seppälä, O. & Valtonen, E. T. 2005. Resistance against eye flukes: naïve versus previously infected fish. *Parasitol. Res.* 95: 55-59.
- Kennedy, C. R. 1978. An analysis of the metazoan parasitocoenoses of brown trout *Salmo trutta* from British lakes. *J. Fish Parasitol.* 13: 255-263.
- Kennedy, C. R. 1990. Helminth communities in freshwater fish: structured assemblages or stochastic assemblages? In: Esch, G. W., Bush, A. O. & Aho, J. M. (eds.), *Parasite communities: patterns and processes*: 131-156. London.
- Koskivaara, M. & Valtonen, E. T. 1991. Paradiplazoon homoion (Monogenea) and some other gill parasites on roach (*Rutilus rutilus*) in Central Finland. *Aqua Fennica* 21:137-43.
- Koskivaara, M. & Valtonen, E. T. 1992. *Dactylogyrus* (Monogenea) communities on the gills of roach in Central Finland. *Parasitology* 104:263-72.
- Koskivaara, M., Valtonen, E. T. & Prost, M. 1991. *Dactylogyrids* on the gills of roach in Central Finland: features of infection and species composition. *Int. J. Parasitol.* 21: 47-55.
- Koskivaara, M., Valtonen, E. T. & Vuori, K.-M. 1992. Microhabitat distribution and coexistence of *Dactylogyrus* species (Monogenea) on the gills of roach. *Parasitology* 104: 273-281.
- Marcogliese, D. J. & Cone, D. K. 1991. Importance of lake characteristics in structuring parasite communities of salmonids from insular Newfoundland. *Can. J. Zool.* 69: 2962-2967.
- May, R. M. 1975. Patterns of species abundances and diversity. In: Cody, M. L. and Diamond, J. M. (eds.), *Ecology and evolution of communities*: 81-120. Harvard University Press, Harvard.
- May, R. M. 1988. How many parasites are there on the earth? *Science* 214:1441-1449.
- Morand, S., Poulin, R., Rohde, K. and Hayward, C. 1999. Aggregation and species coexistence of ectoparasites of marine fishes. *Int. J. Parasitol.* 29: 663-672.
- Morand, S. & Paulin, R. 1998. Density, bodymass and parasite species richness of terrestrial mammals. *Evol. Ecol.* 12: 717-727.
- Morand, S., Simkova, A., Matejusova, I., Plaisance, L., Verneau, O. & Desdevises, Y. 2002. Investigating patterns may reveal processes: evolutionary ecology of ectoparasitic monogeneans. *Int. J. Parasitol.* 32: 111-119.
- Pielou, E. C. 1975. *Ecological diversity*. Wiley Interscience, New York.
- Pojmanska, T. & Dzika, E. 1987. Parasites of bream (*Abramis brama* L.) from the lake Goslawskie (Poland) affected by long-term thermal pollution. *Acta Parasitol. Pol.* 32: 139-61.
- Poulin, R. 1998. *Evolutionary ecology of parasites. From individuals to communities*. Chapman & Hall, London.

- Rohde, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *Am. Nat.* 114: 648-671.
- Rohde, K. 1991. Intra- and interspecific interactions in low density populations in resource-rich habitats. *Oikos* 60: 91-104.
- Rohde, K., Hayward, C., Heap, M. & Gosper, D. 1994. A tropical assemblage of ectoparasites: gill and head parasites of *Lethrinus miniatus* (Teleostei, Lethrinidae). *Int. J. Parasitol.* 24: 1031-1053.
- Sasal, P. & Morand, S. 1998. Comparative analysis: a tool for studying monogenean ecology and evolution. *Int. J. Parasitol.* 28: 1637-44.
- Schoener, T. W. 1986. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-26.
- Siddall, R., Koskivaara, M. & Valtonen, E. T. 1996. *Dactylogyrus* (Monogenea) infections on the gills of roach (*Rutilus rutilus* L.) experimentally exposed to paper and pulp mill effluent. *Parasitology* 114: 439-446.
- Simkova, A., Sasal, P., Kadlec, D. & Gelnar, M. 2001. Water temperature influencing dactylogyrid species communities in roach, *Rutilus rutilus*, in the Czech Republic. *J. Helminthol.* 75: 373-383.
- Smyth, J. D. 1994. *Introduction to Animal Parasitology*. Cambridge.
- Stock, T. M. & Holmes, J. C. 1988. Functional relationships and microhabitat distributions of enteric helminths of crebses (Podicipedidae): the evidence for interactive communities. *J. Parasitol.* 74(2):214-227.
- Syudam, E. L. 1971. The micro-ecology of three species of monogenetic trematodes of fishes from the Beaufort-cape Hatteras area. *Proc. Helminthol. Soc. W.* 38: 240-6.
- Tokeshi, M. 1999. *Species coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.
- Tonn, W. M., Magnuson, J. J., Rask, M. & Toivonen, J. 1990. Intercontinental comparison of small-lake fish assemblages: the balance with local and regional processes. *Am. Nat.* 136: 345-375.
- Valtonen, E. T., Holmes, J. C. & Koskivaara, M. 1997. Eutrophication, pollution and fragmentation: effects on parasite communities in roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in four lakes in Central Finland. *Can. J. Aqu. Fish. Sci.* 54: 572-585.
- Weither, E. & Keddy, P. 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.
- Werner, E. E. 1986. Species interactions in freshwater fish communities. In: Diamond, J. & Case, T. J., *Community ecology*: 344-58. New York. Harper & Row.
- Windsor, D. A. 1998. Most of the species on earth are parasites. *Int. J. Parasitol.* 28: 1939-1941.
- Wootton, R. 1974. The spatial distribution of *Dactylogyrus amphibothrium* on the gills of ruffe *Gymnocephalus cernuus* and its relation to the relative amounts of water passing over the parts of gills. *J. Helminthol.* 48: 167-74.