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Differences Between Four Lakes and the Nature of Dactylogyrid Communities

Academic Dissertation

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MONOGENEANS AND OTHER PARASITES ON THE GILLS OF ROACH (RUTILUS RUTILUS) IN CENTRAL FINLAND
- DIFFERENCES BETWEEN FOUR LAKES AND THE NATURE OF DACTYLOGYRID COMMUNITIES

Mari Koskivaara

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1173 roach were studied between August 1985 and April 1989 for gill parasites. The entire material was used to analyse the occurrence of *Paradiplozoon homoion* on the gills, while gyrodactylid monogeneans on the gills and fins were studied only during the years 1986-87 (767 fish). The dactylogyrid monogenean fauna was studied during 1986 and 1988 (660 roach) and in relation to the community level, during 1988 and 1989 (293 roach). For the material from 1986 the occurrence of other gill parasites was also analysed.

The material was collected from four interconnected lakes, one of which is eutrophic and polluted due to a paper and pulp mill, one of the lakes is oligotrophic and in a natural state and two are eutrophic.

The prevalence of *P. homoion* infection was found to be lowest (1.9%) in the polluted and highest (8.5%) in one of the eutrophic lakes. The abundance was low and no clear seasonal variation was found. Worms with eggs were found from June to September. The proportion of larvae of *P. homoion* was largest on the fourth gill arch, although adults of this parasite was significantly more common on the first arch.

The co-occurrence of gill parasites of roach was found to be random, except for *P. homoion* and *Ichthyophthirius multifiliis*, which were significantly positively associated.

Four *Gyrodactylus* species were found, of which *G. prostae* was the most common in all of the lakes. The total *Gyrodactylus* infection was 8.9-17% on the fins and 6.5-13.3% on the gills of roach. These

monogeneans showed a clear seasonality, with peaks in both prevalence and abundance at the beginning of June. The differing water quality of the lakes is suspected to influence the abundance and site of infection of the gyrodactylids.

Dactylogyrid monogeneans also had a clear seasonal occurrence, but because the prevalence of infection was high throughout period of the study, the seasonality was seen in only the abundance and diversity. The abundance and diversity were found to be significantly higher in the polluted lake. Nine *Dactylogyrus* species were found. *D. crucifer* and *D. nanus* were found to be the core species in all of the component communities. *D. suecicus, D. micracanthus, D. similis, D. fallax* and *D. caballeroi* were secondary species with intermediate prevalences, and *D. sphyrna* and *D. vistulae* were rare satellite species. There were differences in the composition of the *Dactylogyrus* fauna of roach in the lakes studied. The species composition of the polluted lake changed between the two years studied to be more like that of the eutrophic lakes.

When the *Dactylogyrus* fauna was studied at the community level it was found that the component communities tended to be very similar, but some differences were found. Infracommunities on roach in the polluted lake were more often dominated by *D. micracanthus*. The similarities between the infracommunities were higher within the lakes than between the lakes. The differences in dactylogyrid communities are suggested to be due to the differing water quality of the lakes. All seven of the most abundant dactylogyrid species had species-specific preferences for certain gill-arches. These preferences showed some seasonal variation. For some *Dactylogyrus* species niche breadth and species overlap appeared to be unrelated to abundance, indicating possible niche restriction by other species. It is suggested that *Dactylogyrus* communities may be interactive in nature during the peak occurrence of the species.

Key words: Monogenea; gill parasites; roach; pollution; trophic level; seasonality; community structure

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The thesis is based on the following papers, which will be referred to in the text by the Roman numerals I-V:

I. Koskivaara, M. & Valtonen, E. T. 1991: *Paradiplozoon homoion* (Monogenea) and some other gill parasites on roach *Rutilus rutilus* in Finland. - Aqua Fennica 21: 137-143.

II. Koskivaara, M., Valtonen, E. T. & Prost, M. 1991: Seasonal occurrence of gyrodactylid monogeneans on the roach (*Rutilus rutilus*) and variations between four lakes of differing water quality in Finland. - Aqua Fennica 21: 47-55.

III. 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. Parasit. 21: 565-572.

IV. Koskivaara, M. & Valtonen, E. T. 1992: *Dactylogyrus* (Monogenea) communities on the gills of roach in three lakes in Central Finland. - Parasitology 104: 263-272.

V. 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.

Contents

1 Introduction

Studies on parasites, especially fish parasites, have often been at the alpha-taxonomic level. A great deal of work has been carried out describing the parasite species occurring on different hosts in varying environments. In addition, the life-cycles of parasites which utilise intermediate hosts have received great attention.

The first work on the parasites of fish at the community level was that of Dogiel *et al.* (1961). In this work various ways of structuring fish parasite communities were studied by several Russian scientists, although the terminology which they used differed from that currently used in community studies.

Descriptive studies are obviously vital in order to gain information at even the basic level of communities never mind being able to make further conclusions on their function. Consequently, much time consuming and demanding work is necessary to find out what host and parasite species actually form the communities, and what are their prevalences, abundances and patterns of seasonal occurrence. It is also necessary to know what are the main factors in the environment which affect the hosts and their parasites. Questions on host specifity of different species are also important. Before a detailed knowledge on these factors has been acquired, it is impossible to understand the processes involved in the structuring of parasite communities.

The first to use a quantitative approach in studies on parasite communities was Holmes (1961, 1962) when studying the effects of concurrent infections on species of *Cestoda* and *Acanthocephala* in the intestine of laboratory rats. After this Holmes has by many studies promoted the field of community studies on parasites (1971, 1973, 1986, 1990). The same is also true of Kennedy (1978, 1985, 1990,), who has made profound investigations into the question of interactivity and isolation in parasite communities of fish, although only in relation to intestinal communities.

The first publication to use the currently accepted terminology of community parasitology and to review our knowledge on this field was a book published in 1990 and edited by Esch, Bush and Aho. Nevertheless, this work also deals with the helminth communities of hosts other than fish, and as usual, only parasite communities from the intestine of fish are dealt with.

The ectoparasite communities of fish have been studied for

example by Kennedy (1978), Adams (1986), Janovy & Hardin (1988), Leong & Holmes (1981), but the only person who has worked on monogenean communities at the species and infracommunity level is Rohde (1979, 1991). Rohde´s studies concentrate on marine fish monogeneans in a stable marine environment. The communities which he has studied have a very low species diversity and abundance. In marine habitats the macro-environment is very stable, and, therefore, quite different to the variable environmental conditions in the inland waters of northern latitudes.

In the following five publications (later referred to as I, II, III, IV and V) the ectoparasite fauna and, especially, *Dactylogyrus* communities on the gills of roach are studied in four (for *Dactylogyrus* communities in three) interconnected lakes. This is the first time that monogeneans of fish have been studied qualitatively at first, working out the basic population parameters, then comparing these different component communities at a quantitative level, and finally approaching the question of community structure in relation to microhabitat distribution of the dactylogyrids at the infracommunity level. The main hypothesis for these investigations was that the nature of the lake affects populations of these ectoparasites, creating variability in the structure of monogenean communities, and that the dactylogyrid communities studied are interactive in nature during the peaks in species diversity and abundance.

2 Study area

The study area is a part of a large river and lake system called the Kymijoki River System (Fig. 1, II). This kind of chain of lakes connected by narrow straits is typical of Finnish water systems. The waters finally flow through the River Kymijoki to the Gulf of Finland. The research was carried out on four small interconnected lakes. The smallest lake (Vatia) is eutrophic and polluted by waste waters from a paper and pulp mill situated in the town of Äänekoski 15 km upstream. The next two lakes downstream (Saravesi and Leppävesi) are eutrophic and in these the influence of pollution from Lake Vatia is diluted by the sedimentation in Lake Vatia itself, the oxidation of pollutants in rapids between Lakes Vatia and Saravesi and by the inflow of clean water from Lake Kuusvesi into Lake Saravesi. The fourth lake (Peurunka), situated to the side of the main water-way, is oligotrophic and in a natural state; its waters flow to Lake Vatia. It is most important in relation to this study that,

the lakes are interconnected, the migration of roach between them has been prevented for the last 30 years (by rapids, a dam and an electricity plant).

3 Material and methods

3.1 Sampling

The material was collected between August 1985 and April 1989. In 1985 samples were taken during four autumn months from three lakes The materials was published in paper I. During 1986 four lakes were sampled for eight months from February to November and the materials was published in I, II and III. Samples were collected also in 1987 from the four lakes during a six month period and published in I and II. In 1988 and 1989 three lakes were sampled and the samples were collected for eight and three months, respectively. The material from 1988 was published in I, III, IV and V, and that from 1989 in I, IV and V. The total number of roach studied was 1,173. Monthly samples normally consisted of 10 to 15 roach from each lake. The samples from Lake Vatia were the smallest and during some winter months missing, because it was not possible to catch fish at that time of the year.

The roach is known to be one of the most common fish species in all of the lakes studied. Other common species are perch (*Perca fluviatilis*), vendace (*Coregonus albula*) , whitefish (*Coregonus* spp.), ruffe (*Gymnocephalus cernuus*) and pike (*Esox lucius*) in the oligotrophic lake and perch, pike, burbot (*Lota lota*), bream (*Abramis brama*) and zander (*Stizostedion lucioperca*) in the eutrophic lakes (Kurttila and Hyvärinen 1983).

The fish were caught mainly by angling, although also gill nets were used. They were transported to the laboratory in lakewater. Only living roach were used for investigations on their parasites.

3.2 Studying the roach

From the beginning of the research period to the end of the year 1987 the

fish were studied for all parasites at the Laukaa Research Station. The fish were killed and their fins and gills from one side of the body were dissected immediately and studied under a stereo-microscope. All diplozoid, gyrodactylid and ergasilid parasites were collected and preserved, as were dactylogyrids from five infected fish in each sample from each lake. The *Dactylogyrus* spp. from rest of the fish in each sample, *Ichthyophthirius multifiliis* and glochidia were counted. Diplozoids and *Ergasilus* sp. were preserved in 70% ethanol and the dactylogyrids and gyrodactylids in ammonium picroglycerine.

During the years 1988 and 1989 dactylogyrids were identified to species from fresh material . After killing the fish the gills on the left side of the body were dissected. Then all mucus and soft parts from the gill arches were scraped on slides (several slides from each gill arch) and flattened under a cover glass. After this the slides were studied under a microscope in order to count and identify the dactylogyrids. Diplozoids were preserved on slides in ammonium picroglycerine to be stained with Mayer´s paracarmine, identified and measured later.

Monogenean species were identified using Gusev's (1985) description. The identification of the dactylogyrid and gyrodactylid material from 1986 was confirmed by Maria Prost (Agricultural University, Lublin) and that of the diplozoid material by the British Museum (Natural History), London.

Roach were measured and their age was determined from their scales.

3.3 Analyses of the results

ANOVA was used (I and V) to analyse the occurrence of the parasites on different gill-arches. The Fisher exact 2-tail test was used to test the co-occurrence of species (I and IV). The Student´s t-test was used (II and III) to analyse differences between the prevalences and relative proportions of the species and between the lakes and different years. For dactylogyrid community studies (IV) the reciprocal of Simpson´s Index was used to measure diversity (also in V) and for assessing community similarity two indices were used: Jaccard´s index and percentage similarity. Differences between these indices were analysed using the Kruskal-Wallis or Mann-Whitney U-test. Prevalence was used to determine the core, secondary and satellite species (Hanski 1982). Niche breadth was determined (V) by Levins´ Index (1968), and in order to measure the overlap between the species a proportional similarity measure (Schoener 1968) was used. Differences between these measures were tested by the Mann-Whitney U-test.

In papers II and III the term intensity refers to number of parasites

per studied fish. In papers I, IV and V the ecological terms are used according to Margolis, Esch, Holmes, Kuris and Schad (1982).

4 Results

4.1 Species composition on the gills of roach

The occurrence of 17 parasite species on the gills of roach was analysed. Fourteen of these species were monogeneans, 9 *Dactylogyrus* spp. (III), 4 *Gyrodactylus* spp. (II) and one diplozoid (*Paradiplozoon homoion*). One protozoan parasite, *Ichthyophthirius multifiliis*, was included, this species being large and at times very common on roach. The other two non-monogeneans were *Ergasilus briani*, a parasitic copepod, and the glochidium larva of *Anodonta anatina* (I).

The most common species group was the dactylogyrids, with 100% prevalence in all of the lakes studied during 1988-89. The total prevalences of the other species were much lower, partly because of their strong seasonality; none of them had a prevalence greater than 60% in 1986 even during the period of peak occurrence (I). Dactylogyrids, *P. homoion* and *E. briani* parasitise only the gills, but *I. multifiliis* , gyrodactylids and glochidia occur also on the fins and skin. The results on *I. multifiliis* and glochidia concern only the gills (I) while those of the gyrodactylids also include the skin and fins (II).

4.2 *P. homoion* and the relationships between the species-groups

P. homoion was found to be most common in the eutrophic lakes (Saravesi and Leppävesi) and the lowest prevalences were found in the polluted lake (Vatia). Nevertheless, the level of infection was low in all of the lakes studied, varying from 1.9 to 8.5 %. The abundance was also low: 91% of the infected roach had only one or two *P. homoion* specimens. No clear trend existed in the occurrence of this parasite on roach of different ages, neither was there any clear seasonality in the abundance of the parasites, but adults were ovigerous only in summer.

P. homoion were found most often on the first gill-arch (ANOVA, $p<0.001$). The proportion of diporpae (unpaired larvae) and juvenile

paired worms was lowest on the first and highest on the fourth gill-arch.

The relationships of the species-groups were studied from pooled material (composite data from all of the lakes) for the year 1986. Two of these groups have clear seasonal patterns. *Gyrodactylus* spp. have their peak occurrence in June and *I. multifiliis* in July. The species composition of the infracommunities was most variable in July. Co-occurrence was further analysed for the material from June, July and August, the mean number of species-groups per fish being highest during this period. The co-occurrence was found to be random in all but two cases; a positive association was found for *I. multifiliis* and *P. homoion* and a negative one for *I. multifiliis* and *Gyrodactylus* spp.

4.3 Gyrodactylids of roach and their variation between the lakes

The four *Gyrodactylus* species found were *Gyrodactylus prostae, G. gasterostei, G. vimbi* and *G. carassii* (II). Total prevalence of *Gyrodactylus* spp. infection (gills and fins together, year 1986) varied from 11 to 26 %, the highest values being in the eutrophic lakes and lowest in the polluted lake.

Gyrodactylids had a very clear seasonal occurrence in all of the lakes studied and during both years of study. The peak in prevalence occurred in June; only during 1986 in the polluted lake there was no clearly higher prevalence found in June. The same trend was observed concerning the intensities of infection.

A remarkably high proportion of the gyrodactylids found on roach from the polluted lake occurred on the gills of the fish rather than the fins, which are the more usual microhabitats of these parasites. During 1986 only 17% of the worms in the material from the polluted lake were found on the fins, while the average for all of the lakes was 70%. There was a significant ($p<0.001$) increase in the prevalence of infection on the fins of roach in the polluted lake from 1986 to 1987.

4.4 Dactylogyrids in the different lakes, their communities and interrelationships

Dactylogyrids were the most common and most studied species-group in this investigation. Firstly, their species composition and level of infection in the various lakes studied was compared (III) and then the populations and differences between them were considered at the community level (IV). Following this communities were also assessed at the

infracommunity level for microhabitat distribution and interactions between the species (V).

Nine *Dactylogyrus* species were found: *Dactylogyrus crucifer, D. nanus, D. suecicus, D. micracanthus, D. similis, D. caballeroi, D. fallax, D. sphyrna* and *D. vistulae*. All 9 species were found in the eutrophic Lake Saravesi.

The prevalence of dactylogyrid infection was high throughout all seasons in all the lakes, being from 90 to 100% in 1986 and 100% in 1988 and 1989. Although the total prevalence was always high, the number of species varied widely throughout the seasons. Two species, *D. crucifer* and *D. nanus*, had overwhelmingly the highest prevalences in all of the lakes and were also common throughout the year. These species were considered as core species (see Hanski 1982) in the communities. *D. sphyrna* and *D. vistulae* were rare satellite species and the remaining five species with intermediate levels of prevalences were considered secondary species.

All of the species exhibited very clear seasonal changes in their population parameters. This was also apparent for the core species in terms of their abundance, although their prevalence was high all through the year. The highest abundance and highest species diversity occurred in spring and early summer during a short period of only a few weeks. The intensity of *Dactylogyrus* infection was found to be significantly higher in the polluted lake in 1988. During 1986 *D. fallax, D. similis* and *D. suecicus* constituted a high proportion of the dactylogyrid population on roach in the polluted lake and *D. micracanthus* was very common in the eutrophic lakes. During 1988 the relative proportions of the species in the polluted lake were more similar to those in the eutrophic lake.

In 1988 and the spring of 1989 the dactylogyrid populations on the gills of roach were studied at the community level, the populations of the three lakes being treated as component communities and the dactylogyrids on the gills of each roach as infracommunities.

In the oligotrophic lake most fish had 2-3 dactylogyrid species per fish, while in the polluted lake the proportion of roach with a greater number of species was higher. In single species infections the number of specimens per fish was low when compared with concurrent infections. The two core species were found to dominate the infra- and component communities, but in the polluted lake the proportion of infracommunities dominated by *D. micracanthus* (a secondary species) equalled those dominated by *D. crucifer* (a core species).

Although the variation in the number of species, the number of parasites and diversity was found to be high among the infracommunities in each lake, the differences were significant between the component communities.

The similarity indices counted for pairs of infracommunities were

high (over 50%) both within and between the component communities, but higher within the lakes than between.

For closer inspection of the infracommunities, the gills were studied in relation to the species' distributions on the gill-arches. The seven most common species were used to study the abundance of species on different gill-arches, niche breadth and niche overlap between the species.

All species showed a significant species-specific preference for certain gill-arches and these preferences were similar in the three lakes studied. When these preferences were studied monthly, it was seen that they changed seasonally. For example, *D. micracanthus* was most common on the fourth arch in May, but had significantly higher abundances on the middle arches in June. The niche breadth and species overlap were found to be greatest during the period of peak occurrence of the species. Nevertheless, despite of this common trend, in some cases these parameters were unrelated to abundance. For example, species overlap could be higher in June than in May, although the abundance of both species in question was lower in June. The niche overlap between species could also remain stable between the two months, even though the abundance or niche breadth varied.

5 Discussion

5.1 *Paradiplozoon homoion* and the species-groups on the gills of roach

Paradiplozoon homoion infection of roach in Central Finland was found to be low when compared with other studies on diplozoids of fish (Höglund and Thulin 1989, Bovet 1967, Halvorsen 1969, Owen 1963, Wiles 1968, Stranock 1979). The low prevalence is probably the reason why no clear seasonal pattern in the occurrence of this parasite was found. For example, Höglund and Thulin (1989), who studied the thermal effects on *P. homoion* on the gills of roach in brackish water, found a clear seasonal cycle both in prevalence and abundance, and also in the recruitment of the parasites. In Central Finland diporpa larvae were found almost throughout the year, from February to October.

Although the total prevalence was low , there were differences between the four lakes studied that are considered to be due to water quality and the different trophic status of the lakes. The lowest number

of parasites was found from the polluted lake, although the water velocity in this lake is high and, according to Halvorsen (1969), diplozoids of roach are rheophilic. The suggestion that water quality affects the infection is also supported by Stranock (1979), who suggested that some inhibitory factor in water affected diplozoids of roach in a stream in Northern Ireland. There was also a difference in infection prevalences between the oligotrophic and eutrophic lakes, the highest levels of infection being found in the eutrophic lakes.

The microhabitat distribution of *P. homoion* showed a clear preference for the first gill-arch, but it was also observed that the proportion of unpaired larvae increased steadily from the first to the fourth gill-arch. Owen (1963) found that *Diplozoon paradoxum* was most common on the second gill-arch and according to Wiles (1968), the distribution of *D. paradoxum* on the gills of roach was random. Several authors considered that the gill ventilating currents affect the microhabitat distribution of monogeneans (Suydam 1971, Wootten 1974, Arme and Halton 1971, Fernando and Hanek 1976). It is suggested that, in the case of *P. homoion* on roach, the larvae attach most often to the fourth gill-arch, probably because of the nature of the water currents, but that the parasites actively migrate to the first gill-arch.

The parasites on the gills of fish have very rarely been studied at the community level, and usually these studies include only a few species groups. Adams (1986) studied a community on the gills of *Fundulus kansae* consisting of six parasite species, three protozoa, two monogeneans and one copepod. In Central Finland the community on the gill of roach was found to consist of myxosporeans (3 species), monogeneans (14 species), protozoans (*Capriniana piscium, Apiosoma* spp., *Trichodina* spp. *Ichthyophthirius multifiliis*), one copepod and a mollusc (glochidia larvae of *Anodonta anatina*)(Brummer-Korvenkontio *et al.* 1991, I,II,III,IV,V, Halmetoja, Valtonen and Taskinen 1992, Tuuha, Valtonen and Taskinen 1992). Parasites on roach gills form very species rich communities, although gills have often been ignored in parasite community studies on the basis of their depauperate parasite fauna.

Adams (1986) concluded that the significantly positive correlations which she found between some of the parasite species were due to the similar response of the parasite species to the microenvironment or to the ecological conditions of the macroenvironment, i.e. environmental factors were influencing the species in a similar manner.

Of the parasites on the gills of roach, the co-occurrence of five species or species-groups was studied during three summer months. Although only a short period was used for the analysis, it appeared that the distinct seasonality of the species was the reason for a false negative association between gyrodactylids and *I.multifiliis*. The only significant positive relationship was found between *I. multifiliis* and *P. homoion*, and this is considered to be attributable to the physical condition of the

host. Otherwise the co-occurrence of the studied groups was random, indicating that no significant competition exists between them. It is probable that for example, the differences in timing of the periods of peak occurrence is a mechanism for dividing resources and avoiding competition.

5.2 Gyrodactylid populations

Parker (1965) suggested that the main reason for the low prevalence of *G. elegans* on golden shiner (*Notemigonus crysoleucas*) would prove to be a decrease in oxygen supply. In Central Finland the prevalence of gyrodactylids on the fins of roach in the polluted lake increased drastically between the two years studied, and it is also known that the oxygenation of the lake was better in 1987 as compared with 1986 (Granberg 1987, Granberg et al. 1987). This supports Parker's (1965) conclusion. The supply of oxygen may affect the parasites directly but also indirectly via the condition of the host; the secretion of mucus by the host is greater in poor environmental condition and it is possible that the parasites may become dislodged with detaching mucus (Erasmus 1972).

There was also a difference in the localisation of gyrodactylids on the fish. According to Lewis and Lewis (1970), the majority of gyrodactylids occur on the fins and skin of fish, but in the polluted lake in Central Finland a high proportion of the parasites occurred on the gills of roach during 1986. This observation is supported by the studies of Kirby (1981) and Malmberg (1956), who found that gyrodactylids may choose an abnormal attachment site when environmental conditions are unfavourable for them.

The clear seasonality and sharp peak in the occurrence of gyrodactylids might be explained by the spawning of the roach in spring at water temperature of 10 °C (Lind *et al.* 1973), since spawning fish gather together and this enables the parasite transfer. The spawning is also accompanied by a reduced immunological response of the fish host. That the spawning, rather than the water temperature, influences the level of gyrodactylid infection is also indicated by the fact that the prevalences do not rise towards the autumn despite decreasing water temperature.

5.3 Dactylogyrid communities and differences between the lakes

The species composition of the *Dactylogyrus* fauna was very similar in

the four lakes studied, which might have been expected because of the connection between the lakes and the former unrestricted migration of the fish. Nevertheless, one species, *D. fallax*, was not found in the oligotrophic lake, although the relative proportion of this species was large in the polluted lake and these two lakes are situated side by side.

In 1986 the species composition of the polluted lake differed from that of the two eutrophic lakes, but in 1988 the relative proportions of species in the polluted and in the eutrophic lake were similar. In fact there was a change in the environmental conditions in the polluted lake between these two years, caused by changes in the processes used at the paper mill responsible for the pollution (Granberg et al. 1989). Thus the water quality of lakes Vatia and Saravesi was also more similar in 1988. It is possible that changes in environmental conditions may have altered the proportions of *Dactylogyrus* species in Lake Vatia.

The proportions of the species on roach in the oligotrophic lake differed from those from the other lakes studied both during 1986 and 1988, the proportions of the two core species, *D. crucifer* and *D. nanus*, being considerably greater. *D. micracanthus* constituted a greater proportion of the parasites from the eutrophic lakes in 1986 and also from the polluted lake in 1988, when compared with the oligotrophic lake. It is possible that these species are affected by the trophic status of the lakes, the numbers of the core species possibly being restricted when the environmental conditions favour other species.

Of the environmental factors affecting monogeneans, only temperature has been studied in any depth or experimentally (Scott and Nokes 1984, Hanzelova and Zitnan 1985, Gelnar 1987). The importance of other factors is recognised, but mostly only speculated upon (Malmberg 1956, Bauer 1961, Gonzalez-Lanza and Alvarez-Pellitero 1982, Shulman 1989, I), and experimental verification has not been carried out.

It is known that the pollution of Lake Vatia has caused changes in the physiology and immunological response of the fish in this lake (Soivio, Nikunen and Tuurala 1985, Aaltonen, Jokinen and Valtonen, unpubl.). It is also known that these kinds of changes influence the parasitic infections of fish (Malmberg 1956, Ergens 1983). The lowered condition of the host renders the host more susceptible to parasitic infections. Although pollution may have direct negative effects, especially on ectoparasites, which are in direct contact with the surrounding water, the indirect effect through the host may be positive for the parasite.

In Central Finland the abundance of *Dactylogyrus* spp. was found to be highest in the polluted lake (III). It was also found that, at the infracommunity level, the abundance was low in single-species infections (IV). This could mean that the first established species weakens the host's immunological response as its abundance increases, and thus

lowers its resistance to infection by other species. This suggestion is supported by Rohde (1979) in his studies on marine monogeneans. It is also possible that the roach with low level, single-species infections are immunologically more resistant and in good condition and thus the level of infection remains low. The number of species per fish and the number of parasites per fish were highest in Lake Vatia, as was also the total diversity of the component community. It is possible that the high community richness reflects the poorer condition of the fish in the polluted water.

At the community level, considering the dactylogyrids of each lake as a compound community, it was found that the similarities between the communities were high. This indicates a high predictability of the system. Nevertheless, the similarities between the communities were mainly lower than those within component communities. This, and the differences in species proportions and in other community parameters mentioned previously, indicates that there are differences in the structure of *Dactylogyrus* communities of the lakes studied. It is suggested that these differences are not easily detected because the component communities are situated close to each other and the host populations are similar. Another reason for the high predictability of the communities could be associated with the nature of the *Dactylogyrus* community: if the dactylogyrids constitute an interactive community, the community structure is strongly determined by the interactions between the species and thus the effects of the environment are not always apparent.

5.4 The nature of the dactylogyrid community and microhabitat distribution

According to Holmes (1986) and Holmes and Price (1986), important prerequisite for an interactive community is that helminths regularly co-occur at substantial population densities. The ectoparasite communities are often considered to be impoverished in terms of both the number of species and specimens, and this is probably one reason why, for example, communities on the gills of fish have been studied less than species rich intestinal communities.

Dactylogyrids on the gills of roach have been found to form species rich communities with high prevalences and abundances of the species occurring during a certain period of the year (III, IV). In Central Finland nine species of this genus were found to co-exist during May and June, seven of them with a high prevalence and abundance.

It is known that parasite communities may be intermediate in nature, i.e. the components being neither strictly isolationist nor

nature of the community is one or the other of these extremes (Rohde 1979, Bush and Holmes 1986, Stock and Holmes 1988). It is suggested here that communities may also exhibit seasonality, being more isolationist during certain periods of the year and interactive at other times. The *Dactylogyrus* community on the gills of roach may be isolationist during most of the year, when the community is composed almost entirely of the two core species occurring in low numbers, but interactive during the two month period of heavy infection by several species. Secondly, the strength of the interaction between different species may vary, even between species of the same genus. According to Holmes (1990), in multispecies infections each pair of species can exhibit an exclusive interaction or no interaction at all, or they can interact at a reproductive level, where diversity and other community characteristics would not be affected. In Central Finland the possible interaction was thought to be influenced by seasonal changes in prevalence and abundance, and this is why only material from the peak period of spring and summer was used for further studies on the structure of the *Dactylogyrus* community (V).

Rohde (1979) has stated in his studies on marine monogeneans that in communities of these parasites intraspecific factors are more important in structuring the community, the main factor being selection to increase intraspecific contact and thus the possibility of reproduction. Rohde (1991) was also of the opinion that on the gills of marine fishes vacant niches for parasites are usually available, since marine fish species have variable numbers of congeneric parasite species, and potentially competing species have been found to have insignificant effects on microhabitats and infection intensities. Because of these facts, he concluded that interspecific competition has no importance in structuring marine gill parasite communities. In Central Finland the winter communities of dactylogyrids on the gills of roach resemble those on the gills of marine fish, but during the peak occurrences they are quite dissimilar.

The microhabitat distribution of seven species was studied on the basis of distribution on the gill-arches, and all of them showed significant preferences for certain arches. Interestingly these preferences also exhibited seasonal variation (V). The variation was greatest for *D. micracanthus* , which was concentrated on the fourth gill-arch in May but more common on the middle arches in June. The occurrence of parasites on different gill-arches has been studied by Arme and Halton (1972), Wootten (1974), Adams (1986), Buchman (1989) and Dzika and Szymanski (1989). In cases where significant preferences for certain gill-arches have been found, it has been concluded that differences in water currents over the gill-arches or differences in the area of the gill-arches are involved and it is suggested below that parasites at differing developmental stages have differing preference sites (I). It is also

possible that site preferences are a sign of resource partitioning between the species. In dactylogyrid communities on the gills of roach the niche breadth of *D. micracanthus* rose significantly from May to June, simultaneously with the decrease in the abundance of another species, *D. similis* . Between these two months the abundance of *D. micracanthus* did not change significantly. It was also found that, despite variation in the populations of these species, their overlap did not exhibit any significant changes. It is concluded that at least these two species of dactylogyrid community exhibit species interaction, *D. similis* having a restricting effect on *D. micracanthus* . There were also other phenomena involving the timing of peak occurrences, niche breadths and species overlap which strongly suggest that dactylogyrids of roach may be regarded as an interactive community during the time of greatest diversity (V). However, these suggestions need to be verified by experimental work in order to confirm the nature of the community.

Conclusions

The use of parasites as biological tags indicating the state of the environment can be considered as a natural step forward in modern parasitology. As the species composition of parasites in various hosts and in differing environments, and their life cycles and seasonal cycles, have been worked out, it has been possible to investigate how this large group of animals with their extraordinary mode of life reacts to changes in the environment. This is the purpose of the research in four differing lakes in Central Finland.

When parasites have been used as mirrors of the environment the species have usually been studied separately. In this work component communities with differing environmental conditions are compared. Changes in relationships between species may reveal effects that would not be noticed by studying the species separately. This was seen in the study of the dactylogyrid communities.

Ectoparasites of fish are very useful tools for studies on environmental effects. They are in direct contact with the macroenvironment, which is the surrounding water, as well as with the microenvironment, which is the host fish. They often have direct life-cycles with no intermediate hosts, the existence of which may obscure the phenomena being investigated. The monogeneans of fish especially have the advantage of being highly host specific and this reduces the influence of the fish species composition of the study area on the parasite

community occurring on a particular host.

The results of this work indicate that the parasite communities on the gills of roach have distinct differences in different environments, even though the lakes under study are small and interconnected. There was also evidence that the nature of a congeneric monogenean community may be different at different times, being isolationist or interactive according to the season (V).

To verify these results from field data, experimental work is needed, in order to confirm the possible interactions between the species. Certainly, there are differences in the communities between the lakes studied, but, only experimental work will reveal the environmental factors actually influencing the parasites on the gills of roach.

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Selostus

Särjen (*Rutilus rutilus*) monogeenit ja muut kidusloiset Keski-Suomessa - erot neljän järven välillä ja *Dactylogyrus*-yhteisöt

1173 särkeä tutkittiin kidusloisten löytämiseksi vuoden 1985 elokuusta vuoden 1989 huhtikuuhun. Koko aineistoa käytettiin kiduksilla loisivan *Paradiplozoon homoion*in esiintymisen selvittämiseksi. *Gyrodactylus*-suvun monogeenit tutkittiin vuosien 1986-87 materiaalista (767 kalaa). *Dactylogyrus*-suvun monogeenit tutkittiin vuosina 1986 ja 1988 (660 kalaa) ja tämän suvun loisten yhteisörakennetta selvitettiin vuosina 1988 ja 1989 (293 kalaa). Vuoden 1986 materiaalista selvitettiin myös muiden särjen kidusloisten esiintyminen.

Aineisto kerättiin neljästä toisiinsa yhteydessä olevasta järvestä. Yksi järvistä (Vatia) on tyypiltään rehevöitynyt ja lisäksi puunjalostusteollisuuden jätevesien likaama. Peurunkajärvi on oligotrofinen ja luonnontilainen ja kaksi järvistä (Saravesi ja Leppävesi) on rehevöityneitä.

Särjen kidusten *P. homoion* loisinta oli yleisintä (8.5% tutkituista kaloista loisittu) toisessa rehevöityneistä järvistä ja loisittujen kalojen osuus tutkituista oli alhaisin (1.9%) likaantuneessa järvessä. Loisten määrä kalaa kohti oli alhainen eikä vuodenaikaisesiintymisessä havaittu huippuja yhdessäkään tutkituista järvistä. Munallisia loisia löydettiin kesäkuusta syyskuuhun. *P. homoion* oli merkitsevästi yleisempi ensimmäisellä kiduskaarella, mutta toukkavaiheiden osuus löydetyistä loisista oli suurin neljännellä kiduskaarella.

Särjen kidusloisten yhteisesiintymisen havaittiin olevan sattumanvaraista, vain *P. homoion* ja *Ichthyophthirius multifiliis* esiintyivät yhdessä satunnaista useammin.

Gyrodactylus-lajeja löydettiin neljä ja niistä *G. prostae* oli yleisin kaikissa tutkituissa järvissä. 8.9-17%:lla tutkituista kaloista oli *Gyrodactylus*-loisia evillä, kiduksilta näitä loisia löytyi 6.5-13.3%:lta tutkittuja kaloja. Näiden monogeenien esiintymisessä havaitiin selvä vuodenaikaisuus; sekä infektoituneiden kalojen määrä, että loisten määrä kalaa kohti olivat korkeimmillaan kesäkuun alussa. Erojen tutkittujen järvien vedenlaadussa arvellaan vaikuttavan sekä *Gyrodactylus* loisinnan voimakkuuteen, että loisten sijoittumiseen kalalla.

Myös *Dactylogyrus*-suvun monogeeneilla havaittiin selvä vuodenaikaisuus, mutta se näkyi vain loisinnan voimakkuudessa ja lajien määrässä, kun taas loisinta oli yleistä (lähes 100% kaloista loisittu) ympäri vuoden. Sekä loisinnan voimakkuus, että *Dactylogyrus*-lajien

määrä kalaa kohti olivat merkitsevästi voimakkaammat likaantuneessa järvessä verrattuna muihin tutkittuihin järviin. Kaikkiaan *Dactylogyrus*-lajeja löydettiin yhdeksän. *D. crucifer* ja *D. nanus* olivat ydinlajeja kaikissa komponenttiyhteisöissä. *D. suecicus, D. micracanthus, D. similis, D. fallax* and *D. caballeroi* olivat sekundaarisia lajeja (loisinnan yleisyys keskimääräistä), *D. sphyrna* ja *D. vistulae* olivat harvinaisia satelliittilajeja.

Tutkittujen järvien *Dactylogyrus*-faunan koostumuksessa havaittiin eroja. Likaantuneen järven lajisuhteet muuttuivat kahden tutkitun vuoden (1986 ja1988) välillä siten, että vuonna 1988 Vatianjärven lajien suhteelliset osuudet olivat hyvin samanlaiset kuin rehevöityneissä järvissä.

Kun *Dactylogyrus*-lajistoa tutkittiin yhteisötasolla, havaittiin, että komponenttiyhteisöt ovat hyvin samanlaisia, joitakin eroja kuitenkin löydettiin. Likaantuneen järven infrayhteisöjä (yhden särjen *Dactylogyrus*-loiset) hallitsi *D. micracanthus* useammin kuin infrayhteisöjä muissa järvissä. Infrayhteisöjen väliset similariteetti-indeksit olivat korkeammat järvien sisällä, kuin järvien välillä. *Dactylogyrus*-yhteisöjen välisten erojen arvellaan johtuvan eroista järvien vedenlaadussa.

Kaikki seitsemän yleisintä *Dactylogyrus*-lajia olivat selvästi yleisempiä tietyillä kiduskaarilla ja suosituimmuusjärjestys oli lajikohtaista. Kiduskaarten valinnassa havaittiin myös jonkin verran vuodenaikaisvaihtelua. Joillakin tutkituista *Dactylogyrus*-lajeista nitsien leveys ja lajien päällekkäisesiintyminen kiduskaarilla eivät vastanneet lajien runsautta. Tämä viittaa mahdollisesti siihen, että toiset lajit rajoittavat kyseisten lajien nitsejä. On mahdollista, että *Dactylogyrus*-yhteisöt ovat vuorovaikutteisia lajien huippuesiintymisen aikana.

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ORIGINAL PAPERS

I

PARADIPLOZOON HOMOION (MONOGENEA) AND SOME OTHER GILL PARASITES ON ROACH *RUTILUS RUTILUS* IN FINLAND

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by

Mari Koskivaara & E. Tellervo Valtonen

II

SEASONAL OCCURRENCE OF GYRODACTYLID MONOGENEANS ON THE ROACH (*RUTILUS RUTILUS*) AND VARIATIONS BETWEEN FOUR LAKES OF DIFFERING WATER QUALITY IN FINLAND

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III

DACTYLOGYRIDS ON THE GILLS OF ROACH IN CENTRAL FINLAND: FEATURES OF INFECTION AND SPECIES COMPOSITION

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by

Mari Koskivaara, E. Tellervo Valtonen & Maria Prost

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IV

DACTYLOGYRUS (MONOGENEA) COMMUNITIES ON THE GILLS OF ROACH IN THREE LAKES IN CENTRAL FINLAND

Parasitology 104: 263-272

by

Mari Koskivaara & E. Tellervo Valtonen

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V

MICROHABITAT DISTRIBUTION AND COEXISTENCE OF *DACTYLOGYRUS* SPECIES (MONOGENEA) ON THE GILLS OF ROACH

Parasitology 104: 273-281

by

Mari Koskivaara, E. Tellervo Valtonen & Kari-Matti Vuori